

# Integrating social and ecological data to model metapopulation dynamics in coupled human and natural systems

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*Citation:* Van Schmidt, N. D., T. Kovach, A. M. Kilpatrick, J. L. Oviedo, L. Huntsinger, T. Hruska, N. L. Miller, and S. R. Beissinger. 2019. Integrating social and ecological data to model metapopulation dynamics in coupled human and natural systems. *Ecology* 100(6): e02711. 10.1002/ecy.2711

**Abstract.** Understanding how metapopulations persist in dynamic working landscapes requires assessing the behaviors of key actors that change patches as well as intrinsic factors driving turnover. Coupled human and natural systems (CHANS) research uses a multidisciplinary approach to identify the key actors, processes, and feedbacks that drive metapopulation and landscape dynamics. We describe a framework for modeling metapopulations in CHANS that integrates ecological and social data by coupling stochastic patch occupancy models of metapopulation dynamics with agent-based models of land-use change. We then apply this framework to metapopulations of the threatened black rail (*Laterallus jamaicensis*) and widespread Virginia rail (*Rallus limicola*) that inhabit patchy, irrigation-fed wetlands in the rangelands of the California Sierra Nevada foothills. We collected data from five diverse sources (rail occupancy surveys, land-use change mapping, a survey of landowner decision making, climate and reservoir databases, and mosquito trapping and West Nile virus testing) and integrated them into an agent-based stochastic patch occupancy model. We used the model to (1) quantify the drivers of metapopulation dynamics, and the potential interactions and feedbacks among them; (2) test predictions of the behavior of metapopulations in dynamic working landscapes; and (3) evaluate the impact of three policy options on metapopulation persistence (irrigation district water cutbacks during drought, incentives for landowners to create wetlands, and incentives for landowners to protect wetlands). Complex metapopulation dynamics emerged when landscapes functioned as CHANS, highlighting the importance of integrating human activities and other ecological processes into metapopulation models. Rail metapopulations were strongly top-down regulated by precipitation, and the black rail's decade-long decline was caused by the combination of West Nile virus and drought. Theoretical predictions of the two metapopulations' responses to dynamic landscapes and incentive programs were complicated by heterogeneity in patch quality and CHANS couplings, respectively. Irrigation cutbacks during drought posed a serious extinction risk that neither incentive policy effectively ameliorated.

**Key words:** agent-based model; black rail; coupled human and natural system; data integration for population models Special Feature; irrigation; land-use change; metapopulation; rangeland; social-ecological system; stochastic patch occupancy model; Virginia rail; wetland; working landscape.

Manuscript received 15 June 2018; revised 8 November 2018; accepted 2 January 2019. Corresponding Editor: Brian D. Inouye.

**Editors' Note:** Papers in this Special Feature are linked online in a virtual table of contents at: [www.wiley.com/go/ecologyjournal](http://www.wiley.com/go/ecologyjournal)

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## INTRODUCTION

Ecologists have increasingly focused on conserving species in “working landscapes,” where agriculture, forestry, and other forms of resource extraction co-occur with habitat conservation (Franklin and Lindenmayer

2009, Kareiva and Marvier 2012). Working landscapes are frequently characterized by fragmented remnant habitat patches within a matrix of land uses providing less suitable habitat (Gimona and Polhill 2011). Species occupying these patchy landscapes are often structured as a metapopulation (Levins 1969, Hanski 1999). Habitat patches in working landscapes are dynamic because of human-caused changes in land use. Theory suggests that if the rate of patch change exceeds colonization, occupancy will decline, possibly resulting in metapopulation extinction (Anderson et al. 2009). Land-use change can also interact with other aspects of global change, such as climate change and emerging diseases (Wolfe et al. 2005, Brook et al. 2008, Hof et al. 2011, Altizer et al. 2013). Thus, understanding the dynamics of metapopulations in working landscapes requires integrating metapopulation ecology with both biophysical and social sciences to assess the behaviors of key actors that drive change in landscape structure in these coupled human and natural systems (CHANS).

CHANS research uses an interdisciplinary approach to identify and analyze the key system components and the processes linking them across scales (e.g., landowners and regulating agencies), which presents a number of modeling challenges. By its nature, this research generally requires the integration of longitudinal data collected with a diversity of methodological tools from different disciplines (Liu et al. 2015). These data may differ greatly in spatiotemporal scales, resolution, structure, and processes, impeding their combination into a joint likelihood. CHANS tend to be idiosyncratic and context-specific, requiring data integration methods that are flexible enough to be readily adapted to novel data formats and systems. Integrating these data is a serious challenge that has been identified as one of the most pressing questions in CHANS research (Kramer et al. 2017). CHANS frequently have feedback loops, spatiotemporal heterogeneity, and thresholds in system state, which can result in emergent nonlinear dynamics that traditional statistical models fail to predict (Alberti et al. 2011, Liu et al. 2015). This complexity, coupled with the fact that metapopulations occur at a landscape scale that typically impedes experimentation, makes simulation modeling an especially useful tool for understanding land-use change and metapopulation dynamics as a coupled system (Ims 2005).

Here, we present a general framework for integrating social and ecological data to model metapopulations in CHANS by combining agent-based models (ABMs; also called multiagent or individual-based models) with stochastic patch occupancy models (SPOMs), an easily parameterized and commonly used metapopulation simulation tool. We then apply this approach to determine the main drivers of the metapopulation dynamics of two closely related, secretive marsh birds in the wetlands of a working landscape—irrigated rangelands in the foothills of the California Sierra Nevada—and evaluate how various policy options affect the metapopulations.

#### A FRAMEWORK FOR INTEGRATING DATA TO MODEL METAPOPULATIONS AS CHANS

ABMs are a particularly promising tool for analyzing CHANS because they can simulate the behavior of one or more classes of individual agents (e.g., landowners, institutions, wildlife, and habitat patches) to examine the collective patterns and complex dynamics that result (Liu et al. 2015). ABMs emerged from computer science and employed abstract simulations to develop theory, but have become commonly used in CHANS research to link individual or household behaviors to landscape-scale effects (e.g., land-use change; An 2012). ABM software (such as NetLogo; Wilensky 2018) stores sets of dynamic variables for each agent and structures them spatially in a simulated environment, which for CHANS is generally a map constructed from GIS layers. Submodels—individual processes performed by an ABM agent that are usually algorithms (e.g., regression equations)—are programmed to govern the behavior of agents and their effects on other agents. For example, a logistic regression estimating the probability of a “landowner” agent clearing their land of forests could be coded to remove all “forest patch” agents on their property if enacted during the simulation. By mechanistically linking empirical submodels, ABMs can integrate disparate data collected via different disciplinary methodologies to represent system components intuitively as different agents embedded in a common environment (Janssen and Ostrom 2006). Differences in scale and structure among processes are resolved by specifying relationships among agents represented across space and time (An 2012).

An empirical ABM framework that models change in the size and distribution of habitat patches on a landscape can be readily combined with an SPOM that simulates changes in species’ occupancy state (present or absent) in each dynamic patch (Sjögren-Gulve and Hanski 2000) to model the emergent dynamics of land-use and metapopulations in CHANS jointly (Fig. 1). The landscape, represented by cell-based rasters of environmental layers (e.g., elevation), structures the system spatially. At the largest spatial and hierarchical scale, exogenous drivers (e.g., climate) affect one or more of the three classes of agents: governance institutions, resource users, and patches. Government institutions impose policies that incentivize or discourage different decisions of resource users (e.g., landowners) under their jurisdiction. Land-use change decisions of resource users are then modeled as functions of these policies, interactions with neighbors, and their own heterogeneous characteristics, as well as those of their patches (equivalent to individual variation; Plard et al. 2019). For example, in this article we use regression on social survey data to estimate the probability of landowners responding to policies in different ways (a heuristic rule-based decision-making model), but there are many other types of land-use change submodels (see Parker et al. 2003, An

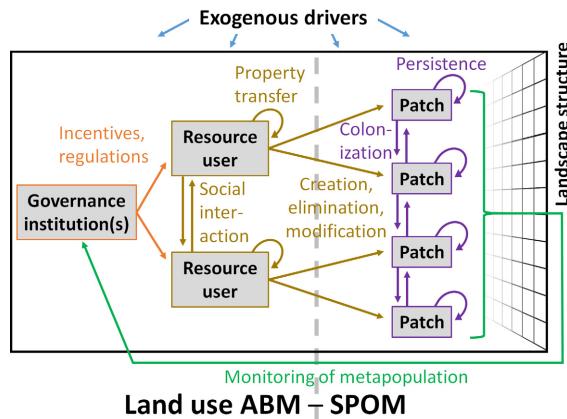


FIG. 1. Conceptual diagram showing how a stochastic patch occupancy model (SPOM; right of dashed line) can be readily combined with an agent-based model (ABM; left of dashed line) to simulate metapopulations over habitat patches in dynamic landscapes. Agents (gray boxes), which may be heterogeneous, exist in a spatially explicit representation of the landscape and execute empirically fit processes (arrows) that affect other agents under their spatial domain.

2012 for reviews). These decisions result in the creation, elimination, or modification of the resource user's patches. Finally, an SPOM is run over the resulting dynamic patches. Each patch's occupancy state is stochastically initialized in the first year with probability  $\Psi$ , and stochastically changes in subsequent years as a first-order Markov process. Occupied patches can go extinct with probability  $\epsilon$ , and unoccupied patches can be colonized with probability  $\gamma$ . These probabilities are patch-specific: theory posits  $\epsilon$  is primarily a function of patch's area and  $\gamma$  of its connectivity to other occupied patches (i.e., sources of colonists), but other habitat covariates can also be included via logistic regression equations in occupancy models (Hanski 1999, MacKenzie et al. 2003). The metapopulation status and provisioning of ecosystem services can then feed back to institutions' decision-making.

Utilizing this ABM-SPOM framework to model metapopulations has a number of advantages. It allows for assessment of conservation strategies that require participation of social actors, such as "payment for ecosystem services" incentive policies (Gimona and Polhill 2011). ABMs can flexibly accommodate a wide range of situations with modular submodels (e.g., this paper includes disease dynamics but excludes interactions between landowners). Previous ABMs integrating land-use change and wildlife have either represented wildlife dynamics simply by using patch characteristics as a proxy for biodiversity (Guzy et al. 2008, Brady et al. 2012, Schouten et al. 2013), or utilized models simulating intra-patch population dynamics or decision-making of individual animals (Guillem et al. 2009, Anselme et al. 2010, Parry et al. 2013, Iwamura et al. 2014). Although the former approach offers limited

insights into metapopulation dynamics in working landscapes, the latter requires knowledge of species-specific population dynamics that, when unavailable, impedes generalization across systems. There is a need for middle-level models that realistically represent important dynamics while being tractable and generalizable (O'Sullivan et al. 2016). SPOMs use detection/nondetection data that are often easier to obtain than estimates of population sizes or vital rates, especially if these vary spatially or temporally (Sjögren-Gulve and Hanski 2000). SPOMs are most suitable for large networks of discrete patches with small local populations, where turnover in patch occupancy may occur between years (Sjögren-Gulve and Hanski 2000). Incidence function models can estimate  $\gamma$  and  $\epsilon$  with patch area and connectivity effects from just a single season of field surveys (Hanski et al. 1996). Surveys over multiple seasons allow for fitting of logistic regression models that incorporate habitat- and year-based covariates of turnover, and multiple resurveys within each season can correct for imperfect detection using hierarchical occupancy models (MacKenzie et al. 2003).

#### APPLYING THE FRAMEWORK TO RAIL METAPOPULATIONS IN THE SIERRA FOOTHILLS

In the foothills of the California Sierra Nevada, irrigation by landowners has greatly increased the size and number of small wetlands (mean area = 0.37 ha; Richmond et al. 2010a). These wetlands support metapopulations of two closely related, secretive marsh birds, the smaller, dispersal-limited black rail (*Lateralus jamaicensis*) and the larger, more vagile Virginia rail (*Rallus limicola*; Richmond et al. 2010b, Hall et al. 2018). The California subspecies of black rail (*L. j. cornicululus*) is listed as a California State Threatened Species because of habitat loss (Eddleman et al. 1988), and the other U.S. subspecies (*L. j. jamaicensis*) is proposed to be listed as Threatened under the Endangered Species Act. In the foothills, occupancy of black rails has declined since 2007, coinciding with the arrival of West Nile virus (WNV), which was a probable cause (Risk et al. 2011). Because wetlands also provide habitat for WNV mosquito vectors, irrigated wetlands may increase regional WNV infection risk. However, 2007–2009 and 2012–2015 were historically severe drought years, offering another possible cause of decline. Drought and climate change not only threaten to dry natural wetlands, they also threaten the stability of regional water supplies that maintain irrigated wetlands, which provide key black rail habitat (Richmond et al. 2010a). Water cutbacks by irrigation districts to conserve water during drought may force landowners to reduce irrigation and encourage the conversion of ranchland to exurban development (Huntsinger et al. 2017). Thus, the persistence of wetlands and rails in the Sierra Nevada foothills strongly depends on the land-use decisions of landowners.

We developed an ABM-SPOM, the Wetlands-Irrigation CHANS Model (WICM; available from Supporting Information), for this region. Modeling CHANS begins by defining a system’s key actors and processes: we focus on climate as an exogenous forcing, irrigation districts and the California Department of Fish and Wildlife (hereafter “the wildlife agency”) as governance institutions, landowners as resource users, and wetlands as patches providing habitat to both rails and WNV (Fig. 2a). We parameterized WICM by collecting data

from five diverse sources: rail occupancy surveys, land-use change mapping, a survey of landowner decision making, climate and irrigation district databases, and mosquito trapping and WNV testing.

The objective of our analysis was to evaluate (1) the dominant drivers of metapopulation dynamics and decline, and potential interactions and feedbacks among them, and (2) the impact of policy options on metapopulation persistence. We selected three policy scenarios for assessment based on pre-survey interviews with stakeholders: water cutbacks by irrigation districts during drought, incentives for landowners to create wetlands, and incentives for landowners to protect wetlands. The wildlife agency is actively developing conservation plans for the black rail; incentives were modeled after similar programs in the adjacent Central Valley (Duffy and Kahara 2011), which do not currently extend to the foothills. Local irrigation districts and the State Water Resource Control Board are under pressure to conserve water in the face of recent severe droughts, which prompted revisions of water cutback policies (Huntsinger et al. 2017). There is a need for the integrated assessment of the potential effects of these policies on the black rail, which can account for the linkages between social, climatic, and disease dynamics, in order to inform state conservation plans and water policy.

We test theoretical predictions of metapopulation dynamics in CHANS by comparing results for the dispersal-limited black rail to the more vagile Virginia rail (Richmond et al. 2010b). Following the conclusions of Gimona and Polhill (2011), we predicted that incentive programs would reduce the importance of other drivers of metapopulation extinction risk because they bolster the species overall. We predicted that wetland creation incentives should lead to landowners increasing the number of small wetlands, which in turn should increase the occupancy of black rails more than Virginia rails because the former can occupy smaller patches (Richmond et al. 2010b) and the resulting connectivity would reduce dispersal limitations (Sjögren-Gulve and Hanski 2000). Conversely, occupancy of black rails should be more sensitive than Virginia rails to higher rates of wetland patch change because they are less able to (re-)colonize patches (Amarasekare and Possingham 2001).

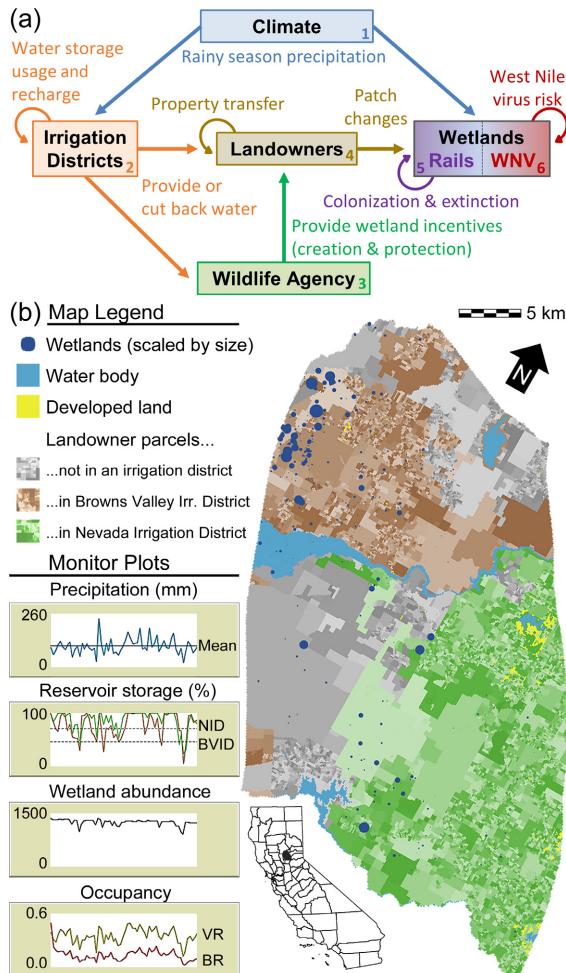


FIG. 2. Design of the agent-based Wetlands-Irrigation CHANS Model (WICM). (a) Simplified flow diagram of main model processes: agents (boxes) execute processes (arrows) that affect other agents under their spatial domain (numbers indicate order of execution). (b) WICM’s graphical user interface. A simulated map displays wetlands, landowners, and irrigation districts, and defines their hierarchical spatial relationships; bottom inset shows study area location in California. Monitor plots let users track how variables change after each simulated year (*x*-axis); the end of a single characteristic run is shown. Reservoir storage (solid lines) and thresholds for drought 20% water cutbacks (dotted lines) are shown for Nevada (NID) and Browns Valley (BVID) Irrigation Districts. BR = black rail and VR = Virginia rail.

METHODS

Data collection

Study area boundaries were the Sierra Nevada Foothills eco-region (U.S. Environmental Protection Agency 2013) for Nevada, Yuba, and southern Butte counties (see Fig. 2b for a map and Appendix S1 for a description). Our climate model was based on projected regional precipitation values from the CCSM RCP 8.5 climate scenario (Flint and Flint 2012), because present greenhouse gas emission trends are closest to this scenario (Sanford et al. 2014). Information on irrigation districts and the

state wildlife agency was obtained from interviews, reservoir databases, and published documents. We acquired a map of 2010 parcel layers from county assessors, and designed and mailed a survey on land and water management to 862 range and oak woodland landowners with properties  $\geq 1.2$  ha from the study area (see Huntsinger et al. 2017 for details and the survey). Parcels  $< 1.2$  ha (a regional cutoff for Residential Agricultural zoning) were excluded from the study and model, as they were suburban and generally lacked wetlands. We obtained 466 valid questionnaires (54% return rate).

We mapped all 1,759 emergent wetlands (minimum mapping unit  $5 \times 5$  m), as well as all open water bodies and rice fields, by manually interpreting summer 2013 0.4 m imagery in Google Earth 7.1.5. We classified wetlands into four geomorphology types: slope (hillside with no open water body), fluvial (edge of creek), fringe (of a pond or rice field), or impoundment (for waterfowl hunting). We classified the water sources of 934 wetlands (53%) as natural only, irrigation only, or both sources. Natural water type was further classified as creek or spring. Irrigation type was classified as pasture, leak, rice, runoff (from multiple properties), or water feature (intentional wetland or pond). We used historical imagery to track wetlands over time (1947–2016; Appendix S2: Table S1) to measure how changes in irrigation created, eliminated, or changed the area of wetlands in this landscape. We recorded the annual area and irrigation state (presence/absence) of all field-surveyed wetlands (see below). We also tracked the parcels of landowner-survey respondents, mapping all wetlands found on parcels in any of the 6 yr preceding our survey (2009–2014). We conducted annual presence–absence broadcast surveys for black rail and Virginia rail occupancy at 273 wetlands (43% of the 2013 acreage) during the breeding season 2002–2016 (methodology described in Richmond et al. 2008, 2010b). We trapped mosquitoes at 80 wetlands from June to October 2012–2014 (6,385 trap nights), with weekly visits where we placed up to three CDC traps baited with dry ice. We used RNA testing to estimate mosquitoes' WNV prevalence. See Appendix S1 for more details on data collection.

#### *Model design and overview*

Studying CHANS and constructing an ABM is an exercise of iterative, incremental progress and redesign (Alberti et al. 2011). We developed the conceptual model in Fig. 2a from observations during early field studies of black rails. WICM was based on disciplinary theories that drove the design of underlying submodels, which were linked regression equations empirically fit from field data. We next refined it via interviews with landowners and water district employees, who helped focus our data collection and modeling on the key processes presented below. After collecting data we reassessed our model, gathering additional data where needed (e.g., reservoir data) and excluding some processes that turned out

unimportant (e.g., baseline rates of new wetland creation). We next provide an overview of the resulting design.

We constructed WICM in NetLogo v6.0.3 (Wilensky 2018). The model represents the CHANS as three types of spatially explicit agents—wetlands, landowners, and irrigation districts—overlaid on a 100-m-resolution raster map of the study area (Fig. 2b). We chose this resolution because it was just below the minimum size of landowner parcels surveyed (1.2 ha), resulting in little information loss while increasing computational efficiency. Raster cells (what NetLogo calls “patches”) have variables representing spatial covariates (elevation and distance to rice) and the spatial domains of landowner parcels and irrigation district service areas. Climate and the state wildlife agency are single entities affecting the whole model. Irrigation districts are agents that provide irrigation to landowners within their service areas. Landowners are agents with their own variables and make decisions that affect wetlands originating on their property. Wetlands are represented as points with associated variables (e.g., area). Rails and WNV are represented as variables stored by wetlands (i.e., wetlands have *black rail occupancy* = 0 or 1). The model starts with a 2013 landscape and runs on an annual time step for 50–100 yr.

Annual processes in WICM are governed chiefly by regression equations parameterized from field data (Table 1) and executed in an order approximating the seasonal cycle or sampling period used when gathering data (Fig. 2a). First, during the winter rainy season, precipitation is generated based on the RCP 8.5 climate scenario (Flint and Flint 2012). Irrigation districts then update their reservoir water storage by subtracting water used over the previous summer and by adding recharge based on winter rainfall, and may implement 20–50% water allocation cutbacks if minimum storage thresholds are not met. The wildlife agency offers wetland protection and creation incentives. The protection incentive program permanently prevents landowners from turning irrigation off for their largest wetland (excluding impoundments, rice fringes, fluvial creeks, and wetlands fed by runoff from other properties). The wetland creation incentive program provides landowners with  $\sim 0.12$  acre-feet/d of water to create a new wetland on their property. Total water allocation for creation incentives was capped at 2% of each district's storage; because created wetlands use additional (i.e., surplus) irrigation water, during water cutbacks they were all turned off and new enrollments suspended. These policies represent different strategies for promoting wetland habitats—one aims to maintain wetlands during drought and one to increase wetlands outside of drought. Landowners may transfer their property to a new landowner due to sale or death and then make a series of irrigation decisions. Wetland patches first stochastically change their irrigation state (on or off) based on empirical baseline rates. Next, landowners can respond to irrigation cutbacks (if implemented) by permanently fixing leaks, temporarily cutting off water from pasture or rice fields until cutbacks are lifted, or deciding to sell their land in the next year (or

TABLE 1. Summary of data integration in our agent-based stochastic patch occupancy model.

| Agent (data source)   | Process                                     | Regression                             | Final submodel   | Tables  |   |
|---|---|--|--|---|---|
| Climate (RCP 8.5 model)   | Rainy season precipitation                  | Summary                                | Precipitation (Nov–May)<br>~ Normal( $\mu, \sigma$ ) <sup>2</sup>  | T/T   |   |
| Irrigation districts<br>(interviews and reservoir<br>databases) | Water storage usage and<br>recharge         | Tobit or summary                       | Water storage used ~ Normal( $\mu, \sigma$ )   | 5/T   |   |
|   |   |  | Water storage recharge ~ Normal<br>(Precipitation, $\sigma$ )  | 5/T   |   |
|   | Provide or cut back water                   | N/A <sup>D</sup>                       | If reservoir levels drop below thresholds,<br>implement water cutbacks   | 5/T   |   |
| Wildlife agency (scenario<br>design)                            | Provide wetland incentives                  | N/A <sup>D</sup>                       | If no cutbacks, provide incentives   | T/T   |   |
| Landowners (mail survey)  | Initialization and property<br>transfer     | Multinomial                            | Landowner typology ~ Property area   | 6/8   |   |
|   |   | Hurdle Poisson                         | Going to sell land ~ Intercept-only<br>Year until sell land ~ Poisson( $\mu$ )   | T/T   |   |
|   |   | Summary                                | Age ~ Normal( $\mu, \sigma$ )  | T/T   |   |
|   | Patches changes (cutback<br>actions)        | Summary                                | Pr(Death) ~ Exponential(Age)   | T/T   |   |
|   |   |  | Pr(Land-seller) ~ Typology   | 9/11  |   |
|   |   | Logistic                               | Pr(Pasture-cutter) ~ Typology<br>+ Elevation + Property area<br>+ Property area <sup>2</sup>   | 9/12  |   |
|   |   |  | Pr(Rice-cutter) ~ Intercept-only   | 9/T   |   |
|   |   |  | Pr(Leak-fixer) ~ Typology<br>+ Property area   | 9/13  |   |
|   |   | Patches changes (incentive<br>actions) | Logistic   | Pr(Protection incentive participant)<br>~ Typology + Elevation                      | 10/14   |
|   |   |  |  | Pr(Creation incentive participant)<br>~ Typology + Elevation + NID                  | 10/15   |
| Wetlands (aerial mapping)                                       | Initialization                              | Multinomial                            | Water source type ~ Geomorphology<br>+ Property area + No irrigation district<br>+ Landowner   | 1/2   |   |
|   |   |  | Irrigation type ~ Both-source<br>+ Geomorphology + Elevation<br>+ Property area + Wetland area<br>+ # wetlands + Landowner   | 2/3   |   |
|   |   | Logistic                               | Natural type ~ Geomorphology<br>+ Landowner  | 3/4   |   |
|   |   |  | Pr(Irrigation initially active)<br>~ Impoundment   | 4/5   |   |
|   | Patch changes (baseline<br>rates)           | Tobit                                  | Both-source wetlands' percent natural area<br>~ Intercept-only   | T/6   |   |
|   |   |  | Logistic   | Pr(Irrigation activation)<br>~ Natural-only + Precipitation<br>+ Impoundment + Site | 7/9   |
|   |   | Summary                                | Pr(Irrigation deactivation)<br>~ Precipitation + Impoundment<br>+ Leak + Pasture + Runoff + Site   | 8/10  |   |
|   |   |  | Summary  | New irrigated size ~ Gamma( $\alpha, \beta$ )                                       | T/T   |
| Wetlands: Rails<br>(presence-absence surveys)                   | Colonization and extinction<br>(black rail) | Occupancy model<br>(logistic)          | $\psi$ ~ Wetland area + Water source<br>+ Slope + Fluvial<br>$\gamma$ ~ Wetland area + Precipitation<br>+ Water source + Geomorphology<br>+ WNV risk + Connectivity<br>$\epsilon$ ~ Wetland area + Precipitation<br>+ Water source + Geomorphology<br>+ WNV risk | 11/16   |   |
|   |   |  | Colonization and extinction<br>(Virginia rail)   | Occupancy model<br>(logistic)   | $\psi$ ~ Wetland area<br>$\gamma$ ~ Wetland area + Precipitation<br>$\epsilon$ ~ Wetland area + Precipitation<br>+ Water source + Elevation |
| Wetlands: WNV (mosquito<br>trapping)                            | WNV risk                                    | Log-normal <sup>D</sup>                | Mosquito abundance ~ % wetland<br>(2.5-km buffer) + Rice distance  | 12/18   |   |
|   |   |  | Mosquito WNV prevalence<br>~ Mosquito abundance<br>+ Rice distance   | 13/19   |   |

Notes: Most submodels are stochastic regressions; “summary” indicates summary statistics (no regression), and superscript D indicates deterministic submodel. “Tables” lists the Appendix S1 table number of the final model/Appendix S2 table number of the model selection table; “T” indicates see text of Appendix S1 (no table).  $\psi$  represents initial occupancy probability,  $\gamma$  colonization probability, and  $\epsilon$  extinction probability. NID, Nevada Irrigation District; WNV, West Nile virus.

some combination of these). When irrigation is turned off, wetlands shrink in size if fed by both irrigated and natural water sources, or are eliminated altogether if fed by irrigation only. Landowners then decide whether to participate in incentive programs, and may enroll in each only once. Next, rail colonization and extinction occur during late spring (matching the onset of our field surveys) by running an SPOM over the new landscape. Wetlands eliminated by turning off irrigation go extinct. Finally, WNV vector strength is determined by wetland distribution as mosquito densities peak in late summer, which affects the probability of rail colonization and extinction in the following year (i.e., due to disease mortality over the winter). In the fall, measurements are taken and time steps forward.

In the following sections, we present a brief summary of each empirical submodel, discuss its implementation in WICM, and describe the coded processes that link submodels. These sections are organized by agent type according to the general framework in Fig. 1 and approximate the schedule of execution of processes described above and in Fig. 2a. Appendix S1 contains a comprehensive description in the standard format for ABMs.

#### *Parameterization of exogenous processes*

*Rainy season precipitation.*—We used the mean monthly precipitation over the rainy season (November–May); this metric accounted for the majority of rainfall and coincided with the timing of districts’ recharge and decision making. We stochastically generated annual precipitation based on the 2017–2099 RCP 8.5 data, to which we fit both a lag-1 autoregressive model (Salas 1993) and a nonautoregressive model using R package *stats* (v3.4.3, R Foundation for Statistical Computing, Vienna, Austria). We used the model without an autoregressive term ( $\mu = 1.023$ ,  $\sigma = 0.189$ ) because it had a lower Akaike’s information criterion (AIC;  $\Delta\text{AIC} = 1.98$ ).

#### *Parameterization of governance institutions*

*Initialization.*—We modeled Browns Valley Irrigation District (BVID) and Nevada Irrigation District (NID) based on polygon maps of water district service areas (U.S. Bureau of Reclamation and California Department of Water Resources 2009). Extents of irrigation district service areas (and landowner properties; see below) were represented in the model by converting polygons to 100-m raster maps and loading them into NetLogo’s raster cells.

*Water storage usage and recharge.*—For each district, we combined information from online databases using summary statistics and normal Tobit regressions to estimate storage usage and recharge per millimeter of precipitation (Appendix S1: Table S5). Annual storage was then updated by subtracting used water (which was proportionately increased by incentive programs or decreased by cutbacks) and adding water recharge, up to the max storage.

*Provide or cutback water.*—If the new storage fell below thresholds (set based on irrigation district reports; Appendix S1: Table S5), 20% or 50% cutbacks were implemented for that year.

*Provide wetland incentives.*—Based on the scenarios we designed, the wildlife agency activates protection policies and creation policies for all irrigation districts without active water cutbacks.

#### *Parameterization of resource users*

*Initialization.*—Landowners were implemented into the model as spatial agents based on 2010 parcel layers, converted to a 100-m raster and loaded into NetLogo. We modeled landowner diversity by conducting factor analysis on survey respondents’ ratings of 24 possible motivations for owning their property (Appendix S2: Table S7), as has been done in other studies (Ferranto et al. 2013). This classified landowners as one of six typologies: investment-, environment-, lifestyle-, profit-, recreation-, or tradition-motivated. These landowner characteristics were then used as covariates for the probabilities of landowners taking actions within the patch change submodels. Private landowners’ characteristics were initialized stochastically via multinomial regression (Appendix S1: Table S6; Appendix S2: Table S8). Public landowners were deterministically assigned and did not change or respond to cutbacks and incentive programs.

*Property transfer.*—New landowner characteristics were assigned (via multinomial regression as above) when property was transferred because landowners either died or reached the year they planned to sell in. Rates were fit from survey data (Appendix S1). If a property was not transferred, the landowner’s age increased and their “years to sell” decreased by one.

*Patch changes (cutback actions).*—Our patch change model simulated a Markov process where an existing wetland transitioned between two irrigation states, on (1) or off (0), based on rates estimated from survey and field data (i.e., a heuristic rule-based model; An 2012). We used this framework, rather than an economic or vegetation successional model, because landowners reported in interviews that water use decision-making was driven by diverse, often noneconomic factors (e.g., tradition or amenities; Huntsinger et al. 2017), and because field observations showed that wetlands were able to form quickly wherever there was sufficient water. We parameterized landowner’s responses to irrigation water cutbacks during drought via four logistic regressions (NLOGIT v5.0, Econometric Software, Inc. Plainview, New York, USA) that assigned landowners to groups based on a survey question asking if they would respond to hypothetical water cuts of  $\geq 20\%$  by (1) selling their land, (2) repairing leaks, (3) reducing pasture irrigation, or (4) reducing rice irrigation (Appendix S1:

Table S9; Appendix S2: Tables S11–S13). These response options were based on landowner interviews; ponds and impoundments were excluded because landowners reported they were unlikely to be affected (see Appendix S1). Landowners in each group took their relevant actions (i.e., turning irrigation off) on their wetlands when cutbacks occurred (see *Model overview*).

*Patch changes (incentive actions).*—We used logistic regression (NLOGIT v5.0) on responses to a survey question asking whether landowners would be interested in protecting a wetland for a one-time payment or creating a wetland if given free water (Appendix S1: S10; Appendix S2: Tables S14 and S15). Landowners that were interested were assigned to protection-landowner and creation-landowner groups when initialized. They then had an annual enrollment probability of 0.0526 (based on observed rates for a similar policy; see Appendix S1). Protection participants received a one-time payment of \$10,000 from the wildlife agency to protect their wetland. Creation participants received enough water to create a ~0.57-ha slope wetland; created wetland size was estimated from State Wildlife Area data (see Appendix S1). The annual water cost, paid by the wildlife agency, was \$550.00 (BVID) or \$893.10 (NID; prices from district documents).

#### *Parameterization of patches*

*Initialization.*—Wetlands were loaded into the WICM as points and had their characteristics assigned based on actual data (if available), or stochastically generated during initialization via regressions (Appendix S1: Tables S1–S4; Appendix S2: Tables S2–S5) following Berger and Schreinemachers (2006). Both-source wetland areas were divided into natural and irrigated areas based on historic tracking data (text of Appendix S1; Appendix S2: Table S5).

*Patch changes (baseline rates).*—We estimated baseline rates of change in wetlands using our patch change data from 2001 to 2016, assuming contemporary rates represented future dynamics. We used mixed logistic regression (R package *lme4* v1.1, Madison, Wisconsin, USA) to estimate probabilities of irrigation activation or deactivation (Appendix S2: Tables S9 and S10; Appendix S1: S7–S8). We included a random effect for site to account for repeat sampling of the same wetlands, as is common for time series data (Bell and Jones 2015). Newly irrigated natural wetlands had their irrigated area predicted with a Gamma distribution ( $\alpha = 0.878$ ,  $\beta = 2.228$ ) fit from mapping data. We did not model the creation of new wetlands because contemporary rates were negligible (Appendix S1).

*Colonization and extinction (black and Virginia rails).*—We modeled the metapopulation as an SPOM, parameterized by fitting multiseason occupancy models (MacKenzie et al. 2003) in R package *unmarked* (v0.12, Laurel, Maryland, USA) to our rail presence–absence

data. These models jointly estimate probabilities of initial occupancy ( $\Psi$ ), colonization ( $\gamma$ ), and extinction ( $\epsilon$ ) with covariates on each parameter. Previous studies found no evidence of competition between black and Virginia rails, so we simulated their dynamics separately (Risk et al. 2011). Connectivity was modeled with an autoregressive buffer radius metric (Appendix S1) that had previously been found to fit best for black rails and was validated with genetic data (Hall et al. 2018). This connectivity metric incorporated occupancy probability at sites within the buffer radius that were unsurveyed or had nondetections. The remaining covariates for  $\gamma$  and  $\epsilon$  were assessed via model selection: precipitation, WNV risk, elevation, geomorphology type, and water source type (Appendix S2: Tables S16 and S17; Appendix S1: Table S11). In WICM, any wetlands smaller than the minimum breeding home range size of radio-tracked black and Virginia rails (0.16 and 0.28 ha, respectively; S. R. Beissinger, *unpublished data*) were automatically set unoccupied.

*West Nile virus risk.*—We used linear regressions to model mosquito abundance (mean # *Culex* spp. caught per trap-night) and WNV prevalence at each wetland as a function of wetland area in a 2.5 km buffer and other covariates (Appendix S2: Tables S18–S20; Appendix S1: Tables S12 and S13). We estimated WNV risk as the product of these metrics (a well-established predictor of spatial variation in WNV cases with a strong theoretical basis; Kilpatrick and Pape 2013).

#### *Simulation analyses*

Simulations were run with the use of R package *RNetLogo* (v1.0.4, Göttingen, Germany). To determine drivers of current CHANS dynamics, we conducted sensitivity analysis with drought cutbacks but no incentives for 50-yr projections. We used  $\pm 25\%$  and  $\pm 10\%$  perturbations for all top-level parameters of the model (i.e., not beta parameters), as well as the beta parameters for rail colonization ( $\gamma$ ) and extinction ( $\epsilon$ ). Initial results showed the system was highly sensitive to precipitation, so we also tested its mean and SD. We replicated simulations 4,000 times and calculated the mean percent change from a no perturbation scenario as

$$\frac{\text{Output metric with perturbation} - \text{Output metric without perturbation}}{\text{Output metric without perturbation}}$$

for three metrics: (1) each species' mean metapopulation size (excluding the first 10 yr as burn-in), (2) each species' minimum metapopulation size for each iteration (as a proxy for quasi-extinction risk; Beissinger and Westphal 1998), and (3) the mean wetland abundance (i.e., the number of wetlands that had natural water sources or were actively irrigated). We defined the metapopulation size as the number of occupied wetlands,

and used this rather than the occupancy rate because wetland abundance varied across simulations.

We assessed the influence of incentive programs after 50 and 100 yr by running scenarios with and without irrigation cutbacks: (1) no incentives, (2) wetland creation incentives, (3) wetland protection incentives, and (4) both incentives. To determine WNV's influence on the system, we also ran a scenario without WNV, incentives, or cutbacks. We replicated simulations 8,000 times and recorded ending and minimum metapopulation sizes for each species. Our model lacked mechanisms to cause extinction vortices, so we choose a minimum metapopulation size threshold of 25 wetlands (<5% occupancy on the 2013 landscape) to represent a quasi-extinction risk, as wetlands in this region are small and often support only a few breeding pairs (Appendix S1). Finally, to test if incentives reduced the importance of other drivers of quasi-extinction risk, we ran sensitivity analyses for a drought cutback scenario with both incentives (4,000 replicates) with  $\pm 25\%$  perturbation. We then compared the absolute percent changes to the corresponding percent changes from the no incentives scenario, using Welch's *t*-tests (Benjamini-Hochberg correction for a 0.05 false discovery rate) to identify significant differences.

#### Model validation

We used 2017–2018 rail occupancy data that was not included in model fitting to validate WICM's ability to accurately predict metapopulation dynamics. To estimate 2017 and 2018 colonization and extinction rates corrected for detection probability, we fit multiseason occupancy models with different annual  $\gamma$ ,  $\epsilon$ , and  $p$  intercepts for each year to the field data. We then ran simulations, replicated 2,000 times, that were initialized in 2002 and run through 2018 with the observed annual precipitation values and with WNV first entering the system in 2007. We only used wetlands with identical site boundaries between the field data set and model ( $n = 260$ ). To validate our land-use change model, we randomly selected 10% of regional wetlands ( $n = 176$ ) and assessed their active water sources in 2017 via Google Earth imagery. We replicated simulations 2,000 times, initialized to 2013 and run through 2017 with observed precipitation values. Following Schreinemachers and Berger (2011), we tested whether each metric's measured 95% CIs included the mean simulated rates for the same sets of wetlands.

## RESULTS

#### Model behavior

Validation tests indicated our model accurately predicted metapopulation and land-use change dynamics (Fig. 3). Modeled values were within the 95% CI of independent field data for all measures except Virginia rail colonization in 2017, which fell just below the

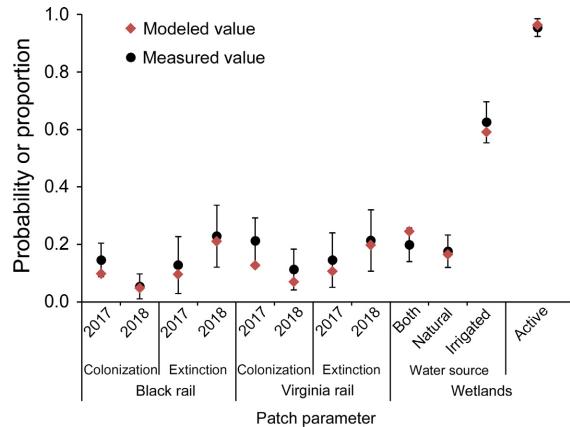


FIG. 3. Validation analysis comparing sampled probabilities of colonization and extinction for black and Virginia rail metapopulations ( $n = 260$  sites for 2017 and 2018), and proportions of wetlands fed by natural, irrigated, or both water sources, and with at least one active water source ( $n = 176$  sites for 2017 only), to a Wetlands-Irrigation CHANS Model (WICM) simulation of the California Sierra Nevada foothills that used actual precipitation values. Bars represent 95% CIs.

confidence limit. The model correctly predicted an increase in occupancy for both species in 2017, which was the second rainiest year on record in California. However, it slightly underestimated the occupancy increase due to unusually high October 2017 rainfall, which was not captured in our precipitation metric (mean November–May, the typical rainy season); adding this extra precipitation to the model boosted model values close to expected values for both species (data not shown).

A characteristic run illustrating CHANS dynamics with drought cutbacks and no incentive policies is shown in Fig. 2b. Simulations exhibited relatively stable wetland numbers with balanced wetland irrigation activation and deactivation rates, but periodic drops in wetland numbers occurred when landowners reduced irrigation during drought cutbacks. Severe droughts typically caused cutbacks in only one irrigation district, while rarer, exceptional droughts caused cutbacks in both. Black rail occupancy declined in early years, because initial occupancy ( $\psi$ ) was fit from pre-WNV levels; thereafter, occupancy reached a stochastic equilibrium. However, severe droughts caused occupancy declines that required up to a decade to recover. Virginia rail dynamics similarly stabilized at a stochastic equilibrium punctuated by drought-induced drops in occupancy, but exhibited greater annual stochasticity. The two species had fairly synchronous dynamics due to similar effects of precipitation. WNV risk was not retained in Virginia rail occupancy models during model selection (Appendix S1: Table S18), but was detrimental to both colonization and extinction rates of black rails (Appendix S2: Table S11). Wetlands near rice fields in the Central Valley had an order-of-magnitude higher

WNV risk compared to wetlands upslope and away from rice agriculture ( $\sim 1.5$  vs.  $\sim 0.15$  infected *Culex* per trap/night), similar to elsewhere in California (Kovach and Kilpatrick 2018). Wetlands with more wetland land cover within 2.5 km also had higher WNV risk (Appendix S3: Table S19). Thus, WNV introduced a negative feedback between wetland abundance and rail occupancy that most affected large, well-connected wetlands, which were otherwise the most likely to be occupied.

#### *Drivers of rail metapopulation dynamics*

This CHANS of wetlands in a working landscape was more sensitive to variation in precipitation by an order of magnitude compared to other modeled processes, with rail metapopulation dynamics (Fig. 4), quasi-extinction risk (Appendix S3: Fig. S1), and abundance of wetlands (Appendix S3: Fig. S2) all exhibiting similar patterns of sensitivity. A precipitation term was in seven submodels; it was retained in every AIC model selection procedure in which it was tested (Appendix S2). Sensitivity to precipitation was driven primarily by its mean, but quasi-extinction risk also showed sensitivity to changes in precipitation variability. Irrigation district water storage capabilities and usage also exerted moderate effects for rails (Fig. 4) and strong effects for wetland abundance (Appendix S3: Fig. S2). After precipitation, the strongest drivers of metapopulation dynamics were those that directly affected occupancy and the colonization and extinction rates ( $\gamma$  and  $\epsilon$ ); mean metapopulation size was equally sensitive to  $\gamma$  and  $\epsilon$  (Fig. 4), whereas quasi-extinction risk was more sensitive to  $\epsilon$  (Appendix S3: Fig. S1). Virginia rails were generally less sensitive than black rails, but exhibited similar patterns. However, Virginia rails were relatively more sensitive to their minimum wetland size for occupancy (Fig. 4b) because it was larger than for black rails, so a similar percent change caused more wetlands to be affected. There were other differences in sensitivity between rail species as well, with strong to moderate effects of connectivity, slope geomorphology, and WNV for black rails, and of patch change rates and elevation for Virginia rails. Most other parameters, including landscape and landowner initialization parameters (Appendix S3: Figs. S2 and S3), had insignificant effects (Appendix S3).

#### *Effects of irrigation cutback and wetland incentive policies*

Prior to the arrival of WNV, black rails had higher occupancy than Virginia rails, but models suggested the virus more than halved black rail metapopulation size while Virginia rails were unaffected (Pre-WNV vs. None in Fig. 5a, b; see Appendix S3: Fig. S5 for actual occupancy trends). Likewise, in all other scenarios black rail ending and minimum metapopulation size (Fig. 5a, b) after 50 yr was about half that of Virginia rails

(Fig. 5c, d). Results were similar for 100-yr projections (Appendix S3: Fig. S4a, b).

Minimum black rail occupancy reached precariously low levels when irrigation districts implemented water cutbacks during drought. Then, over a quarter of the simulations dropped below 25 occupied wetlands ( $\sim 5\%$  occupancy; Fig. 5c, red dashed line) within 50 yr, and nearly half fell to that level within 100 yr (Appendix S3: Fig. S4c, d).

Wetland creation incentives were effective at bolstering metapopulation size of both species outside of drought years, but also increased variation in occupancy (Fig. 5a, b). Creation incentives increased the total metapopulation size for Virginia rails more than for black rails, due to higher overall occupancy rates of Virginia rails. However, creation incentives were more effective at increasing the proportion of wetlands occupied for black rails, increasing their ending occupancy by 45.6% of its original value compared to 19.6% for Virginia rails. In the absence of drought cutbacks, creation incentives increased black rails' minimum metapopulation size over 50 yr by 78.5% on average (Fig. 5c), greatly reducing their quasi-extinction risk. However, this benefit disappeared with water cutbacks during drought (reduced to only a 9.3% increase). Similar patterns were seen for Virginia rails but, because this species was widely distributed beyond the boundaries of our study area and had higher colonization rates, it faced little risk of metapopulation extinction (Fig. 5d). Creation incentives had high landowner participation rates, as this program reached the 2% reservoir storage cap on water allocation within a mean of 5 yr. There were  $277.0 \pm 0.2$  SD new wetlands created at an annual cost for water of \$233,336.

Wetland protection incentives had little effect ( $<5\%$  change) on ending or minimum metapopulation size of either rail species after 50 yr in all scenarios (Fig. 5). This was partly because protection incentives had lower landowner participation rates than creation incentives; participation was uncapped and grew linearly from  $170.7 \pm 11.6$  wetlands by year 50 to  $310.0 \pm 14.1$  protected wetlands by year 100. After 100 yr, protection incentives had a small effect for black rails when coupled with drought cutbacks, increasing their ending and minimum metapopulation size by 7.3% and 12.2% (seven and three more occupied wetlands, respectively). Virginia rail ending and minimum metapopulation size were still unaffected after 100 yr ( $\leq 5\%$  change). The mean annual cost of protection incentives for the first 50 yr was \$33,509 (3.35 wetlands/yr).

There was a moderate reduction in quasi-extinction risk when wetland protection incentives were combined with wetland creation incentives (Fig. 5c, d). The combination increased black rail minimum metapopulation size 15.8% after 50 yr and 18.8% after 100 yr (about five new occupied wetlands in both cases) compared to the scenario without incentives. For Virginia rails, combining incentives showed weak effects only at 100 yr (a

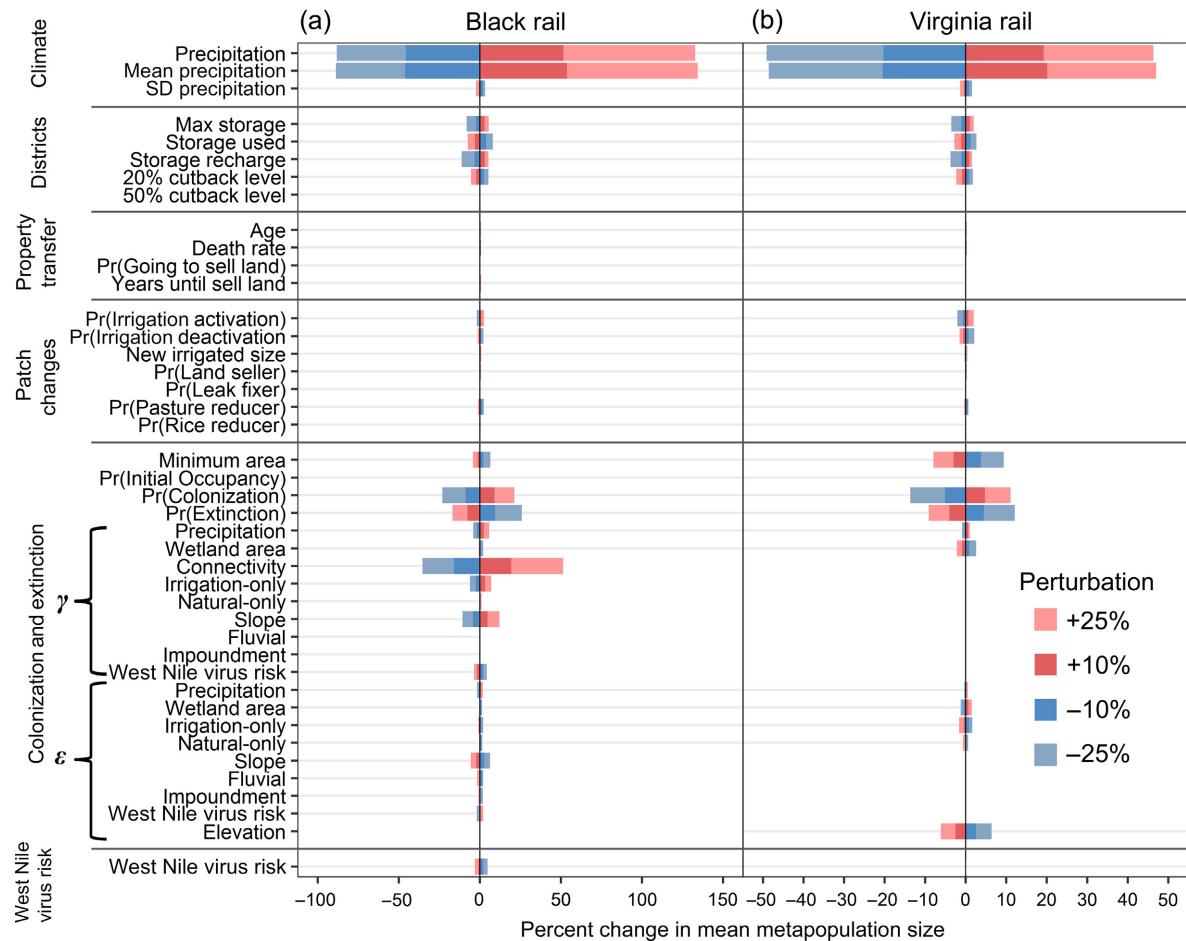


FIG. 4. Sensitivity analysis of (a) black and (b) Virginia rail for Wetlands-Irrigation CHANS Model (WICM) input parameters used in the simulation of the California Sierra Nevada foothills with drought cutbacks and no wetland incentives. Virginia rails were less sensitive to system dynamics overall. Parameters labeled  $\gamma$  and  $\epsilon$  are regression parameters for colonization and extinction probabilities, respectively.

6.1% increase), due to their larger minimum metapopulation size.

Incentive policies made black rail quasi-extinction risk more sensitive to precipitation and irrigation storage, as well as slope geomorphology wetlands (the type created by incentives; Fig. 6). They reduced sensitivity to several parameters, all of which were not tied to the dynamics of creation-incentive wetlands, such as the proportion of landowners that turned off pasture wetlands during drought and precipitation’s direct effects on rail extinction rates.

## DISCUSSION

### *Drivers of metapopulation dynamics in a CHANS*

Our model showed that the precipitous decline of the California black rail metapopulation was caused by a combination of WNV and drought. WNV halved the occupancy, and droughts created periodic spikes in

extinction probability and reductions in colonization probability (Appendix S3; Fig. S5). The ability to deduce drivers of observed metapopulation dynamics by reproducing emergent, qualitative patterns is an important benefit of ABMs (Grimm et al. 2005). We found little evidence of WNV impacting Virginia rails (Appendix S1: S37); WNV infection and mortality rates vary substantially among avian species (Kilpatrick et al. 2013).

The CHANS was strongly driven by precipitation and the ability of irrigation districts to store it in reservoirs, further illustrating the importance of severe drought events (Fig. 4). The RCP 8.5 climate scenario projects a 6.6% drier climate with 19.5% greater variance compared to contemporary levels for the study region. Even these levels of change could cause large shifts in system state because of the extremely high sensitivity of rail metapopulation dynamics and wetland numbers in our model to precipitation. Precipitation affected rails directly as a covariate for colonization and extinction

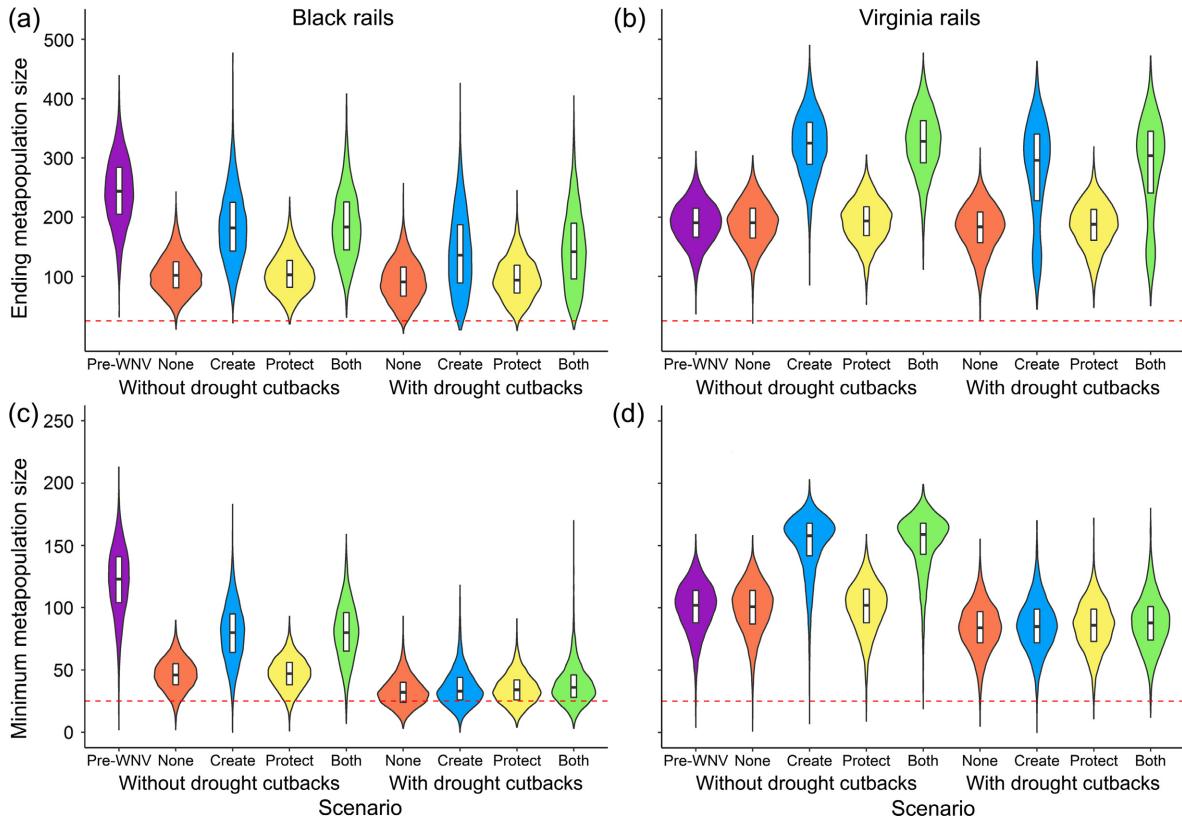


FIG. 5. Ending metapopulation size and minimum metapopulation size (used as a measure of quasi-extinction risk) for black rails and Virginia rails in the California Sierra Nevada foothills, projected for 50 yr in Wetlands-Irrigation CHANS Model (WICM) for eight different scenarios. Bar shows median, and box plots show first–third quartiles. WNV, West Nile virus.

(Appendix S1: Table S11), by increasing the baseline probability of irrigation being turned or kept off in drier years (Appendix S1: Tables S7 and S8), and by landowner responses to drought cutbacks (Appendix S1: Table S9). Occupancy was less sensitive to direct effects of precipitation on colonization and extinction (Fig. 4a), indicating that sensitivity to precipitation was caused chiefly by irrigation decisions of landowners that changed wetland abundance. However, quasi-extinction risk was sensitive to effects of precipitation as a covariate for extinction probability (Appendix S3: Fig. S1a), suggesting that natural drying of wetlands during drought (observed in the field; S. R. Beissinger, unpublished data) is also a risk to the metapopulations. Irrigation cutbacks are thus a synergistic threat, causing wetlands to disappear when rails are already stressed from drying wetlands. Both species were surprisingly insensitive to parameters controlling the number of landowners that responded to drought cutbacks, indicating that the frequency of drought disturbance was more important than its magnitude.

The complexity of CHANS makes anticipating threats and controlling system behavior difficult, so fostering CHANS’ resilience to different disturbances is an important management goal (Schlüter et al. 2012).

Gimona and Polhill (2011) found that incentive programs reduced the sensitivity of metapopulation extinction risk to all other model parameters, creating resilience to perturbations of the other components of the CHANS. In contrast, we found that the addition of incentives greatly increased metapopulation sensitivity to precipitation (Fig. 6), although incentives did reduce sensitivity to some threats (e.g., landowners reducing pasture irrigation). This occurred in WICM because the provisioning of water for wetland creation incentives was conditional on staying above drought thresholds, whereas the Gimona and Polhill incentive programs were decoupled from system dynamics. Thus, an incentive scheme’s ability to reduce extinction risk sensitivity may depend on whether the policy is exogenous to the CHANS dynamics.

Species differences in wetland habitat preferences complicated relationships between patch change (i.e., elimination and creation) rates and colonization abilities predicted by theory. The limited dispersal abilities of black rails should make them more sensitive to patch change rates than Virginia rails because black rails are at greater risk of patch changes outpacing (re-) colonization abilities (Amarasekare and Possingham 2001). However, Virginia rails showed greater sensitivity to

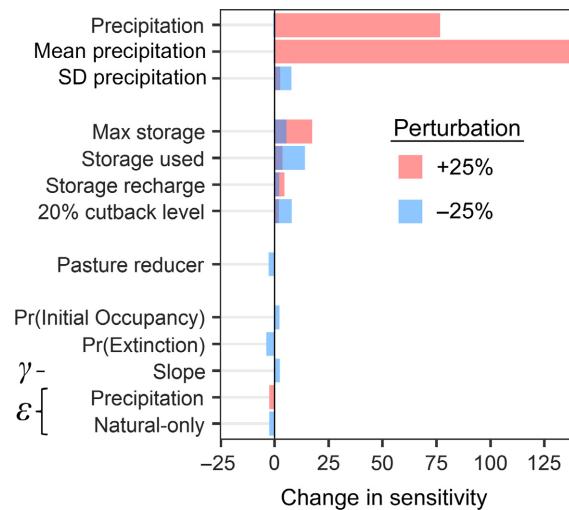


FIG. 6. Significant differences (Welch's  $t$ -tests with Benjamini-Hochberg 0.05 false discovery rate) in sensitivity (percent change in minimum black rail metapopulation size) between scenarios with drought cutbacks and incentives, compared to scenarios without incentives (the baseline).

baseline patch change rates (Fig. 4). This likely occurred because Virginia rails used impoundment wetlands, which frequently dried and were reirrigated (Appendix S1: Tables S16–S18), but black rails rarely used these sites (Appendix S1: Table S11) which often are flooded too deeply (Richmond et al. 2010a). However, black rails were much more sensitive than Virginia rails to patch change due to drought, as shown by their greater sensitivity to precipitation and irrigation district parameters (Fig. 4). This difference may also be partly due to wetland heterogeneity; cutbacks affected pasture- and leak-fed wetlands, which were more often of the slope geomorphology type (Appendix S1: Table S2) preferred by black rails (Fig. 4a). Metapopulation theory has increasingly focused on the effects of patch quality differences and patch dynamics (Ranius et al. 2014). Our results show that in CHANS these processes can interact in complex ways, with heterogeneity in patch quality able to overshadow or exacerbate the influence of different drivers of patch change.

#### *Utility and limitations of data integration via agent-based modeling*

The ABM-SPOM framework allowed us to combine quantitative field data from wildlife occupancy surveys, social science surveys, land-use change mapping, climate models, and insect disease vector trapping. This integration resulted in important findings—such as direct effects of drought on wetland drying appearing to be much less important than its impacts on landowner irrigation behavior, and incentive schemes to foster resilience being less effective if coupled to CHANS dynamics. These findings would not have been evident from a

standard SPOM or from the assessment of field data because they emerged from the coupling of multiple processes. A traditional SPOM would likely underestimate the true risk of metapopulation extinction by failing to account for the threat posed by irrigation cutbacks, which was identified from our ABM. Another key benefit of ABMs is their ability to model individual heterogeneity (Parker et al. 2003). This was crucial to our finding that the theoretical relationship between dispersal and patch change rates in metapopulations was not borne out in this system because patch heterogeneity affected colonization, extinction, and patch change rates in different ways.

Integrating different kinds of data to model CHANS is an evolving process (Alberti et al. 2011) that is enabled by the flexible ABM framework. Constructing an ABM-SPOM for a new system may seem daunting, but it begins by simply developing a conceptual model of the key social actors and ecological processes (i.e., Fig. 2), which can be coded into an initial draft of an ABM. Coding an ABM with “fake” parameters before beginning data collection has numerous benefits: it can clarify ambiguities in thinking, ensure that the correct data are gathered, provide an ongoing base for data integration, and be iteratively redesigned as necessary. NetLogo's simple programming language makes coding submodels remarkably easy, and the ABM-SPOM framework can be implemented in more advanced programming languages if needed.

Data types differ in their ease of incorporation into an ABM. Occupancy data for SPOM parameterization are relatively easy to collect and analyze. On the other hand, land-use change ABMs can be difficult to parameterize (Bousquet and Le Page 2004). However, if some parameters lack data, a range of plausible values can be estimated from expert opinion and the uncertainty this introduces into model behavior can be assessed via sensitivity analysis (c.f., Iwamura et al. 2014). In other situations, it may be pragmatic for ecologists to gather and integrate SPOM data into existing land-use change ABMs focused on farmland (Guillem et al. 2009, Brady et al. 2012, Schouten et al. 2013), urban growth (Guzy et al. 2008), vegetative succession (Anselme et al. 2010), or other systems (Parker et al. 2003), rather than reinvent the wheel. Such efforts could rapidly expand the number of studies of metapopulations in CHANS and help to identify general principles for their conservation.

Uncertainty in model outcomes arises from uncertainty in model input parameter estimates, alternative model design choices, errors in data collection, and errors in model construction, all of which propagate through model results (Evans 2012). The use of sensitivity analyses to assess uncertainty is standard in ABMs because of their complexity (Evans 2012, Lee et al. 2015). Our sensitivity analyses showed extreme sensitivity to precipitation, suggesting that uncertainty in climate change models likely overwhelms other sources. However, model construction choices also added

uncertainty to WICM, because data availability necessitated simplifications that reduced realism. Our reservoir model was a statistical approximation that did not model hydrologic flows or temperature increases, which threaten water supplies by reducing snowpack and increasing evaporation from reservoirs. Also, our model of water cutbacks during drought only focused on wetlands fed by pasture, rice, or irrigation leaks, and assumed that landowners responded by ceasing irrigation and drying these wetlands entirely rather than by reducing wetland size, which may happen in some situations. Thus, our results likely overestimated some effects of drought on wetland persistence, but this was offset by our assumption that water- feature- and runoff-fed wetlands were unaffected by irrigation water cutbacks (Appendix S1). Lastly, we did not model parcel subdivision and land-use change outside of wetlands, which may have important effects in this CHANS over the coming decades. Thus, our results are best viewed as a useful approximation of CHANS behavior, rather than representing the system with total accuracy.

#### *Conservation implications*

Achieving sustainable CHANS requires an integrated systems approach to avoid “solutions” to natural resource problems that produce unforeseen negative consequences. ABMs are a particularly promising tool for quantitatively assessing such tradeoffs (Liu et al. 2015). Our model suggests that a negative externality may arise as a result of recently revised water conservation policies in California for increased water cutbacks during drought (Huntsinger et al. 2017). In the absence of water cutbacks during drought, only 5% of model runs had black rail metapopulation size falling below a threshold within 50 yr where extinction could become a grave concern, and wetland creation incentives were effective at reducing this risk (Fig. 5b). However, a serious extinction risk to black rails occurs if irrigation districts mandate water cutbacks during drought, with one-quarter and one-half of the model iterations falling below this threshold within 50 and 100 yr, respectively.

Although our simulations should not be viewed as predictions of future conditions, they do provide information on how this CHANS is likely to respond, which can inform decisions (Bousquet and Le Page 2004, Liu et al. 2015). Neither of our assessed incentive policies—protecting wetlands and providing free water to landowners outside of drought cutback years—was effective at ameliorating risk to black rails from drought or reducing their sensitivity to precipitation. Creation-incentive wetland programs had high rates of landowner interest (Appendix S2: Table S15), but were more expensive and their gains in occupancy during normal precipitation years disappeared when irrigation water was cut back during drought. Thus, adding wetlands outside of drought years did not bolster overall occupancy sufficiently to reduce the risk posed by drought cutbacks.

Wetland protection schemes designed to encourage landowners to continue irrigating their wetlands were cheaper, but yielded only slight reductions in extinction risk over very long time periods. Sensitivity analysis (Fig. 4) suggested additional ways to reduce extinction risk, especially by increasing the water storage capacity of irrigation districts (Appendix S3). If combined with guaranteed water allocations for wetlands that were preserved during drought, this may be a politically feasible middle ground, providing landowners with additional and more secure water supplies and environmental benefits to trade off against the impacts of reservoir construction.

We found that water conservation policies encouraging landowners to reduce irrigation “waste” that feeds wetlands, even if only during drought years, may reduce rail metapopulations to near extinction thresholds. Recent studies have documented similar systems where irrigation runoff and leaks have created numerous patchy wetlands that support bird communities in Europe (Moreno-Mateos et al. 2009) and semi-arid regions in the western United States (Sueltenfuss et al. 2013, Palta et al. 2017). Our study is the first to assess how water conservation policies impact such systems, and suggests caution is needed. Humans have caused profound loss of natural wetlands, and existing environmental policies have focused on preventing further degradation. However, some wetland species may have suffered an “extinction debt” (Tilman et al. 1994) from loss of natural wetlands and are persisting primarily because of the presence of irrigated wetlands. Integrating accidental wetlands into regional water management goals may provide more cost-effective conservation benefits than attempting to restore a lost “natural” state.

#### ACKNOWLEDGMENTS

This research was funded by the National Science Foundation (DEB-1051342, CNH-1115069), the Sierra Foothills and Sacramento Audubon Societies, the Salvador de Madariaga program (PRX16/00452) of the Spanish Ministry of Culture and Education, and the U.S. Department of Agriculture National Institute of Food and Agriculture. We thank our field technicians, the Sierra Foothills Research and Extension Center, and our landowner participants for making this research possible.

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