Two-species occupancy models: a new parameterization applied to co-occurrence of secretive rails

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Abstract. Two-species occupancy models that account for false absences provide a robust method for testing for evidence of competitive exclusion, but previous model parameterizations were inadequate for incorporating covariates. We present a new parameterization that is stable when covariates are included: the conditional two-species occupancy model, which can be used to examine alternative hypotheses for species' distribution patterns. This new model estimates the probability of occupancy for a subordinate species conditional upon the presence of a dominant species. It can also be used to test if the detection of either species differs when one or both species are present, and if detection of the subordinate species depends on the detection of the dominant species when both are present. We apply the model to test if the presence of the larger Virginia Rail (*Rallus limicola*) affects probabilities of detection or occupancy of the smaller California Black Rail (*Laterallus jamaicensis coturniculus*) in small freshwater marshes that range in size from 0.013 to 13.99 ha. We hypothesized that Black Rail occupancy should be lower in small marshes when Virginia Rails are present than when they are absent, because resources are presumably more limited and interference competition should increase. We found that Black Rail detection probability was unaffected by the detection of Virginia Rails, while, surprisingly, Black and Virginia Rail occupancy were positively associated even in small marshes. The average probability of Black Rail occupancy was higher when Virginia Rails were present (0.74 ± 0.053, mean ± SE) than when they were absent (0.36 ± 0.069), and for both species occupancy increased with marsh size. Our results contrast with recent findings from patchy forest systems, where small birds were presumed to be excluded from small habitat patches by larger competitors.

Key words: Black Rail; detection probability; interspecific competition; Laterallus jamaicensis coturniculus; Rallus limicola; *species co-occurrence; two-species occupancy models; Virginia Rail.*

INTRODUCTION

Interspecific competition plays an important role in structuring ecological communities (Rosenzweig 1995). For example, larger species may exclude smaller ones from territories or high-value food resources through interference competition (Persson 1985, Pimm et al. 1985, Robinson and Terborgh 1995, St-Pierre et al. 2006), and these interactions are expected to be strongest under conditions of resource limitation (Wiens 1989). Recent studies of avian communities in fragmented forest systems (Brown and Sullivan 2005, Brown 2007) used patch size as a proxy for resource availability and showed that, in small fragments, large- and medium-sized bird species increased in abundance while small bird species declined, offering circumstantial evidence for interspecific competitive exclusion. However, using differences in observed species occurrences as evidence of competitive exclusion may lead to incorrect inferences

about both the magnitude and direction of competition unless analyses account for two important factors: false absences and habitat covariates (Lynch and Johnson 1974, MacKenzie et al. 2004, 2006). The development of robust and flexible methods for characterizing species interactions is needed, particularly for species distribution modeling applications that have become central to predicting community responses to climate change (Elith and Leathwick 2009).

MacKenzie et al. (2004, 2006) developed a flexible, likelihood-based two-species occupancy model that accounts for imperfect detection for analyzing species co-occurrence patterns from repeated presence–absence survey data. The model directly estimates a "species interaction factor" (hereafter SIF) that is a ratio of how likely the two species are to co-occur compared to what would be expected under a hypothesis of independence. This two-species occupancy model has been used to examine co-occurrence patterns of terrestrial salamanders (MacKenzie et al. 2004), vipers (Luiselli 2006), and owls (Bailey et al. 2009). In addition to providing unbiased estimates of co-occurrence, their model can be used to examine how the presence or detection of one
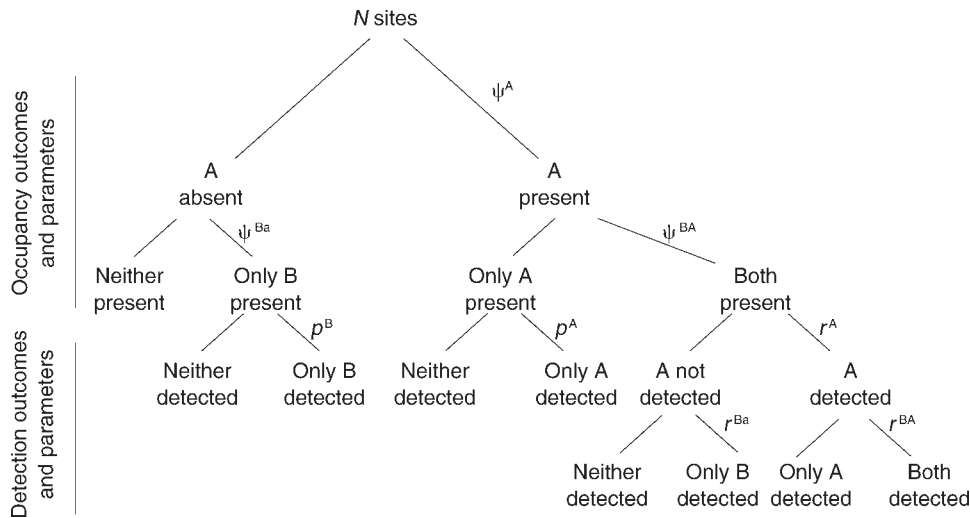
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Fig. 1. Model structure for the conditional parameterization of the single-season two-species occupancy model, where species A is assumed to be dominant and species B subordinate. Parameters are the probabilities of occupancy (ψ), detection where one species is absent (p), and detection where both species are present (r); superscript "a" indicates that species A is absent (for ψ^{Ba}) or is present but not detected (for r^{Ba}). See Table 1 for all definitions. All unlabeled branches correspond to one minus the opposite labeled branch (e.g., the unlabeled branch opposite ψ^A is equal to $1 - \psi^A$).

species might affect the detection probability of the other. For example, Bailey et al. (2009) found evidence that the detection probability of Barred Owls (*Strix varia*) and Northern Spotted Owls (*Strix occidentalis caurina*) was negatively influenced by the presence of the congeneric species. However, a limitation of the two-species model parameterization of MacKenzie et al. (2004, 2006) is that it can fail to converge when covariates are included and a SIF is directly estimated. Developing a two-species occupancy model that successfully incorporates habitat covariates is crucial because habitat preferences are a major factor determining species distributions (Morrison et al. 2006) and they can generate co-occurrence patterns that may incorrectly be interpreted as a product of interspecific competitive exclusion.

Here we present a new parameterization for the two-species occupancy model called the "conditional two-species occupancy model" that successfully incorporates covariates. We then apply it to examine co-occurrence patterns of two secretive wetland birds, the California Black Rail (*Laterallus jamaicensis coturniculus*) and Virginia Rail (*Rallus limicola*), across a range of marsh sizes. Understanding co-occurrence patterns for Black and Virginia Rails is important because competitive interactions are a potential factor that may influence the sparse and patchy distribution of the Black Rail throughout North America (Eddleman et al. 1994) and in California, where it is legally protected as a threatened subspecies (California Department of Fish and Game 2008). We first examine factors that may affect the detection probability for each species, and then test for evidence of an association between Black and Virginia Rail occupancy. Lastly, we test three

predictions for co-occurrence patterns related to patch area: (1) Black Rails should have a higher probability of occupancy in small marshes than Virginia Rails because they have a smaller home range; (2) in small marshes where resources are presumably more limited, Black Rail occupancy should be lower when Virginia Rails are present than when they are absent because interference competition should increase; and (3) the probability of occupancy for both species should increase with marsh area, because larger marshes should provide a wider range of microhabitats and contain more resources to support both species.

PARAMETERIZATION OF THE CONDITIONAL TWO-SPECIES OCCUPANCY MODEL

The conditional two-species occupancy model can be represented as a hierarchical tree of conditional occupancy and detection probabilities, where species A is assumed to be dominant and species B subordinate. The top branch of the model (Fig. 1, Table 1) represents the unconditional probability of occupancy (ψ^A) or absence ($1 - \psi^A$) for species A. The second, lower, set of branches represent the probabilities of occupancy (ψ^{BA}) or absence ($1 - \psi^{BA}$) for species B conditional on species A being present, and the probability of occupancy (ψ^{Ba}) or absence ($1 - \psi^{Ba}$) for species B conditional on species A being absent. The remaining lower branches represent probabilities of detection for species A and B that are conditional on the occupancy status of both species (Fig. 1, Table 1; further details on detection will be provided). Note that the probability of detection is not equivalent to the probability of detecting an individual of a given species, but rather is the probability of detecting at least

TABLE 1. Descriptions of the parameters used in the conditional two-species occupancy model.

Parameter	Description
ψ^A	Probability of occupancy for species A
ψ^{BA}	Probability of occupancy for species B, given species A is present
ψ^{Ba}	Probability of occupancy for species B, given species A is absent
p^A	Probability of detection for species A, given species B is absent
p^B	Probability of detection for species B, given species A is absent
r^A	Probability of detection for species A, given both species are present
r^{BA}	Probability of detection for species B, given both species are present and species A is detected
r^{Ba}	Probability of detection for species B, given both species are present and species A is not detected

Note: Species A is assumed to be dominant, and species B subordinate.

one individual of a species at a site that may contain multiple individuals.

This new model structure differs from the parameterization developed by MacKenzie et al. (2004, 2006) in three main ways: (1) In the previous parameterization, the probabilities of occupancy for both species were unconditional, whereas in the new parameterization the probability of occupancy for species A is unconditional and the probability of occupancy for species B is conditional on either the presence or absence of species A. The unconditional probability of occupancy for species B can be calculated using the parameters in the new model as $\psi^B = \psi^A \psi^{BA} + (1 - \psi^A)\psi^{Ba}$. (2) The probability of both species being present at a site (ψ^{AB}) is not estimated directly but can be calculated using the parameters in the new model as $\psi^{AB} = \psi^A \psi^{BA}$. (3) A SIF, designated in Mackenzie et al. (2004) as "γ" and in MacKenzie et al. (2006) and hereafter as "φ," is not estimated directly. The SIF of MacKenzie et al. (2004, 2006) was expressed as: $\varphi = \psi^{AB}/\psi^A \psi^B$, where ψ^A is the unconditional probability of occupancy for species A and ψ^B is the unconditional probability of occupancy for species B. From the parameters in our new model, the SIF can be calculated as

$$\varphi = \frac{\psi^A \psi^{BA}}{\psi^A \left(\psi^A \psi^{BA} + (1 - \psi^A)\psi^{Ba} \right)}$$

(Fig. 1, Table 1). If the two species occur independently, then the SIF is equal to one. An SIF less than one indicates that species B is less likely to co-occur with species A than expected under a hypothesis of independence (i.e., avoidance), whereas values greater than one indicate that species B is more likely to co-occur with species A than expected under a hypothesis of independence (i.e., aggregation).

Data used in the conditional two-species occupancy model are detection histories that consist of sequences of detections (1) and non-detections (0) for each visit or sampling occasion at N sites for each species during a given sampling period or season. Sites are assumed to be closed to changes in occupancy state for each species for the duration of each season. Thus, a species is assumed to be either always present or always absent at a given site during a season. As a general example, we present a case with three independent surveys conducted at each sample location. The detection history $X_i^A = 110$ signifies that location i was surveyed on three occasions during one season, and species A was only detected on the first and second visits. The detection history $X_i^B = 000$ signifies that location i was surveyed on three occasions, and species B was not detected on any visit. We will describe the model, following the general framework presented by MacKenzie et al. (2004, 2006), but incorporating the new conditional parameterization.

For each site there are four possible occupancy states for two species: (1) both species A and B are present; (2) only species A is present; (3) only species B is present; or (4) neither species is present. Using the new parameters in Table 1 and Fig. 1, we define a row vector for the probability of location i being in each of the four respective states as in Eq. 1 (below), where the elements of $\boldsymbol{\phi}_i$ sum to 1.

The probability of observing the detection histories for the two species, conditional on the occupancy state of the site, can be stated in terms of detection parameters. Considering the example detection histories presented above ($X_i^A = 110$ and $X_i^B = 000$), there are two possible occupancy states. First, the surveyors could have failed to detect species B and the location is actually occupied by both species, in which case the probability of observing the given detection histories is

$$\Pr(X_i^A = 110 \text{ and } X_i^B = 000 \,|\, \text{both species present})$$
$$= r_{i1}^A(1 - r_{i1}^{BA})r_{i2}^A(1 - r_{i2}^{BA})(1 - r_{i3}^A)(1 - r_{i3}^{Ba}) \quad (2)$$

where r^A is the probability of detecting species A when both species are present, r^{BA} is the probability of detecting species B when both species are present and A is detected, r^{Ba} is the probability of detecting species B when both species are present but A is not detected (Table 1 and Fig. 1), i corresponds to the location, and the subscript number corresponds to the visit number. Alternatively, if the site is only occupied by species A, the probability of observing the detection histories is

$$\Pr(X_i^A = 110 \text{ and } X_i^B = 000 \,|\, \text{only species A present})$$
$$= p_{i1}^A p_{i2}^A(1 - p_{i3}^A) \quad (3)$$

where p^A is the probability of detecting species A when only A is present (Table 1, Fig. 1). The probability of

$$\boldsymbol{\phi}_i = [\psi_i^A \psi_i^{BA} \quad \psi_i^A(1 - \psi_i^{BA}) \quad (1 - \psi_i^A)\psi_i^{Ba} \quad (1 - \psi_i^A)(1 - \psi_i^{Ba})] \quad (1)$$

observing the given detection histories for the other two possible occupancy states (occupied by species B only and occupied by neither species) is 0, because species A was detected and the model, as parameterized, does not consider false presences.

We define a column vector,

$$\mathbf{p}_i^{\{X^A\},\{X^B\}}$$

representing the probabilities of observing the example detection histories, conditional upon each occupancy state and described by the parameters in Table 1 and Fig. 1, as follows:

$$\mathbf{p}_i^{\{110\},\{000\}} = \begin{bmatrix} r_{i1}^A(1 - r_{i1}^{BA})r_{i2}^A(1 - r_{i2}^{BA})(1 - r_{i3}^A)(1 - r_{i3}^{Ba}) \\ p_{i1}^A p_{i2}^A(1 - p_{i3}^A) \\ 0 \\ 0 \end{bmatrix}.$$
$$(4)$$

We then calculate the unconditional probability of observing the detection histories as

$$\Pr(X_i^A, X_i^B) = \boldsymbol{\phi}_i \mathbf{p}_i^{\{X^A\},\{X^B\}}. \qquad (5)$$

Assuming that the collection of the detection histories at the N locations was independent, we define the model likelihood as follows:

$$L = \prod_{i=1}^{N} \Pr(X_i^A, X_i^B). \qquad (6)$$

Missing observations that apply to both species at a given survey occasion contribute no information about model parameters (MacKenzie et al. 2006). This is accomplished by removing the respective detection parameters from the probability equation for a given detection history. For example, if the detection histories $X_i^A = 1$-- and $X_i^B = 0$-- are obtained (where "-" represents a missing observation), then

$$\mathbf{p}_i^{\{1--\},\{0--\}} = \begin{bmatrix} r_{i1}^A(1 - r_{i1}^{BA}) \\ p_{i1}^A \\ 0 \\ 0 \end{bmatrix}. \qquad (7)$$

In situations where a missing observation occurs for one species but not the other on a given survey, all possibilities for the missing observation (that the species in question was present and detected, was present and not detected, or was absent) are included within the probability statement for the detection history (MacKenzie et al. 2006).

We test for species interactions related to occupancy and detection probabilities by obtaining the maximum likelihood estimates (MLEs) of the parameters in Eq. 6 and then use a model selection approach (Burnham and Anderson 2002) to rank competing models. Specifically, we can test three biological questions: (1) Does the probability of occupancy of the subordinate species depend on the presence of the dominant species? (2) Does the detection probability of the subordinate species depend on the presence of the dominant species? (3) Does the detection probability of the subordinate species depend on the detection of the dominant species when both species are present? The first question is usually of greatest biological interest and is relevant to studies that aim to test, for example, hypotheses of competitive exclusion. The second question is relevant for cases in which the presence of one species, for example, a predator, may affect the behavior of a prey species by lowering (or raising) its probability of detection. The third question is relevant for cases in which the detection of a dominant species may affect the probability of detecting a subordinate species, assuming both species are present. For example, a call playback survey that stimulates a vocal response from a dominant species may either increase or decrease the probability of detecting a subordinate species.

The preceding biological hypotheses can be explicitly tested using different formulations of the two-species model. We can determine if occupancy of the subordinate species depends on the presence of the dominant species by comparing model performance when ψ^{BA} and ψ^{Ba} are estimated separately (i.e., the presence of species B is conditional on the presence of species A), or when $\psi^{BA} = \psi^{Ba}$ (i.e., the presence of species B is unconditional). We can determine if the detection of the subordinate species is conditional on the presence of the dominant species or is unconditional by comparing model performance when p^B (the probability of detecting species B when only B is present; Table 1, Fig. 1) is estimated separately from r^{BA} and r^{Ba} (assuming $r^{BA} = r^{Ba}$), or when $p^B = r^{BA} = r^{Ba}$. Although we do not consider it in our case study, the model formulation can be used to determine if the detection probability of the dominant species is conditional on the presence of the subordinate species by comparing model performance when p^A and r^A are estimated separately, or when $p^A = r^A$. This circumstance could potentially arise if a predator became more secretive in the presence of a prey species, e.g., while hunting. Finally, we can determine if the detection of the subordinate species is conditional on the detection of the dominant species when both are present or is unconditional by comparing model performance when r^{BA} and r^{Ba} are estimated separately or when $r^{BA} = r^{Ba}$.

Covariates such as environmental or temporal variables can be incorporated into occupancy and detection probability estimation using the multinomial logistic model:

$$\theta_i^k = \frac{\exp(\mathbf{Y}_i \boldsymbol{\beta}_k)}{1 + \sum_{k=1}^{m-1} \exp(\mathbf{Y}_i \boldsymbol{\beta}_k)} \qquad \text{for } k = 1, 2, \ldots, m-1 \qquad (8)$$

where θ_i^k is the probability of occupancy or detection, $\mathbf{Y}_i$ is a row vector of the covariate values for the ith

location, $\boldsymbol{\beta}_k$ is a column vector of the coefficients to be estimated, and m is the number of discrete occupancy or detection outcomes. Eq. 8 reduces to the binomial logistic model in cases when there are two outcomes (present/absent or detected/not detected). In Eq. 8, θ_i^k is constrained to be in the interval (0, 1) by the structure of the equation. In previous parameterizations (MacKenzie et al. 2004), some parameters such as the SIF were not constrained to this interval, but instead were constrained to the interval (0, ∞) by omitting the denominator. This can lead to possible values for beta parameters that are impossible occupancy probabilities (e.g., $\gamma = 7.33$, $\psi^A = 0.5$, and $\psi^{AB} = 2.2$). Computation of the likelihood value based on these parameters was the source of the convergence problems in the likelihood function optimization in the previous two-species occupancy model (MacKenzie et al. 2004). The new conditional two-species model parameterization is stable when covariates are incorporated and is an improvement upon the previous model that directly estimated a species interaction factor (MacKenzie et al. 2004, 2006).

METHODS

Case study: Black and Virginia Rails

We applied the conditional two-species occupancy model to co-occurring Black and Virginia Rails that inhabit a network of freshwater palustrine emergent persistent wetlands in the Sierra Nevada foothills of California, USA (Richmond et al. 2008). Limited information on food preferences suggests that Black and Virginia Rails have similar diets (Eddleman et al. 1994, Conway 1995), and our preliminary analyses of stable isotopic signatures from feathers suggests diet overlap (S. R. Beissinger, *unpublished data*). Both species feed mainly on small aquatic invertebrates and the seeds of emergent plants, and other aspects of their natural history are similar (Eddleman et al. 1994, Conway 1995). Virginia Rails weigh up to three times as much as Black Rails, have larger home ranges, and are much more widely distributed throughout North America than Black Rails (Eddleman et al. 1994, Conway 1995). Very little is known about interactions between cryptic rallids, although Virginia Rails appear tolerant of the slightly smaller Sora (*Porzana carolina*) in other parts of their range (Pospichal and Marshall 1954, Kaufmann 1989).

We surveyed for rails from June through August at 166 freshwater marshes in 2005 and 192 marshes in 2006 in Butte, Nevada, and Yuba counties, California, as described in Richmond et al. (2008). We mapped marsh perimeters using a backpack Trimble GPS unit (Trimble, Sunnyvale, California, USA) capable of determining three-dimensional positions with 0.5-m accuracy. We excluded large areas of open water and areas with non-emergent vegetation (non-rail habitat) from marsh area calculations. Marsh area averaged 1.17 ± 1.80 ha (mean ± SD) with a range of 0.01–13.99 ha and a median area of 0.52 ha.

We surveyed for the presence of rails at each marsh using call playback surveys, a standard method used with secretive wetland birds (Evens et al. 1991, Legare et al. 1999, Spear et al. 1999, Conway et al. 2004). In each year, we visited marshes up to three times to survey for Black Rails using a removal design (MacKenzie et al. 2006), where in each year we did not revisit a marsh after the first Black Rail detection. During all Black Rail surveys, we concurrently surveyed for Virginia Rails even if Virginia Rails had already been detected at that marsh; thus, at some sites we detected Virginia Rails on multiple visits within a year. We conducted call playback surveys for Black Rails following methods described in Richmond et al. (2008). For Virginia Rails we conducted playback surveys at up to two locations per marsh in 2005 and at up to half of the Black Rail playback stations in 2006. Thus, on average, there were more Virginia Rail playback stations in 2006 per marsh than in 2005. The Virginia Rail playback sequence was always played after the Black Rail sequence and consisted of 2 min of silent listening and two sets of interspersed "tick-it" and "grunt" calls (Conway 1995) lasting 30 s each, followed by 30 s of listening between sets.

Analyzing factors affecting detection probability and co-occurrence patterns

Candidate model sets for the conditional two-species parameterization can become very large because it has a minimum of 4–8 parameters, depending on whether occupancy and/or detection probabilities are modeled conditionally or unconditionally, that can each be fit with combinations of covariates. This necessitated a two-step process for model selection. First, we identified the best detection models for each species by evaluating the effect of covariates on detection probabilities separately (16 models for Virginia Rails and 8 models for Black Rails) using single-season, single-species occupancy models in Program PRESENCE, version 2.4 (Hines 2006). Using the best detection covariates for each species from this analysis, we then developed a set of 108 candidate models for simultaneously testing the effect of: (1) Virginia Rail presence and detection on Black Rail detection probability; (2) Virginia Rail presence on Black Rail occupancy; and (3) patch area and year on occupancy for both species. In this step we fit single-season, two-species occupancy models in Program PRESENCE, version 2.4 (Hines 2006) using the conditional two-species model parameterization, termed the "psiBa parameterization" in PRESENCE. The two-step approach to model selection allowed us to simplify the structure of nuisance (detection) parameters when examining the comparisons of greatest interest. Had we not taken this approach, our model set would have consisted of ~20 480 candidate models. Details of each step are presented next.

To identify the best detection model, we held occupancy constant ($\psi(.)$) and fit: (1) 16 single-season,

single-species occupancy models for Virginia Rails to test the effects of Julian day (day 1 = 1 January), time of day, year, and visit on detection probability (Appendix A); and (2) 8 models for Black Rails with the same detection covariates, except that we did not fit models where detection probability varied by visit because Black Rail surveys were conducted using a removal model design, which resulted in no repeat detections in a given year (Appendix A). We predicted that detection probability would increase with Julian day for both species because incubation can suppress the responsiveness of breeding adults to playbacks early in the survey period (Legare et al. 1999, Spear et al. 1999) and fledglings increase the number of potential responders later in the breeding season. We had no a priori prediction for whether morning or evening surveys would be associated with higher detection probabilities, because previous studies reported conflicting results (Spear et al. 1999, Conway et al. 2004). We tested models where detection probability varied by visit for Virginia Rails because there is evidence that rallids (Huxley and Wilkinson 1979) and other birds (Dong and Clayton 2009) can habituate to playback over time. We predicted that detection probability would be: (1) higher for Virginia Rails in 2006 compared to 2005 because there were more Virginia Rail playback stations per site in 2006 compared to 2005; and (2) stable across years for Black Rails because their survey protocol was consistent. To evaluate if the detection covariate analysis was affected by the choice of the occupancy model, we ran the same detection candidate model sets for each species using a global occupancy model that included all potential occupancy covariates and interactions, and found that the AIC rankings of the detection covariates were unchanged (O. M. W. Richmond and S. R. Beissinger, *unpublished data*).

We then used the best detection covariates for each species in the conditional two-species occupancy model to simultaneously test whether the detection probability of Black Rails was conditional on the presence or detection of Virginia Rails, whether Black Rail occupancy was conditional on the presence of Virginia Rails, and whether occupancy for each species was influenced by covariates. We predicted that the detection of Virginia Rails would have no effect on the detection probability of Black Rails when both were present, because we always played Black Rail vocalizations first in the playback sequence. However, if Virginia Rails act as dominant competitors, their presence might be expected to reduce Black Rail detection probability and/or occupancy. We examined the effects of marsh area, area^2, and year on occupancy for both species. We fit models with area × species and area^2 × species interactions, where Black Rail occupancy was modeled as either conditional or unconditional on the presence of Virginia Rails. We also fit models with year × species interactions, where Black Rail occupancy was modeled unconditionally, and we fit additive models that included combinations of covariates and species interactions. A total of 108 candidate models were in the final model set (Appendix B). We model-averaged the top 20 models, which had a cumulative AIC weight of 0.952, to obtain estimates of the probability of occupancy for each species as a function of marsh area and year (Burnham and Anderson 2002). We calculated the SIF as a function of marsh area using the model-averaged occupancy estimates for each species. We applied the delta method (Kendall and Stuart 1969) to estimate confidence intervals for the probabilities of occupancy for each species and for the SIF using the function "deltamethod" in the msm package in Program R version 2.7.2 (R Development Core Team 2008). Means are presented ± one standard error (SE).

Results

Effect of covariates on rail detection probability

Factors affecting detection rates differed between rail species (Appendix A). For Virginia Rails, the model with the most support included visit-specific detection probabilities and year as a detection covariate; models with year had a cumulative Akaike weight of 0.75 and models with visit-specific detection had a cumulative Akaike weight of 0.57. Mean detection probability calculated from the best Virginia Rail detection model declined with visit (0.75 ± 0.010, 0.62 ± 0.013, and 0.59 ± 0.014 for the first, second, and third visits, respectively) and, as expected, Virginia Rails had a higher mean probability of detection in 2006 (0.73 ± 0.017) than in 2005 (0.56 ± 0.013). For Black Rails, the detection model with the most support included Julian day (cumulative Akaike weight of 0.60); as predicted, there was a positive association between detection probability and Julian day. Mean detection probabilities for a single survey (visit) calculated from the top model for each species (Appendix A) were higher for Black Rails (0.85 ± 0.033) than for Virginia Rails (0.65 ± 0.076).

Modeling rail co-occurrence patterns

Black Rail detection probability did not appear to be affected by Virginia Rail detection when both species were present (Tables 2 and 3). Models that assumed no effect of Virginia Rail detection on Black Rail detection probability received strong support (Table 3), with a cumulative Akaike weight of 0.87. The relationship between Black Rail detection probability and the presence of Virginia Rails yielded similar but more ambiguous results. Models that assumed no effect of Virginia Rail occupancy on Black Rail detection probability had a cumulative Akaike weight of 0.58, whereas models that assumed an effect had a cumulative Akaike weight of 0.42 (Table 3). The average detection probability for Black Rails was slightly higher when Virginia Rails were present (0.87 ± 0.040) than when they were absent (0.82 ± 0.059); these results were obtained by model-averaging estimates from the 12

TABLE 2. The 20 top-performing two-species occupancy models examining interactions between Black and Virginia Rails (*Laterallus jamaicensis coturniculus* and *Rallus limicola*) out of a total set of 108 models (see Appendix B for the entire model set and additional model details).

Occupancy model	Occupancy covariates	Detection model	K	ΔAIC	w
$\psi^A\psi^{BA}\psi^{Ba}$	Area, Area × Species(C), Area², Area² × Species(C)	$p^A p^B$	15	0.00	0.204
$\psi^A\psi^{BA}\psi^{Ba}$	Area, Area × Species(C), Area², Area² × Species(C), Year	$p^A p^B$	16	0.46	0.162
$\psi^A\psi^{BA}\psi^{Ba}$	Area, Area × Species(C), Area², Area² × Species(C)	$p^A p^B r^B$	16	1.32	0.105
$\psi^A\psi^{BA}\psi^{Ba}$	Area, Area × Species(C), Area², Area² × Species(C), Year	$p^A p^B r^B$	17	1.81	0.082
$\psi^A\psi^{BA}\psi^{Ba}$	Area, Area × Species(C), Area², Area² × Species(C), Year, Year × Species(U)	$p^A p^B$	17	2.41	0.061
$\psi^A\psi^{BA}\psi^{Ba}$	Area, Area × Species(C)	$p^A p^B$	12	2.89	0.048
$\psi^A\psi^{BA}\psi^{Ba}$	Area, Area × Species(C), Area², Area² × Species(C)	$p^A p^B r^{BA} r^{Ba}$	17	3.05	0.044
$\psi^A\psi^{BA}\psi^{Ba}$	Area, Area × Species(C), Year	$p^A p^B$	13	3.30	0.039
$\psi^A\psi^{BA}\psi^{Ba}$	Area, Area × Species(C), Area², Area² × Species(C), Year	$p^A p^B r^{BA} r^{Ba}$	18	3.52	0.035
$\psi^A\psi^{BA}\psi^{Ba}$	Area, Area × Species(C), Area², Area² × Species(C), Year, Year × Species(U)	$p^A p^B r^B$	18	3.75	0.031
$\psi^A\psi^{BA}\psi^{Ba}$	Area, Area × Species(C)	$p^A p^B r^B$	13	4.52	0.021
$\psi^A\psi^{BA}\psi^{Ba}$	Area, Area × Species(U)	$p^A p^B$	11	4.54	0.021
$\psi^A\psi^{BA}\psi^{Ba}$	Area, Area × Species(C), Year	$p^A p^B r^B$	14	4.99	0.017
$\psi^A\psi^{BA}\psi^{Ba}$	Area, Area × Species(C), Year, Year × Species(U)	$p^A p^B$	14	5.16	0.015
$\psi^A\psi^{BA}\psi^{Ba}$	Area, Area × Species(U), Year	$p^A p^B$	12	5.34	0.014
$\psi^A\psi^{BA}\psi^{Ba}$	Area, Area × Species(C), Area², Area² × Species(C), Year, Year × Species(U)	$p^A p^B r^{BA} r^{Ba}$	19	5.47	0.013
$\psi^A\psi^{BA}\psi^{Ba}$	Area, Area × Species(U)	$p^A p^B r^B$	12	5.53	0.013
$\psi^A\psi^{BA}\psi^{Ba}$	Area, Area × Species(C)	$p^A p^B r^{BA} r^{Ba}$	14	5.94	0.010
$\psi^A\psi^{BA}\psi^{Ba}$	Area, Area × Species(C), Year	$p^A p^B r^{BA} r^{Ba}$	15	6.29	0.009
$\psi^A\psi^{BA}\psi^{Ba}$	Area, Area × Species(U), Year	$p^A p^B r^B$	13	6.37	0.008

Notes: The cumulative Akaike weight for the top 20 models was 0.952. Occupancy covariates included Area, Area², Year, and interactions by species (Area × Species, Area² × Species, and Year × Species). For Black Rails, the interactions by species were either unconditional (U) or conditional (C) on the presence of Virginia Rails. K is the number of parameters, ΔAIC is the difference in AIC relative to the best model, and w is the Akaike weight that indicates the relative support for each model.

models in the top 20 that included an effect of Virginia Rail presence on Black Rail detection probability.

The probabilities of occupancy for Black and Virginia Rails were strongly positively associated. Models that assumed that Black Rail occupancy was conditional on the presence of Virginia Rails greatly outperformed models that assumed an independent relationship (cumulative Akaike weight of 0.99 vs. 0.01; Tables 2 and 3). The mean probability of Black Rail occupancy, model-averaged over the top 20 models, was greater when Virginia Rails were present (0.74 ± 0.053) than when Virginia Rails were absent (0.36 ± 0.069).

The unconditional probabilities of occupancy for Black and Virginia Rails had similar positive, nonlinear

TABLE 3. Relative support for different formulations of a two-species occupancy model where Black Rail occupancy was either conditional (C) or unconditional (U) on Virginia Rail occupancy, and where Black Rail detection probability was either conditional or unconditional on Virginia Rail occupancy or detection, respectively.

Effect of Virginia Rail occupancy on Black Rail occupancy	Effect of Virginia Rail occupancy on Black Rail detection	Effect of Virginia Rail detection on Black Rail detection	N	w_+
C	U	U	18	0.579
C	C	U	18	0.2936
C	C	C	18	0.127
U	C	C	18	0.000
U	U	U	18	0.000
U	C	U	18	0.000

Notes: N is the number of models and w_+ is the relative importance weight: the summed Akaike weights for all models sharing a given model structure in the set of 108 models (Appendix B).
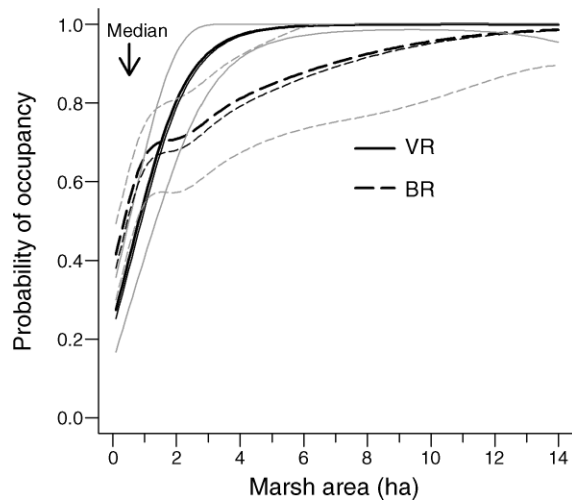
FIG. 2. Estimated unconditional probabilities of occupancy for Virginia Rails (VR; *Rallus limicola*) and Black Rails (BR; *Laterallus jamaicensis coturniculus*) as a function of marsh area and survey year. Results were model-averaged across the top-performing 20 models presented in Table 2 (cumulative Akaike weight of 0.952) out of a total set of 108 models (Appendix B). "Median" is the median marsh area. Thin lines are 2005 data, and heavy lines are 2006 data. Gray lines show the 95% confidence intervals. Because there was little difference in confidence interval by year, only the widest confidence intervals (either from 2005 or 2006) are displayed.

relationships with marsh area, but the response differed between species (Fig. 2, Tables 2 and 4). Models with area, area^2, and interactions with species (for Black Rails conditional on the presence or absence of Virginia Rails) were particularly well supported (cumulative Akaike weight = 0.63) and there were small differences

in occupancy between years (Tables 2 and 4). Our prediction that occupancy for Black Rails should be higher in smaller marshes than for Virginia Rails was supported (Fig. 2), although both species sometimes occurred in very small marshes. Black Rails were present in marshes as small as 0.01 ha, whereas Virginia Rails occurred in marshes as small as 0.06 ha. At median-sized marshes (Fig. 2), Black Rails had a higher model-averaged unconditional probability of occupancy (0.54 ± 0.041 in 2005; 0.57 ± 0.039 in 2006) than Virginia Rails (0.37 ± 0.049 in 2005; 0.40 ± 0.046 in 2006), while Virginia Rails had a higher probability occupancy in larger marshes (>1.5 ha), although confidence intervals for the two species overlapped across the range of marsh sizes (Fig. 2).

Contrary to our expectation, Black Rails had a higher probability of occupancy in both small and large marshes when Virginia Rails were present compared to when they were absent (Fig. 3). In fact, Black and Virginia Rails were most likely to co-occur in the smallest marshes and appeared to be distributed independently at larger marshes. The model-averaged SIF at median sized marshes was 1.33 (95% CI = 1.13–1.53) in 2005 and 1.29 (95% CI = 1.12–1.47) in 2006, was above 1 for marshes <5 ha in area, and was approximately equal to 1 for marshes >5 ha (Fig. 4). This relationship differed only slightly between years (Fig. 4).

DISCUSSION

The conditional two-species occupancy model presented here introduces a powerful tool for examining species co-occurrence patterns. Improving on the previous parameterization of MacKenzie et al. (2004,

TABLE 4. Relative support for two-species occupancy models for Black and Virginia Rails with occupancy covariates and species × covariate interaction terms.

Occupancy covariates	N	w_+
Area, Area × Species(C), Area^2, Area^2 × Species(C)	3	0.353
Area, Area × Species(C), Area^2, Area^2 × Species(C), Year	3	0.279
Area, Area × Species(C), Area^2, Area^2 × Species(C), Year, Year × Species(C)	3	0.105
Area, Area × Species(C)	3	0.080
Area, Area × Species(C), Year	3	0.065
Area, Area × Species(U)	6	0.039
Area, Area × Species(U), Year	6	0.026
Area, Area × Species(C), Year, Year × Species(U)	3	0.026
Area, Area × Species(U), Year, Year × Species(U)	6	0.011
Area, Area × Species(U), Area^2, Area^2 × Species(U)	6	0.008
Area, Area × Species(U), Area^2, Area^2 × Species(U), Year	6	0.005
Area, Area × Species(U), Area^2, Area^2 × Species(U), Year, Year × Species(U)	6	0.002
Area, Area^2, Year	6	0.000
Area, Area^2	6	0.000
Area, Area^2, Year, Year × Species(U)	6	0.000
Area, Year	6	0.000
Area	6	0.000
Area, Year, Year × Species(U)	6	0.000
(.)	6	0.000
Year	6	0.000
Year, Year × Species(U)	6	0.000

Note: U stands for unconditional; C stands for conditional; N is the number of models; w_+ is the relative importance weight, the summed Akaike weights for all models sharing a given model structure in the set of 108 models (Appendix B).
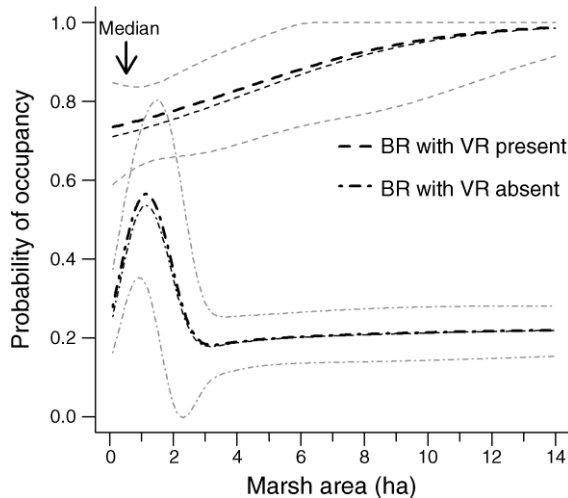
FIG. 3. Estimated probabilities of occupancy for Black Rails (BR) conditional on the presence or absence of Virginia Rails (VR) as a function of marsh area and survey year. Results were model-averaged across the top-performing 20 models presented in Table 2 (cumulative Akaike weight of 0.952) out of a total set of 108 models (Appendix B). "Median" is the median marsh area. Thin lines are 2005 data, and heavy lines are 2006 data. Gray lines show 95% confidence intervals. Because there was little difference in confidence interval by year, only the widest confidence intervals (either from 2005 or 2006) are displayed.

interactions between species pairs for which there might be a priori reasons to hypothesize an interaction. However, demonstrating (or failing to demonstrate) a negative association between two species only provides circumstantial evidence that interspecific competition is present or absent (Wiens 1989): an occupancy pattern that appears to be consistent with competitive exclusion could be driven by habitat or other factors that are excluded from the model, or competition could be operating on a different spatial scale than the scale at which observations were made. Identifying a negative association between two species may indicate competition, but this observation should be followed up, if possible, by direct experiments.

A potential drawback of two-species occupancy models can be the large number of parameters required for estimation. Candidate sets for two-species models can quickly amplify when up to eight parameters must be estimated (Fig. 1) and due to the multiplicative effect of adding covariates; for example, each combination of covariates for species A can be tested against every combination for species B in both conditional and unconditional formulations. To reduce the candidate set to a manageable number of models, we used a two-stage approach to model fitting, in which we first examined covariates for detection and then used the best detection covariates in the second modeling stage to test the main

2006), it successfully incorporates occupancy covariates to allow stronger inferences to be made about co-occurrence patterns. Like the MacKenzie et al. (2004, 2006) parameterization, it improves over past studies of interspecific competition that relied on observations of community composition but did not account for false absences (Diamond 1975, Schluter 1984, Minot and Perrins 1986). The conditional two-species parameterization also models the effects of the presence or detection of one species on the detection probability of the other species. Such effects could be especially important for species pairs with strongly asymmetric competition, or when the presence of one species may suppress the detection of another, as in a predator–prey pair. For example, Barred Owl (*Strix varia*) and Northern Spotted Owl (*Strix occidentalis*) presence each had negative effects on the detection probabilities of the other species (Olson et al. 2005, Bailey et al. 2009).

Two-species occupancy models that incorporate detection probabilities and covariates can make important contributions to studies of species co-occurrence across environmental gradients. A strength of the conditional two-species model parameterization is that covariates can be modeled simultaneously with the species interaction, allowing alternative explanations of observed species distribution patterns to be examined (e.g., species-specific responses to habitat characteristics, patch size, elevation, isolation, and so forth). At present, the best use of two-species models is for examining
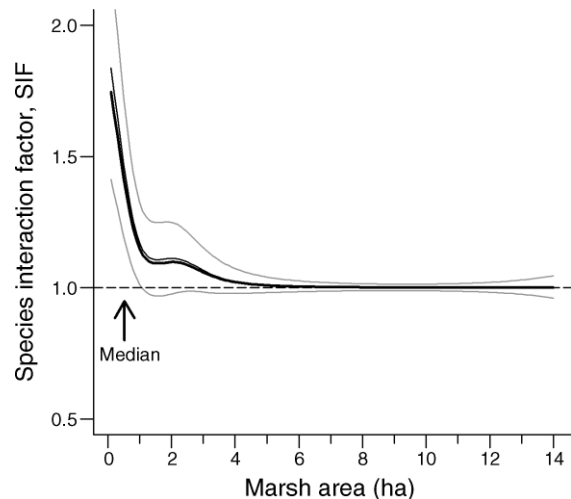

FIG. 4. The species interaction factor (SIF) as a function of marsh area and survey year. Results were model-averaged across the top-performing 20 models presented in Table 2 (cumulative Akaike weight of 0.952) out of a total set of 108 models (Appendix B). An SIF >1 indicates that the two species occur together more often than expected by chance, whereas an SIF <1 indicates that the two species occur together less often than expected by chance; SIF = 1 indicates that the two species occur independently (no aggregation or avoidance). "Median" is the median marsh area. Thin lines are 2005 data, and heavy lines are 2006 data. Gray lines show 95% confidence intervals. Because there was little difference in confidence interval by year, only the widest confidence intervals (either from 2005 or 2006) are displayed.

hypotheses. Careful consideration of appropriate covariates and critical thinking during the formulation of the candidate model set is essential (Burnham and Anderson 2002). The large number of parameters necessitates very large data sets and may make it difficult to apply similar model structures to multispecies communities (MacKenzie et al. 2006).

Two-species occupancy models provide a useful method for making inferences about interactions between cryptic species, such as the secretive rails in this study, because direct observations of such species' interactions are exceedingly rare. We found no evidence that the presence or detection of Virginia Rails affected the detection probability of Black Rails, and the two species showed a positive association across a range of marsh sizes. The positive occupancy association could suggest overlapping habitat preferences at the patch level, where coexistence may be maintained by microhabitat or resource partitioning (Chesson 2000). Differences between these rail species in bill size, leg length, and feeding behavior support this contention (Eddleman et al. 1994, Conway 1995). Although we found no evidence of competitive exclusion, the relationship between occupancy and marsh size differed slightly by species; for Black Rails it depended on the occurrence of Virginia Rails, albeit in an unexpected manner. Surprisingly, Black Rails were more likely to occur in small marshes that were occupied by Virginia Rails than in marshes without Virginia Rails (Figs. 3 and 4). Perhaps small marshes that are high in overall habitat quality can support both rail species, whereas low-quality sites can support neither species. Although occupancy of both species increased with marsh area, Black Rails were more likely to occupy smaller marshes than Virginia Rails (Fig. 3), probably due to their smaller home range requirements.

Our findings for wetland rails contrast with studies of birds in which large- and medium-sized species appeared to outcompete small species for space or resources in patchy forest systems (Brown and Sullivan 2005, Brown 2007) and within nectarivorous bird assemblages (Grey et al. 1997, Mac Nally and Timewell 2005). Black and Virginia Rails coexist, even in very small wetlands where resources are presumed to be more limiting. This suggests that body size difference alone may be a poor indicator of interspecific competitive exclusion in some guilds.

The conditional two-species occupancy model provides a useful tool for testing hypotheses of co-occurrence and could make important contributions to projecting future species distributions with climate change. Future research could focus on expanding two-species occupancy models to more complex multispecies communities. Also, extending the model to multiple sampling periods (MacKenzie et al. 2006) would allow stronger inferences to be made about underlying species interactions. A multi-season two-species model would include parameters for local colonizations and extinctions of a species that are conditional on the presence of another species. Finally, a potentially powerful application for two-species or multiple-species models is in the prediction of community responses to climate change. Most conventional species distribution models treat species as distinct units that respond individualistically to climatic conditions (Elith and Leathwick 2009). The SIF derived from two-species or multiple-species models provides a measure of interaction that could be incorporated into species distribution models to create more mechanistic projections of species ranges under alternative climate change scenarios. Such models will further improve our ability to examine species interactions and distributions in ecological communities.

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APPENDIX A

Evaluation of the effect of covariates on detection probability for Black Rails (*Laterallus jamaicensis coturniculus*) and Virginia Rails (*Rallus limicola*) in palustrine emergent wetlands in the northern Sierra Nevada foothills, California, USA, 2005–2006 (*Ecological Archives* A020-073-A1).

APPENDIX B

Complete model set examining the effects of covariates on occupancy probability for Black Rails (*Laterallus jamaicensis coturniculus*) and Virginia Rails (*Rallus limicola*) in palustrine emergent wetlands in the northern Sierra Nevada foothills, California, USA, 2005–2006 (*Ecological Archives* A020-073-A2).