EASTERN BLACK RAIL (*LATERALLUS JAMAICENSIS JAMAICENSIS*)

OCCUPANCY AND ABUNDANCE ESTIMATES ALONG

THE TEXAS COAST WITH IMPLICATIONS

FOR SURVEY PROTOCOLS

by

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LIST OF ABBREVIATIONS

Abbreviation	Description
AIC	Akaike Information Criterion
AIC_C	Akaike Information Criterion corrected for small sample size
ΔAIC	The difference in AIC units of the top model and a specified model included in a model selection analysis
ΔAIC_C	The difference in AIC_C units of the top model and a specified model included in a model selection analysis
Diel	Time of day
CO	Call order
CI	Credible Interval
GPS	Global Positioning System
Herbaceous	Non-*Spartina* herbaceous species
Herb.	Non-*Spartina* herbaceous species
INTM	Intermediate-brackish marsh
JD	Julian Date
Lunar	Lunar phase
Noise	Ambient noise
NWR	National Wildlife Refuge
PB	Barometric Pressure
SE	Standard Error
Sky	Cloud cover
Spartina	*Spartina* species
spp.	Species, plural
Temp.	Temperature
TSS	Time after dawn survey start time
Wind	Wind speed
Woody	Woody species

ABSTRACT

Eastern black rails (*Laterallus jamaicensis jamaicensis*) are a subspecies of conservation concern. These birds vocalize infrequently and inhabit dense vegetation making them difficult to detect. I conducted the first large scale study of black rail occupancy and abundance in Texas. I repeated point count surveys at 308 points spread across 6 study sites from mid-March to late-May in 2015 and 2016. Each survey at a point was a 6-minute call-playback broadcast where birds were detected acoustically. My study sites were located at Anahuac, Brazoria, and San Bernard National Wildlife Refuges, Mad Island Wildlife Management Area, Clive Runnel's Mad Island Marsh Preserve, and Powderhorn Ranch Preserve. I estimated the fit of 19 occupancy and 19 abundance models that also accounted for imperfect detection. Black rail detection increased with moon phase and temperature but decreased with wind speed and ambient noise. Occupancy and abundance increased with woody, *Spartina*, non-*Spartina* herbaceous, and intermediate marsh cover. Black rail occupancy and abundance estimates were similar between years. From the estimated detection probabilities I determined that ~ 16 repeated surveys could establish black rail presence at survey points. I reached two main conclusions. One, black rail management during the breeding season, in Texas, should focus on *Spartina* cover as occupancy and abundance estimates were highest when *Spartina* cover was high. Two, effort to establish black rail presence from naïve occupancy estimates is impractical. Monitoring efforts of black rails should design studies that estimate distribution and abundance while accounting for imperfect detection.

I. EASTERN BLACK RAIL (*LATERALLUS JAMAICENSIS JAMAICENSIS*) OCCUPANCY AND ABUNDANCE ESTIMATES ALONG THE TEXAS COAST WITH IMPLICATIONS FOR SURVEY PROTOCOLS

Knowledge of a species' distribution and abundance forms the bedrock for any species conservation effort. Distribution, or occupancy, is the extent of area inhabited by populations. Abundance is the number of individuals in a population. Knowledge of a species' distribution provides a spatial reference for survey efforts and management actions. Estimating abundance is needed to monitor population trends over time. Both state variables, occupancy and abundance, are used to set conservation goals and establish conservation status of a species. Therefore, reliable estimates of occupancy and abundance are vital to the conservation of a species (Kéry et al. 2005, MacKenzie et al. 2006, Hunt et al. 2012, Veech et al. 2016). Species behavior and habitat often influence the reliability of occupancy and abundance estimates (Royle 2004, Kéry et al. 2005, MacKenzie et al. 2006, Hunt et al. 2012, Veech et al. 2016). Detection of individuals or a species is rarely 100% (MacKenzie et al. 2002, Royle 2004, MacKenzie et al. 2006, Veech et al. 2016). For example, abundance and occupancy estimates of cryptic species, those species that allude detection, tend to be biased low. Therefore, techniques that account for imperfect detection are needed to obtain less biased estimates of occupancy and abundance.

Conceptually, population estimation can be expressed by the following formula:

$$\widehat{N} = \frac{C}{\hat{p}} \qquad\qquad 1$$

where $\widehat{N}$ is the estimated abundance, C is the number of individuals counted, and $\hat{p}$ is the estimated probability of detecting an individual when it is available to be detected in a survey area (Nichols 1992). Correcting for detectability is often difficult (Royle 2004, MacKenzie et al. 2006), nonetheless, numerous estimators have been developed to estimate $\hat{p}$. Royle (2004) discussed the impracticalities and the inadequacies of some of these techniques, such as mark-recapture estimates of $\hat{p}$ and subjective selection of $\hat{p}$. He argued that mark-recapture is not feasible on a large scale and that arbitrary selection of $\hat{p}$ can yield unrealistic abundance estimates.

Counts obtained from systematic surveys are often used as indices for abundances. Indices are useful approximations of abundance when surveys represent a constant proportion of the actual population size (Johnson 1995, White 2005, Weckerly 2007). Yet, the assumption of constant proportionality is rarely met (Nichols 1992, Johnson 1995, Anderson 2001, Royle and Nichols 2003, Weckerly 2007) because detection of individuals can vary spatially and temporally (Royle et al. 2005, Veech et al. 2016). Such variation in detections may result in counts that misrepresent true variation in population abundance. Johnson (2008) relaxed the condition of constant proportionality and showed that as long as the variation in detectability was less than the variation in counts, indices capture abundance dynamics correctly. Detection of cryptic species, however, is low and probably varies with a variety of environmental factors

(Legare et al. 1999, MacKenzie et al. 2002, Conway and Gibbs 2005, MacKenzie et al.
2006, Conway 2011). Therefore, variation in counts may not actually capture variation in
abundance (Nichols 1992, MacKenzie and Kendall 2002, Royle 2004, MacKenzie et al.
2006, Hunt et al. 2012).

Difficulties in estimating abundance due to variation in detection has led
researchers to use occupancy as a surrogate for abundance (MacKenzie et al. 2002,
MacKenzie et al. 2006). MacKenzie et al. (2002) developed a method for modeling
occupancy in a closed population that incorporates detection probability. A closed
population is one in which there is no dispersal of individuals in or out of the survey area
during the time surveys are conducted. Presence and non-detection data, from repeated
surveys, of spatially referenced survey points is needed to estimate detection probability
and occupancy based on covariates that could affect either detection or occupancy.
MacKenzie et al. (2003; 2006) further expanded the model to incorporate changes in
occupancy over time. These multi-season models could also include covariates that
influence the decrease or increase in occupancy.

Much like occupancy models, N-mixture models use count data from repeated
surveys of spatially referenced survey points and covariates to estimate abundance and
detection probability (Royle 2004, Kéry et al. 2005, Hunt et al. 2012, Veech et al. 2016).
N-mixture models use statistical distributions such as the Poisson, zero-inflated Poisson
and negative binomial distributions to estimate abundance and the binomial distribution
to estimate detection probabilities (Royle 2004, Kéry et al. 2005, Veech et al. 2016).
Like multi-season occupancy estimation, N-mixture models can also accommodate

temporal changes in abundance via parameters estimating recruitment and apparent survival (Dail and Madsen 2011, Hostetler and Chandler 2015).

Black rails (*Laterallus jamaicensis*) represent a model species for the use of occupancy and *N*-mixture models. These rails are small (~15 cm total length), secretive marsh birds found in North, Central, and South America as well as the Caribbean Islands (Taylor 1998). In North America there are two subspecies: the California black rail (*L. j. courturnicops*) and the eastern black rail (*L. j. jamaicensis*) (Eddleman et al. 1988, Taylor 1998). Eastern black rails occur in coastal marshes along the Gulf and Atlantic states (Eddleman et al. 1988, Eddleman et al. 1994, Taylor 1998). There are some interior populations which breed inland in the Midwest and Appalachian states (Eddleman et al. 1988, Eddleman et al. 1994, Taylor 1998, Butler et al. 2015). Although the California black rail has been studied (Evans et al. 1991, Evans and Nur 2002, Spautz et al. 2005, Richmond et al. 2008, Risk et al. 2011), the eastern subspecies has received less attention. Some studies have been conducted in Florida and along the Atlantic seaboard yet there has been little work on estimating distribution and abundance of black rails along the Texas coast (Legare et al. 1999, Watts 2016).

The eastern black rail subspecies is in review for listing under the Endangered Species Act. This status assessment was instigated because populations are perceived as declining throughout the eastern and southeastern United States (Watts 2016). With eastern black rails under probable decline in the Atlantic states, it is important to assess the status of black rails in Texas. Texas populations have not been monitored at a large scale and baseline occupancy and abundance data are rare (except see Butler et al. 2015).

A majority of Rallidae, or rails, are secretive because these birds inhabit and conceal themselves in densely vegetated habitats and their vocalizations are infrequent (Eddleman et al. 1988, Taylor 1998). Additionally, rails generally dwell on the ground, run to escape danger rather than fly, and rarely perch on vegetation (Taylor 1998, Sibley 2000). The escape behavior, infrequent calling, and concealment in dense habitats makes detection of rails challenging. Eastern black rails are no exception to the overall character of this taxa. They inhabit marshes and wet prairies containing dense stands of cordgrasses (*Spartina* spp.), sea oxeye daisy (*Borrichia frutescens*), and glassworts (*Salicornia* spp.) (Legare et al. 1999, Butler et al. 2015). In addition, their calling rate is relative low. Legare et al. (1999) reported that radio tagged females and males called a maximum of 20% and 50% of the time, respectively, during surveys conducted in the breeding season. Given this information, perhaps it is unsurprising that Butler et al. (2015) estimated a maximum detection probability of 0.16. The prevailing evidence indicates that eastern black rails are difficult to detect by sight or sound.

To elicit black rails, and rails in general, to call, broadcast surveys of vocalizations are used to increase detection (Legare et al. 1999, Spear et al. 1999, Conway et al. 2004, Conway 2011, Butler et al. 2015). Most often, call-playback broadcast surveys (hereafter call surveys) are conducted at points systematically placed across the landscape (Evans et al. 1991, Evans and Nur 2002, Spautz et al. 2005, Richmond et al. 2008, Richmond et al. 2010). Black rail surveys are also generally conducted at night or during the morning and evening (Evans et al. 1991, Lagare et al. 1999, Evans and Nur 2002, Spautz et al. 2005, Butler et al. 2015). During these times,

black rails are considered to call most frequently and hence most likely to respond to a played call.

My overarching goals were to estimate eastern black rail habitat associations, distribution, and abundance while accounting for factors affecting detection along the Texas coast. To my knowledge, Butler et al. (2015) is the only study to estimate eastern black rail detection and occupancy in Texas and they did not integrate their detection models with their occupancy models. Additionally, this is the first study to estimate black rail abundance with *N*-mixture models in Texas. I conducted repeated call broadcast surveys at 6 study sites along the Texas coast. Also, I measured a set of covariates I thought would influence black rail detection, occupancy, and abundance. My specific objectives were to: (1) determine influential covariates affecting detection of the eastern black rail; (2) determine habitat covariates that were related to black rail occupancy and abundance; (3) develop a monitoring protocol to estimate black rail occupancy and abundance.

STUDY AREA

The 6 sites were at Anahuac National Wildlife Refuge (NWR) in Chambers County, Brazoria NWR in Brazoria County, San Bernard NWR in Brazoria and Matagorda Counties, Mad Island Wildlife Management Area and Clive Runnells Family Mad Island Marsh Preserve (Mad Island Marsh) in Matagorda County, and Powderhorn Ranch Preserve in Calhoun County (Figure 1). These sites represent a diversity of land ownership from federally owned NWRs to non-governmentally owned Mad Island Marsh and Powderhorn Ranch.

Anahuac NWR is transected by bayous running north and south which are flanked by thickets, rice fields, freshwater marshes, moist-soil units, and bluestem prairies in the north. The freshwater marshes and prairies give way to brackish and salt marshes. Finally, the marshes are replaced by estuaries and the Intracoastal Waterway at the refuge's southern extent. The 13,759 ha of Anahuac NWR receive ~ 145 cm of precipitation per year with the greatest precipitation events occurring in the summer (Baker et al. 1994). Temperatures can exceed 32˚C in the summer and be lower than 6˚C in the winter (Baker et al. 1994).

Brazoria NWR has 17,973 ha of bluestem uplands, freshwater, brackish, and salt marshes in addition to ponds and woody thickets. The bluestem uplands of Brazoria NWR are intermixed with the woody thickets and freshwater, brackish, and salt marshes throughout the northern extent of the refuge. Brackish and salt marshes dominate the southern part of the refuge and recede inland from the estuaries and bays at the southern and southeastern boarders of the refuge. Where Brazoria NWR is a contiguous refuge, the 21,853 ha of San Bernard NWR are spread across Brazoria and Matagorda counties. San Bernard contains, north to south, Columbia hardwoods, cypress swamps, freshwater, brackish, and salt marshes. Freshwater marshes, lakes, Gulf Coastal Prairies, and invasive monocultures make up the remainder of San Bernard NWR. The greatest precipitation events at San Bernard and Brazoria NWRs occur in autumn (Baker et al. 1994). These refuges receive < 127 cm of precipitation each year and seasonal changes are evident from summer highs in the 30s˚C and winter lows in the 10s˚C (Baker et al. 1994).

Mad Island Wildlife Management Area consists of 2,913 ha of brushy and coastal

prairie uplands that are protected from coastal flooding by salt and freshwater marshes.

Mad Island Marsh, which borders Mad Island Wildlife Management Area to the west, is

made up of 2,858 ha of fresh and saltmarshes and by bushy thickets and inland tallgrass

prairie. The Mad Islands receive ~ 114 cm of annual precipitation (Baker et al. 1994).

Precipitation events are highest in autumn with temperatures reaching 31˚C in the

summer and lows of ~ 5˚C in the winter (Baker et al. 1994).

Powderhorn Ranch comprises 6,981 ha of scrub woodlands, virgin coastal live

oak (*Quercus agrifolia*) forests, and bluestem grasslands. Additionally, the preserve has

extensive saltmarshes around Powderhorn Lake's periphery and bayou fed freshwater

wetlands interspersed throughout the property. Annual precipitation at the Ranch is 106

cm (Baker et al. 1994). Summer temperatures reach up to 33˚C and winter temperatures

are as low as 7˚C (Baker et al. 1994).

METHODS

Call broadcast surveys were conducted at least 3 times at each study site during the black

rail breeding season, which begins in late March and ends in late May (Conway 2011).

Across that time there should be constant residence status and "population closure"

(MacKenzie et al. 2006). I assumed that all wintering black rail migrants had left for

their breeding grounds before the initiation of my surveys (Conway 2011). Call surveys

were used because they tend to increase detection of black rails (Conway and Gibbs

2005), which should result in less biased estimates of abundance and occupancy

(MacKenzie et al. 2002).

For ease of access surveys were conducted along roads, levees, and fire breaks that permeated presumed black rail habitat. I established 375 point count stations across the 6 study sites, with 105 points at Anahuac NWR, 80 points at Brazoria NWR, 65 points at San Bernard NWR, 84 points at Mad Island Wildlife Management Area and Mad Island Marsh, and 41 points at Powderhorn Ranch. Point count stations were established with the following stratified random approach. Points were plotted 400 meters apart in ArcGIS (Environmental Systems Research Institute, Inc., Redlands, CA) along all roads, levees, and fire breaks at each study sites. The 400-meter spacing between survey points was used to ensure independence of detections across survey points (MacKenzie et al. 2006, Conway 2011). Points were then divided into survey routes containing 4 to 10 points. These routes were then numbered and a subset of the total routes available at each study site were then selected randomly. Surveys were conducted from ~ 30 minutes before sunrise to ~ 2 hours after sunrise and ~ 2 hours before sunset to ~ 30 minutes after sunset (Conway 2011). Routes were reversed and surveyed during evening and morning survey periods. Reversal of the order of points surveyed was used to reduce potential bias from time-of-day (Hunt et al. 2012).

Moon phase was recorded for each survey as a discrete variable ranging from 0 to 15 (where 0 = no moon and 15 = full moon [Spear et al. 1999]). Temperature and barometric pressure were recorded at the beginning and end of each route. Time of survey, average wind speed, could cover, and ambient noise level were recorded at each survey point before initiating the survey (Conway 2011). Wind speeds, temperatures, and barometric pressures were measured with Kestrel® 2500 Pocket Wind Meters (Nielsen-Kellerman, Boothwyn, PA). Ambient noise level was recorded as a discrete

variable on a 0 to 9 scale (0 = no noise, 1 = faint noise, 2 = loud noise; may not be able to hear birds beyond 100 m, 3 = intense noise some birds may not be heard beyond 50 m, 4 = very intense noise birds may be missed within 50 meters and 9 = no detections recorded due to noise [Conway 2011]). These covariates were used to assess their possible influence on black rail detection.

For each broadcast survey a passive period followed by a black rail and clapper rail (*Rallus crepitans*) calling sequence was played. Clapper rail calls were used in an attempt to increase black rail detection. Conway and Nadeau (2010) reported that heterospecific marsh bird calls increase black rail detection. The call sequence was: 4 minutes of passive surveying, 30 seconds of black rail *kik-kik-kir* and *grr* calls, 30 seconds of passive surveying, 30 seconds of clapper rail *clatter, kek*, and *kek-bur* calls, and a final 30 seconds of passive surveying. The segment containing species calls was reversed between surveys to assess if species order influenced detection in broadcast surveys (Conway and Gibbs 2005). Calls were broadcasted from a wireless Bluetooth© speaker (Bluetooth Ver 3.0 3W, 3W©) at 80 dB placed at the edge of the marsh (Conway 2011). Speaker intensity was tested with a Digital Sound Meter (Extech Instruments©, Waltham, MA).

Black rails seen or heard in each minute of the survey period were recorded by 1 to 4 observers. Bearing to detected rails was measured. Distance to detected rails was estimated in 4, 50 meter bands (0 – 50 m, 50 – 100 m, 100 – 150 m, and > 150 m). These data were used to assess if individual birds were detected at consecutive points. The data were also used to assess if black rails responded to playback more when the speaker was pointed in their general direction. I ensured surveys were performed at the same location

at each replication by locating survey points with etrex 20 GPS units (Garmin, Olathe, KS) and flagging the survey point.

Habitat Sampling

Vegetation and habitat variables were measured to assess their influence on occupancy and abundance of black rails. Percent cover of *Spartina* spp., non-*Spartina* herbaceous spp., and woody spp. were visually estimated in a 50-meter radius at each survey point with Daubenmire coverage classes (hereafter *Spartina*, herbaceous, and woody). The placement of survey points along roads, levees, and fire breaks provided high vantage points to assess the surrounding vegetative cover accurately. These variables provided measures of vegetation structure that influence black rail habitat selection (Flores and Eddleman 1995, Spautz et al. 2005, Tsao et al. 2009). In addition to vegetation variables, I also recorded management actions that were occurring at each point. Grazing was recorded as a binomial variable with un-grazed points as the reference category. Points were considered grazed by cattle if cattle, moist tracts, and/or feces of cattle were seen around the survey point during the survey season. There were 111 points grazed in 2015 and 81 points grazed in 2016. Grazing occurred at all study sites except Brazoria and San Bernard NWR. The use of prescribed fire between 2015 and 2016 at points was recorded as a binomial variable. There were 67 points burned between 2015 and 2016. The intensity of the burn and the burning frequency of each site was not considered in this study. Prescribed fire is a management tool that was used at all 6 study sites between 2015 and 2016. Both management activities, grazing and prescribed fire, have been reported to influence black rail habitat use (Grace et al. 2005, Richmond et al. 2012, J. Wilson, United States Fish and Wildlife Service, unpublished data).

In addition to the point level covariates above, I measured site level covariates. A

United States Geological Survey raster file (Enwright et al. 2015) was used in ArcGIS to

estimate percent cover of two habitat types for each study site. I used the extract by mask

tool with shapefile overlays for each study site to extract this raster data. The habitat

types in the USGS raster included: fresh water wetlands (salinity = 0.1 – 3.4 parts per

thousand [ppt]), intermediate-brackish marsh (salinity = 3.4 – 8.3 ppt), salt marsh

(salinity >8.3 ppt), open water, and other (all other land uses [Enwright et al. 2015]). The

raster dataset on habitat type was measured from satellite images taken in 2013 and was

the most recent raster dataset I could find with these marsh types. I used intermediate-

brackish marsh (intermediate marsh) cover because both *Spartina spartinae* and *Spartina*

patens dominate this habitat type (Enwright et al. 2015, Stutzenbaker 2010) and

preliminary observation showed most black rail detections were in this habitat type.

Open water was used as a proxy for discontinuity in habitat at the site level. These

covariates were used to evaluate site level influences on black rail occupancy and

abundance.

Data Analysis

I used package "unmarked" in program R to model occupancy and abundance (R Version

3.2.4, www.r-project.org, accessed 15 February 2017, Fisk and Chandler 2011). I used

package "AICcmodavg" for occupancy model selection analyses and goodness-of-fit

tests. All continuous and discrete covariates were standardized before data analyses

(Royle et al. 2004, MacKenzie et al. 2006).

Occupancy analysis.—I evaluated covariate influences on detection in two steps

(Appendix A). First I estimated single-season occupancy models for each candidate

covariate while holding occupancy constant. Covariates were considered influential if

the 85% ($|Z| \geq 1.41$, $P \leq 0.15$) confidence level of the parameter estimate excluded 0

(Arnold 2010). I then used the influential covariates to estimate multi-covariate detection

models again holding occupancy constant (Comte and Grenouillet 2013, Hamel et al.

2013). I selected the top model from an AIC_C model selection analysis. I used the

number of points where a black rail was detected as my sample size (*n*) for calculating

AIC_C. For estimation of detection probability, I selected the model with the lowest AIC_C

and when all other models had a $\Delta AIC_C > 2.00$ (Burnham and Anderson 2002). Models

were considered competing if they had a $\Delta AIC_C < 2.00$. If competing models were

nested and had similar log-likelihoods I chose the model with the fewest number of

parameters over models with more parameters that were not statistically significant (*P* >

0.15, Arnold 2010). I then used the selected detection covariates to estimate models

where occupancy varied by year and habitat covariates.

I used multi-seasonal models to estimate black rail occupancy because I expected

occupancy to change between 2015 and 2016 (McKenzie et al. 2006). I considered the

years of the study to be my primary periods with secondary periods consisting of surveys

conducted in each year. I estimated 19 models, where occupancy could vary by point

level habitat influences (e.g., areas that were grazed or un-grazed, percent cover of

woody, herbaceous, and *Spartina*) and site level landscape variables (percent cover of

intermediate marsh and open water). The rationale for building these 19 model was

based on the following competing hypotheses: (1) black rail occupancy is influenced by

one of the habitat covariates I measured, (2) black rail occupancy is influenced at the

spatial scale of the site by one or more of the measured covariates, (3) black rail

occupancy is influenced at the spatial scale of the point by one or more of the measured covariates, (4) black rail occupancy is influenced by covariates at both the spatial scale of the point and the scale of the site by one or more of the measured covariates, and (5) black rail occupancy is more influenced by *Spartina*, herbaceous, intermediate marsh cover than the other measured covariates. I also considered different combinations within each overarching hypothesis to examine importance of those covariates I thought would be most influential: *Spartina*, herbaceous, and intermediate marsh cover. I did this by including models that excluded those covariates. I did not examine all possible combinations of the covariates because I thought there was little biological rational for that approach. I included two null models to test the hypothesis that one or more of the measured covariates influenced black rail occupancy. These models were, a model where all covariates were held constant and one where detection and colonization were allowed to vary by covariates found to be significant in preliminary analyses.

I allowed colonization (points occupied in 2016 that were unoccupied in 2015) to vary by whether or not survey points had been burned. This was based on the idea that some sites may have either lost vegetation structure that black rails are attracted to for territorial establishment or vegetation components may have been reduced by fire to increase attractiveness of an area for black rails to establish territories. For this binomial covariate, points that had not been burned between the survey seasons of 2015 and 2016 were coded as the reference category. I choose this covariate because a preliminary analysis indicated that burning influenced colonization. Also, preliminary analyses revealed that none of my covariates influenced extinction. Therefore, I held extinction constant in all of the occupancy models. I evaluated the fit of the global model using

MacKenzie and Bailey's (2004) goodness-of-fit test with 1,000 bootstrapped iterations. I also estimated Nagelkerke R^2 for each model (Fiske and Chandler 2011).

I selected the top model with an AIC_C model selection process. I then estimated mean occupancy for both 2015 and 2016 using the top model and the smoothing method described by Weir et al. (2009). This smoothing method allows for more precise estimates of site occupancy when the same sites are surveyed from season to season (Weir et al. 2009). The standard error for mean yearly occupancy was estimated from a nonparametric bootstrap of 10,000 samples.

I used the top occupancy model to estimate the survey effort needed to have a 0.95 probability of detecting a black rail given presence at a single survey point during a single survey season. To do this, I estimated the species detection probability with the means of detection and occupancy covariates. I then used the following standard formula:

$$p = 1 - (1 - \hat{p})^k \qquad\qquad 2$$

where p is the probability of detecting one or more rails at a single point within a single survey season, $\hat{p}$ is the mean probability of detecting one or more rails within a single survey, and k is the total number surveys. I started at $k = 1$ and then estimated p with increasing k by a factor of 1 until p reached 0.95.

Abundance analysis.—I used single-season *N*-mixture models to assess influences on detection of individual black rails. For this analysis I assumed abundance to have a Poisson distribution (Royle 2004). This was to limit the number of different combination of models. I held abundance constant and allowed individual detection to vary with the same detection covariates I used in the occupancy analysis. I also used an 85%

confidence level to eliminate uninformative covariates and the AIC model selection process to find the set of covariates that influenced detection of individual black rails (Arnold 2010). I used AIC (instead of AIC_C) because there has been no consensus on what to use for n in AIC_C analyses for N-mixture models (Fiske and Chandler 2011). I then used the selected detection covariates to model the covariates that influenced abundance.

Once detection covariates were selected, I used these covariates to generate 3 global abundance models with 3 different distributions. To evaluate which mixture model best fit the abundance data, I ran bootstrapped, χ^2 goodness-of-fit tests for the global model under the Poisson, negative binomial, and zero inflated Poisson distributions (Kéry et al. 2005, Fisk and Chandler 2015). The reason for evaluating these models after the detection selection model was so that the number of parameters in each global model was not excessive. I used open models where 2015 and 2016 were my primary periods and surveys within those years were my secondary periods. I then selected the distribution which had a $\hat{C}$ closest to one and was statistically nonsignificant indicating the model fit the data. The selected distribution was used in all further analyses.

Like occupancy, I estimated 19 models including a global model, where abundance varied by the aforementioned point level habitat influences and site level landscape variables. The logic behind the construction of these models was the same as for the occupancy models. I allowed recruitment (the increase in number of rails at a point from 2015 to 2016) to vary by the binomial-covariate, burn. This variable was included because it had a significant influence on recruitment in preliminary analyses.

Much like extinction in the occupancy analyses, a preliminary analysis indicated no
influential covariate on apparent survival (i.e., proportion of rails at a point that was
similar from 2015 to 2016). Therefore, I held apparent survival constant in all of the
abundance models. I ran 30 permutations of each model to ensure that parameter
estimates did not vary between iterations. This number of permutations had constant
estimates of the model parameters and had more than twice the maximum number of
detections at a single site in a single survey (Fiske and Chandler 2011). I used an AIC
model selection process to select the top N-mixture model (Fiske and Chandler 2011).
The Nagelkerke R^2 was also estimated for each model (Fiske and Chandler 2011). I
used the top model to estimate the empirical Bayes averages for abundance in 2015 and
2016 and 95% credible intervals for those years.

RESULTS

There were 3,425 call playback surveys conducted and vegetation was sampled at 308
points from mid-March to the end of May, 2015 and 2016. Vegetation was not sampled
or surveys were not conducted at 67 points in 2015 because of flooding of roads and
other logistical constraints. There was a mean of 11.12 surveys per point count station
with a minimum of 3 and a maximum of 8 surveys per year. Over the two years I had a
total of 190 detections of one or more black rails (hereafter species detection) at 92
survey points. I had a total of 239 individual black rail detections. With 151 detections
of 1 rail per survey, 32 detections of 2 rails per station, 5 detections of 3 rails per survey,
1 detection of 4 rails per survey, and 1 detection of 5 rails per survey. The distances of
229 of these rails from the survey point were recorded. There were 87 detections within
50 meters of the survey point, 81 between 50 to 100 meters of the survey point, 49

between 100 to 150 meters from the survey point, and 12 beyond 150 meters of the survey point.

Occupancy

I examined the influences of 15 covariates on species detection with single-season occupancy models while keeping occupancy constant. I found the most influential covariates to be lunar phase, wind speed, and average survey temperature (Appendix A). Detection increased with more moonlight and hotter temperatures and declined with increasing wind speed. These three covariates were then used to model species detection probability in all subsequent models estimating occupancy (see below).

With regard to estimating occupancy, the global model (contained all six covariates) appeared to fit the data well ($\chi^2 = 2780.443$, $P = 0.141$). The global model also had low over-dispersion ($\hat{C} = 1.19$). The fit of the global model gives credence to the use of the measured covariates in the model selection analysis (MacKenzie and Bailey 2004). As the top model, I selected the point-level and site-level model (mixed-level) where occupancy was influenced by herbaceous, *Spartina*, woody, and intermediate marsh cover. I choose this model because it had the lowest AIC_C and differed from all other models by > 3.00 ΔAIC_C units (Table 1). The selected model had an estimated Nagelkerke's $R^2 = 0.30$.

Black rail occupancy increased with herbaceous (min = 0%; max = 97.5%), *Spartina* (min = 2.5%; max = 97.5%), and woody (min = 2.5%; max = 97.5%) cover, at the level of the point count station (Figure 2 [a, b, d], Table 2). Occupancy also increased with the site level covariate, intermediate marsh cover (Figure 2c). The highest estimated

occupancy was associated with *Spartina* cover. When a survey point had more than 90% cover of *Spartina*, black rail estimated occupancy was greater than 70% (Figure 2).

Mean black rail occupancy was virtually the same between 2015 ($\bar{\psi} = 0.27$, SE = 0.03) and 2016 ($\bar{\psi} = 0.27$, SE = 0.04). Yet, there was some colonization of survey points in 2016. Mean colonization was 0.12 (SE = 0.04). I did not, however, detect any extinction (Table 1). Whether or not a survey point was burned between 2015 and 2016 survey seasons did not appear to influence colonization of survey points by one or more black rails (Table 1).

I used the top occupancy model to estimate the total survey effort required to have a 0.95 probability of detecting one or more black rails at a single point, in a single season under mean conditions assuming presence (detection: wind = 6 – 10 km/hr, lunar phase = half-moon [7.8], average survey temperature = 23.25 ˚C; occupancy: herbaceous = 38.44%, *Spartina* = 35.58%, woody = 26.31%, intermediate marsh = 42.02% [Figure 3]). The mean species detection probability was 0.18 (SE = 0.02). Using formula 2, it takes ~ 16 surveys to have a 0.95 probability of detecting one or more black rails when they are actually present at a survey point.

Abundance

As with occupancy, I examined the influence of the same 15 covariates on individual black rail detection probabilities as estimated in Poisson *N*-mixture models. I found that wind speed, lunar phase, average survey temperature, and ambient noise level influenced individual black rail detection the most (Appendix B). Individual detection increased

with moon phase, average survey temperature, and decreased with increasing ambient noise and wind speed (Appendix B).

The mixture model with the lowest dispersion ($\hat{C} = 1.06$) was the global, negative binomial model. That model also appeared to fit the data ($\chi^2 = 3{,}769.3$, $P = 0.077$). The global models with Poisson and the zero-inflated Poisson distributions had $\hat{C}$ values of 1.12 and 1.10, respectively. The goodness-of-fit statistics for the Poisson mixture model suggested a lack of fit ($\chi^2 = 3{,}816.8$, $P = 0.003$) but the zero-inflated Poisson mixture ($\chi^2 = 3{,}796.8$, $P = 0.118$) did fit the data. I chose the negative binomial mixture because it had the lowest $\hat{C}$ and this model appeared to fit the data. Nevertheless, findings from both mixture models were similar (Appendix C).

I evaluated 19 nested models for the negative binomial mixture (Table 3). I selected the multi-scale model where herbaceous, *Spartina*, woody, and intermediate marsh cover influenced abundance. This model had a ΔAIC $= 1.22$ with the second smallest AIC behind the global model. The additional parameters in the global model seemed to have little influence ($P > 0.15$). I therefore used the concept of parsimony to select the simpler model where most of the parameters were statistically significant. Furthermore, the deviance of the two models were fairly similar (within 5) so the global model explained a similar amount of variation in the data as the selected model (Arnold 2010).

For the selected model, abundance increased with increases in point level (*Spartina*, herbaceous and woody cover) and site level covariates (intermediate marsh cover, Figure 4 and Table 4). The Nagelkerke's R^2 for the selected model was 0.32.

Mean abundance declined from 0.96 rails/point (95% credible interval [CI] = 0.28 – 3.13) in 2015 to 0.91 rails/point (CI = 0.28 – 2.45) in 2016 although the difference was not significant given the substantial overlap of the CIs. Mean recruitment was only 0.21 rails/points (SE = 0.08) in areas that were not burned between years but 7.19 rails/point (SE = 2.73) in areas that were burned between 2015 and 2016. The mean proportion of rails that were similar at points between 2015 and 2016 was 0.43 rails/point (SE = 0.11). The negative-binomial dispersion parameter, $\hat{\alpha}$ = 0.073 (SE = 0.420), was not statistically significant. Mean individual detection was 0.07 (SE = 0.02).

DISCUSSION

My results indicate that black rail species detection was influenced most by wind speed, temperature, and moon phase. The same covariates, in addition to ambient noise, influenced individual black rail detection. Black rail occupancy and abundance were influenced at the spatial scales of the point, by *Spartina*, herbaceous, and woody cover and the site, by intermediate-brackish marsh cover. Black rails occupied areas in 2016 that were not occupied in 2015. The proportion of rails similar between years was ~ 40% per point and there was an increase in the number of rails at points that were burned. Yet, black rail occupancy and abundance were similar between 2015 and 2016. Similarities in annual occupancy and abundance might be because differences were slight and beyond what could be detected with inter-point variation in colonization, extinction, recruitment, and survivorship. Recruitment varied widely and points that were burned made up a minority of the total points (~ 22%). The low number of burned points along with the variation in recruitment between points may have reduced the ability to detect increases in abundance.

Black rails were most vocal and easiest to hear when wind speeds were low (below 11 km/hr), the moon was full the night before the survey, temperatures were above 21˚C, and ambient noise levels were low. Black rail vocalizations were not influenced by time of day, time of survey, or Julian date. For individual covariates, these results are similar to those found in other black rail studies yet the combined influence of wind, temperature, moon phase, and noise level is unique to my study. Spear et al. (1999) reported that both moon phase and temperature influenced California black rail vocalizations. Legare et al. (1999) did not examine moon phase, but did report that temperature had a positive influence on eastern black rail vocalizations. Previous studies did not report wind as an influential variable (Legare et al. 1999, Spear et al. 1999, Butler et al. 2015). Wind was an important influence in my model and probably decreases an observer's ability to hear birds vocalizing and may decrease vocalization rates (Conway 2011). I conducted some surveys when wind speeds were ≥ 11 km/hr (Butler et al. 2015) and 25 km/hr (Evens et al. 1991, Legare et al. 1999, Spear et al. 1999, Conway 2011), recommendations of wind speeds when surveys should not be conducted. Wind speeds are often highly variable and can change quickly on the Texas coast. Logistically, stopping and starting surveys when these thresholds had been breached would have been impractical.

Cloud cover variables have been reported to influence black rail vocalizations (Spear et al. 1999, Butler et al. 2015). Yet none of my cloud cover covariates greatly influenced black rail vocalizations (Appendices A and B). The influence of cloud cover variables is inconsistent across studies, Spear et al. (1999) reported vocalizations to decrease with cloud cover, while Butler et al. (2015) reported the opposite relationship,

and Legare et al. (1999) reported cloud cover to be uninfluential. It is also difficult to assess the importance of the cloud cover variables in the studies that reported them as influential. Butler et al. (2015) only reported the cumulative AIC weight of cloud cover and did not report the magnitude of influence (covariate coefficient) while Spear et al. (1999) was not looking for the most parsimonious model to estimate black rail detection and thus did not perform a model selection analysis. As such, the magnitude of influence from cloud cover variables is difficult to assess in particular studies much less in the context of a species.

I also detected no effect from Julian day or diel period, yet, prior studies have reported both as influencing black rail vocalization frequency (Legare et al. 1999, Spear et al. 1999, Conway et al. 2004, Butler et al. 2015). It is not surprising that Julian date was not influential in my study. Though both time of year and month have been reported to influence black rail vocalizations I conducted my surveys when breeding is thought to occur in Texas. Others surveyed outside of and during the breeding season (Spear et al. 1999, Conway et al. 2004). My focus on the breeding season likely prevented the detection of a possible relationship between calling frequency and Julian date because the breeding season is when black rails are most vocal (Legare et al. 1999, Spear et al. 1999, Conway et al. 2004). Diel periods or time of day has often been shown to influence black rail vocalizations. Mornings, evenings, and nights are times in which black rails are vocal with nights reported to be the peak in vocalizations (Reynard 1974, Eddleman et al. 1994). Studies that report differences in vocalization frequency between mornings and evenings might have conducted a dissimilar number of surveys between the two periods. This amount of unevenness in survey effort might have influenced findings especially

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considering the low detection probability of black rails. I had similar survey effort in the morning and evening.

Additionally, the differences between my results and others could be a result of geographic variation and taxa-specific behavior. It has been reported that different populations of black rails vary in vocalization peaks throughout the day and night (Kerlinger and Wiedner 1990, Conway et al. 2004). Eastern black rails and California black rails are known to differ in vocalization behaviors (Conway et al. 2004, Butler et al. 2015). Therefore, the detection patterns I report may be unique to black rails inhabiting the Texas coast.

If vocalizations vary by region and subspecies then mean species detection might also vary. I estimated that, during one survey in a single season under mean conditions, I had an 18% (SE = 2.0) chance of detecting the species if present. This is similar to the night detection probability (0.16 ± 0.05) but lower than the mean species detection probability (0.09 ± 0.04) previously reported for Texas eastern black rails (Butler et al. 2015). My estimated species detection is also similar to Legare et al.'s (1999) detection probability for female eastern black rails in Florida. California black rails, however, have been consistently reported to have much higher detection probabilities (0.75 – 0.85; Conway et al. 2004, Richmond et al. 2008). The eastern black rail subspecies, therefore, seems to have a lower detection rate than their California counterparts.

Very low individual detection of species (< 15%) can have adverse effects on the estimation of abundance with *N*-mixture models (Royle 2004, Veech et al. 2016). Veech et al. (2016), applied *N*-mixture models to simulated data. Their findings, indicated that when individual detection drops below 5%, estimates of abundance may be biased high.

Consequently, when detection probability is < 0.15, *N*-mixture model estimates should be viewed with caution. However, their simulations considered density dependent and random heterogeneity in detection, wherein calling rate and detection of birds is not constant but increases with abundance. Density dependence heterogeneity may be reduced when calls are elicited by call-playback. If this is the case for black rails, my survey techniques may have reduced any heterogeneity in detection induced by differences in density. My estimates of mean abundance 0.91 and 0.96 rails/point are similar to those which have estimated abundance in California (0.08 – 2.10 rails/station; Evens et al. 1991). Therefore, my estimates of abundance appear plausible.

If *N*-mixture models are reliable models for estimating black rail abundance my results do not reveal whether the negative binomial or zero-inflated Poisson distributions fits the black rail abundance distribution. Both theoretical distributions may describe black rail abundance. The zero-inflated distribution would be appropriate when a large number of sites were not occupied by black rails (that is, true zeros were common in the data set [Royle 2004]). The negative binomial distribution would be appropriate if there was clumping of black rails across a landscape (Royle 2004, Veech et al. 2016). As there were points with extremely low occupancy rates (Figure 2), there might have been sites unoccupied by black rails. The zero-inflated mixture should then match the black rail abundance distribution. Nevertheless, I did have a wide range in the number of individual detections in a single survey (1-5) which could indicate clumping of rails under certain habitat conditions. Indeed, both mixtures might provide plausible estimates.

Estimates of occupancy and abundance can be biased by a lack of independence between survey points. Butler et al. (2015) attempted to decrease autocorrelation in black rail detections by spacing points 800 meters apart instead of the 400 meters suggested by Conway (2011). Nevertheless, in my results relatively few rails seemed to be detected more than 150 meters away from my survey points (15/234). The decrease in detections beyond 150 meters that I observed, is similar to other studies which have examined detection of black rails in relation to distance (Spear et al. 1999, Legare et al. 1999, Conway 2004). Spacing survey points 400 meters apart is likely adequate to circumvent the detection of the same individuals between adjacent survey points. Additionally, black rail home ranges, in other populations, are relatively small (0.62 – 1.3 ha; Legare and Eddleman 2001). If home ranges of Texas black rails are similar it is unlikely individual rails moved between survey points within the breeding season. Therefore, I think point count stations were likely independent during my study.

I conducted my surveys along roadsides, roadbeds, and along fire breaks. This may have biased my estimates of occupancy and abundance by limiting survey sites to edge habitat (Bart et al. 1995, Keller and Scallan 1999) in otherwise expansive marsh areas. Nonetheless, limiting my points to these areas allowed for quick and efficient navigation to and between survey points. The efficiency of this method allowed me to sample far more points than would have been possible in a completely random design. Additionally, roadside sampling reduces habitat disturbance (i.e. trampling of the marsh vegetation); which has been speculated to decrease black rail detection probability (Butler et al. 2015). Proponents of this idea, suggest black rails may hunker down and not vocalize or run from disturbed areas thus decreasing their detectability. Thus in

addition to their efficiency, roadside surveys may have higher detection rates than survey conducted within the marsh.

Occupancy and abundance were influenced by environmental factors (model covariates) at two spatial scales, the site level and the point level. Black rail abundance and occupancy increased with the cover of intermediate-brackish marsh cover. The magnitude of influence, however, of this covariate was relatively low. The low influence may be the product of temporal inconsistency. That is, the raster data (Enwright et al. 2015) I used to estimate the percent cover of intermediate-brackish marsh per site was collected in 2013 whereas my data was collected in 2015 and 2016. It is possible that the percent cover of intermediate-brackish marsh increased in those years at some of my study sites and decreased in others. However, it is unlikely that the percent cover would very that drastically over the spatial extent I examined. Another interpretation for the low magnitude of influence is an ecological one. Black rails are territorial and are likely distributed despotically across the landscape (Freckleton et al. 2005). In this case, there may be quality intermediate-brackish marsh habitat that is simply not occupied by black rails because they are a rare species. Thus the low magnitude of influence could be a result of black rail scarcity on the landscape.

At the point level, habitats with high *Spartina* cover were most often occupied by black rails and had the highest estimated number of black rails. *Spartina* cover consisted of two species of cordgrass, saltmeadow cordgrass (*S. patens*), and gulf cordgrass (*S. spartinae*). Although smooth cordgrass (*S. alterniflora*) was recorded in this general category very few of my points were dominated by this species. Other authors have reported and suggested that black rail habitat preferences are based on structure rather

than specific species of vegetation (Rundle and Fredrickson 1981, Flores and Eddleman 1995, Tsao et al. 2009). This structure is characterized by high stem counts and a closed canopy of grasses and forbs (Tsao et al. 2009). Saltmeadow and gulf cordgrass are inherently very dense. Gulf cordgrass is this way because of its high stem count and the closeness of individual bunches (Butler et al. 2005). Saltmeadow cordgrass achieves this structure through a rhizomatous growth habit that gives raise to tall, dense, monocultures.

Woody and herbaceous cover were also included in the top occupancy and abundance models but the regression coefficients for these covariates were much less than for *Spartina*. The woody component might have been influential because high marsh and coastal prairie, which are dominated by saltmeadow and gulf cordgrass in Texas, often has dispersed patches of eastern baccharis (*Baccharis halimifolia*) and/or Jesuit's bark (*Iva frutescens*), both shrub species. Black rails might have occupied areas with high herbaceous cover when it had high stem count.

Black rail occupancy was not influenced by burning yet number of black rails increased in burned areas. The influence of fire on black rails is inconsistent in the literature. Black rails have been reported to increase in abundance a few years after a burn (J. Wilson, United States Fish and Wildlife Service, unpublished data). On the other hand, fire has been reported to have no influence on black rail spatial patterns (Conway et al. 2010). Clearly, more work is needed to assess the influence of burning on habitat and black rail movement and demography.

In summary, black rails, in Texas, are easiest to detect when wind speeds are low, temperatures are high, the moon is full the night before the survey, and ambient noise is low. Black rail occupancy and abundance are highest in areas with high gulf cordgrass

and/or saltmeadow cordgrass cover. Other variables such as intermediate-brackish marsh, herbaceous and woody cover may influence black rail occupancy and abundance but at a very low magnitudes. More research is needed on how black rails respond to the implementation of fire and what type of *N*-mixture model is best for estimating black rail abundance.

MANAGEMENT IMPLICATIONS

Black rail distribution and abundance appears to be strongly tied to *Spartina* cover. As such, habitat management for the species should focus on the enhancement and maintenance of *Spartina* stands along the Texas coast.   I also suggest that surveys for black rails in Texas should first focus on wet prairies and marshes dominated by gulf cordgrass and/or saltmeadow cordgrass. Black rail survey points that are 400 meters apart seem to have low chance of detecting the same birds at adjacent points. To maximize detection of black rails, surveys should be conducted when wind speeds are below 11 km/hr, temperatures are above 21˚C, ambient noise is low, and the moon is more than half full.   The low probability of detecting black rails on the Texas coast appears to result in excessive effort for estimating population states from raw counts or naïve estimates of occupancy. With up to 16 surveys required to establish presence of black rails at a single point, in each survey season, it is probably impractical to expect to be able to conduct that number of surveys in an 8 – 10 week breeding season. Estimation of breeding season occupancy and abundance from models that account for imperfect detection and environmental heterogeneity is likely the most practical way of attaining reliable estimates of black rail population states. These recommendations apply to monitoring of black rails during the breeding season because that is when my surveys

took place. More research should be conducted to determine effective monitoring

methods of black rail populations outside the breeding season.

Table 1. Model selection summary of multi-season occupancy models of black rail (*Laterallus jamaicensis*) occupancy. Primary periods were 2015 and 2016 and secondary periods were 3 to 8 repeated call broadcast surveys from March to May (2015 and 2016). Included in models were combinations of multiscale occupancy ($\hat{\psi}$) covariates (point level and site level), a binomial influence on colonization ($\hat{\gamma}$), constant extinction ($\hat{\varepsilon}$), and detection probability ($\hat{p}$) influences. Point level covariates were: percent cover of non-*Spartina* herbaceous spp. (herb.), *Spartina* spp. (*spartina*), and woody species (woody); and if points were grazed (grazed). Site level covariates were percent cover of intermediate marsh (INTM) and open water. Colonization was influenced by a binomial covariate where unburned was the reference category. Detection probability influences were wind speed (wind), lunar phase (lunar), and average survey temperature (temp.). Included in the table are model statements (Model), number of parameters (K), the difference between the top ranked model's AIC_C and model$_i$'s AIC_C (ΔAIC_C), the model deviance (deviance), and each model's estimated Nagelkerke's R^2 (R^2).

Model	K	$\Delta AICc$	Deviance	R^2
$\hat{\psi}$(herb. + spartina + woody + INTM), $\hat{\gamma}$(burned), $\hat{\varepsilon}$(.), $\hat{p}$(wind + temp. + lunar)	12	0.00	1,155.14	0.30
$\hat{\psi}$(herb. + spartina + woody + graze + INTM + open water), $\hat{\gamma}$(burned), $\hat{\varepsilon}$(.), $\hat{p}$(wind + temp. + lunar)	14	3.02	1,152.65	0.30
$\hat{\psi}$(herb. + spartina + INTM), $\hat{\gamma}$(burned), $\hat{\varepsilon}$(.), $\hat{p}$(wind + temp. + lunar)	11	3.38	1,161.17	0.28
$\hat{\psi}$(herb. + spartina), $\hat{\gamma}$(burned), $\hat{\varepsilon}$(.), $\hat{p}$(wind + temp. + lunar)	10	7.95	1,168.33	0.27
$\hat{\psi}$(spartina + INTM), $\hat{\gamma}$(burned), $\hat{\varepsilon}$(.), $\hat{p}$(wind + temp. + lunar)	10	7.96	1,168.34	0.27
$\hat{\psi}$(spartina + woody + INTM), $\hat{\gamma}$(burned), $\hat{\varepsilon}$(.), $\hat{p}$(wind + temp. + lunar)	11	9.32	1,167.11	0.27
$\hat{\psi}$(herb. + spartina + woody + graze), $\hat{\gamma}$(burned), $\hat{\varepsilon}$(.), $\hat{p}$(wind + temp. + lunar)	12	9.92	1,165.06	0.27
$\hat{\psi}$(spartina + woody + graze + INTM + open water), $\hat{\gamma}$(burned), $\hat{\varepsilon}$(.), $\hat{p}$(wind + temp. + lunar)	13	10.75	1,163.17	0.28

Table 1 continued.

Model	K	ΔAICc	Deviance	R^2

$\hat{\psi}$(spartina),
    $\hat{\gamma}$(burned), $\hat{\varepsilon}$(.),
    $\hat{p}$(wind + temp. + lunar)
	9	18.90	1,181.79	0.23

$\hat{\psi}$(herb. + woody + graze + INTM + open water),
    $\hat{\gamma}$(burned), $\hat{\varepsilon}$(.),
    $\hat{p}$(wind + temp. + lunar)
	13	34.46	1,186.89	0.22

$\hat{\psi}$(herb. + Spartina + INTM),
    $\hat{\gamma}$(burned), $\hat{\varepsilon}$(.),
    $\hat{p}$(wind + temp. + lunar)
	11	37.03	1,194.81	0.20

$\hat{\psi}$(INTM + open water),
    $\hat{\gamma}$(burned), $\hat{\varepsilon}$(.),
    $\hat{p}$(wind + temp. + lunar)
	10	47.13	1,207.50	0.16

$\hat{\psi}$(INTM),
    $\hat{\gamma}$(burned), $\hat{\varepsilon}$(.),
    $\hat{p}$(wind + temp. + lunar)
	9	50.32	1,213.21	0.15

$\hat{\psi}$(open water),
    $\hat{\gamma}$(burned), $\hat{\varepsilon}$(.),
    $\hat{p}$(wind + temp. + lunar)
	9	51.47	1,214.36	0.14

$\hat{\psi}$(herb.),
    $\hat{\gamma}$(burned), $\hat{\varepsilon}$(.),
    $\hat{p}$(wind + temp. + lunar)
	9	52.95	1,215.85	0.14

$\hat{\psi}$(woody),
    $\hat{\gamma}$(burned), $\hat{\varepsilon}$(.),
    $\hat{p}$(wind + temp. + lunar)
	9	56.53	1,219.43	0.13

$\hat{\psi}$(.),
    $\hat{\gamma}$(burned), $\hat{\varepsilon}$(.),
    $\hat{p}$(wind + temp. + lunar)
	8	59.88	1,225.24	0.11

$\hat{\psi}$(graze),
    $\hat{\gamma}$(burned), $\hat{\varepsilon}$(.),
    $\hat{p}$(wind + temp. + lunar)
	9	61.71	1,224.60	0.12

$\hat{\psi}$(.), $\hat{\gamma}$(.), $\hat{\varepsilon}$(.), $\hat{p}$(.)	4	86.97	1,261.60	0.00

Table 2. Parameter estimates of the selected multi-season occupancy model for black rails (*Laterallus jamaicensis*) on the Texas coast. Primary periods were 2015 and 2016 and secondary periods were 3 to 8 repeated call broadcast surveys from March to May (2015 and 2016). Included in the model were multiscale occupancy ($\hat{\psi}$) covariates (point level and site level), an influence on colonization ($\hat{\gamma}$), constant extinction ($\hat{\varepsilon}$), and influences on detection probability ($\hat{p}$). Point level covariates were: percent cover of non-*Spartina* herbaceous spp. (herb.), *Spartina* spp. (*spartina*), and woody species (woody) and a site level covariate: percent cover of intermediate marsh (INTM). Colonization was modeled to influence immigration by a binomial covariate with unburned as the reference category. Detection probability influences were wind speed (wind), lunar phase (lunar), and average survey temperature (temp.). Intercept coefficients are denoted by b0.

Parameter	Estimate	SE	*P*
$\hat{\psi}_{b0}$	- 1.596	0.284	< 0.001
$\hat{\psi}_{herb.}$	1.656	0.560	0.003
$\hat{\psi}_{spartina}$	2.795	0.608	< 0.001
$\hat{\psi}_{woody}$	0.696	0.282	0.014
$\hat{\psi}_{INTM\ marsh}$	0.695	0.235	0.003
$\hat{\gamma}_{b0}$	- 1.952	0.321	< 0.001
$\hat{\gamma}_{burned}$	0.949	0.646	0.141
$\hat{\varepsilon}_{b0}$	- 0.450	0.385	0.242
$\hat{p}_{b0}$	- 1.514	0.120	< 0.001
$\hat{p}_{wind}$	- 0.439	0.105	< 0.001
$\hat{p}_{temp.}$	0.181	0.094	0.054
$\hat{p}_{lunar}$	0.338	0.095	< 0.001

Table 3. Model selection analysis for multi-season *N*-mixture models of black rail (*Laterallus jamaicensis*) abundance. Primary periods were 2015 and 2016 and secondary periods were 3 to 8 repeated call broadcast surveys from March to May (2015 and 2016). Included were combinations of multiscale abundance ($\hat{\lambda}$) covariates (point level and site level), a binomial recruitment ($\hat{\gamma}$) influence, constant apparent survival ($\hat{w}$), and individual detection probability ($\hat{r}$) influences. Point level covariates were: percent cover of non-*Spartina* herbaceous species (herb.), *Spartina* species (*spartina*), and woody species (woody); and if points were grazed (grazed). Site level covariates were: percent cover of intermediate marsh (INTM) and open water. Recruitment was influenced by a binomial covariate where unburned was the reference category. Influences on $\hat{r}$ were wind speed (wind), lunar phase (lunar), average survey temperature (temp.), and ambient noise (noise). The negative binomial dispersion parameter ($\hat{\alpha}$) was used to fit each model. Included in the table are model statements (Model), number of parameters (*K*), and the difference between the top ranked model AIC and model$_i$'s AIC (ΔAIC), the model deviance (deviance), and each model's estimated Nagelkerke's R^2 (R^2). Two models were ranked as competing models (within 2 ΔAIC of the top ranked model).

Model	K	ΔAIC	Deviance	R^2
$\hat{\lambda}$(herb. + spartina + woody + graze + INTM + open water), $\hat{\gamma}$(burned), $\hat{w}$(.), $\hat{r}$(wind + temp. + lunar + noise), $\hat{\alpha}$	16	0.00	1,460.41	0.33
$\hat{\lambda}$(herb. + spartina + woody + INTM), $\hat{\gamma}$(burned), $\hat{w}$(.), $\hat{r}$(wind + temp. + lunar + noise), $\hat{\alpha}$	14	1.22	1,465.63	0.32
$\hat{\lambda}$(herb. + spartina + INTM), $\hat{\gamma}$(burned), $\hat{w}$(.), $\hat{r}$(wind + temp. + lunar + noise) $\hat{\alpha}$	13	2.95	1,469.36	0.31
$\hat{\lambda}$(spartina + woody + graze + INTM + open water), $\hat{\gamma}$(burned), $\hat{w}$(.), $\hat{r}$(wind + temp. + lunar + noise) $\hat{\alpha}$	15	5.19	1,467.60	0.32
$\hat{\lambda}$(spartina + INTM), $\hat{\gamma}$(burned), $\hat{w}$(.), $\hat{r}$(wind + temp. + lunar + noise) $\hat{\alpha}$	12	7.46	1,475.86	0.30
$\hat{\lambda}$(spartina + woody + INTM), $\hat{\gamma}$(burned), $\hat{w}$(.), $\hat{r}$(wind + temp. + lunar + noise) $\hat{\alpha}$	13	8.83	1,475.24	0.30
$\hat{\lambda}$(herb. + spartina), $\hat{\gamma}$(burned), $\hat{w}$(.), $\hat{r}$(wind + temp. + lunar + noise) $\hat{\alpha}$	12	12.97	1,481.37	0.29

Table 3 continued.

Model	K	ΔAIC	Deviance	R^2
$\hat{\lambda}$(herb + spartina + woody + graze), $\hat{\gamma}$(burned), $\hat{w}$(.), $\hat{r}$(wind + temp. + lunar + noise) $\hat{\alpha}$	14	15.76	1,480.16	0.29
$\hat{\lambda}$(herb. + woody + graze + INTM + open water), $\hat{\gamma}$(burned), $\hat{w}$(.), $\hat{r}$(wind + temp. + lunar + noise) $\hat{\alpha}$	15	25.14	1,487.54	0.27
$\hat{\lambda}$(spartina), $\hat{\gamma}$(burned), $\hat{w}$(.), $\hat{r}$(wind + temp. + lunar + noise) $\hat{\alpha}$	11	25.64	1,496.04	0.25
$\hat{\lambda}$(herb. + woody + INTM), $\hat{\gamma}$(burned), $\hat{w}$(.), $\hat{r}$(wind + temp. + lunar + noise) $\hat{\alpha}$	13	34.45	1,500.85	0.24
$\hat{\lambda}$(INTM + open water), $\hat{\gamma}$(burned), $\hat{w}$(.), $\hat{r}$(wind + temp. + lunar + noise) $\hat{\alpha}$	12	37.88	1,506.29	0.22
$\hat{\lambda}$ (INTM), $\hat{\gamma}$(burned), $\hat{w}$(.), $\hat{r}$(wind + temp. + lunar + noise) $\hat{\alpha}$	11	46.59	1,516.99	0.20
$\hat{\lambda}$(open water), $\hat{\gamma}$(burned), $\hat{w}$(.), $\hat{r}$(wind + temp. + lunar + noise) $\hat{\alpha}$	11	52.18	1,522.59	0.18
$\hat{\lambda}$(herb.), $\hat{\gamma}$(burned), $\hat{w}$(.), $\hat{r}$(wind + temp. + lunar + noise) $\hat{\alpha}$	11	56.89	1,526.91	0.17
$\hat{\lambda}$(woody), $\hat{\gamma}$(burned), $\hat{w}$(.), $\hat{r}$(wind + temp. + lunar + noise) $\hat{\alpha}$	11	57.89	1,528.30	0.17
$\hat{\lambda}$(.), $\hat{\gamma}$(burned), $\hat{w}$(.), $\hat{r}$(wind + temp. + lunar + noise) $\hat{\alpha}$	9	64.98	1,539.38	0.14
$\hat{\lambda}$(graze), $\hat{\gamma}$(burned), $\hat{w}$(.), $\hat{r}$(wind + temp. + lunar + noise) $\hat{\alpha}$	11	65.05	1,535.46	0.15
$\hat{\lambda}$(.),$\hat{\gamma}$(.), $\hat{w}$(.),$\hat{r}$(.),$\hat{\alpha}$	5	101.78	1,584.19	0.00

Table 4. Parameter estimates of the selected multi-season *N*-mixture model for black rail (*Laterallus jamaicensis*) abundance on the Texas coast. Primary periods were 2015 and 2016 and secondary periods were 3 to 8 repeated call broadcast surveys from March to May (2015 and 2016). Included in the model were multiscale abundance ($\hat{\lambda}$) covariates (point level and site level) and constant recruitment ($\hat{\gamma}$) influences, apparent survival ($\hat{\omega}$), and individual detection probability ($\hat{r}$) influences. Point level covariates were: percent cover of non-*Spartina* herbaceous spp. (herb.), *Spartina* spp. (*Spartina*), and woody spp. (woody) and a site level covariate: percent cover of intermediate marsh (INTM). Recruitment was influenced burned areas (burned) where unburned was the reference category. Detection probability influences were wind speed (Wind), lunar phase (Lunar), and average survey temperature (Temp.). Included in the table are parameter estimates, standard error for parameter estimates (SE), and the associated *P*-values (*P*). Intercept coefficients are denoted by b0.

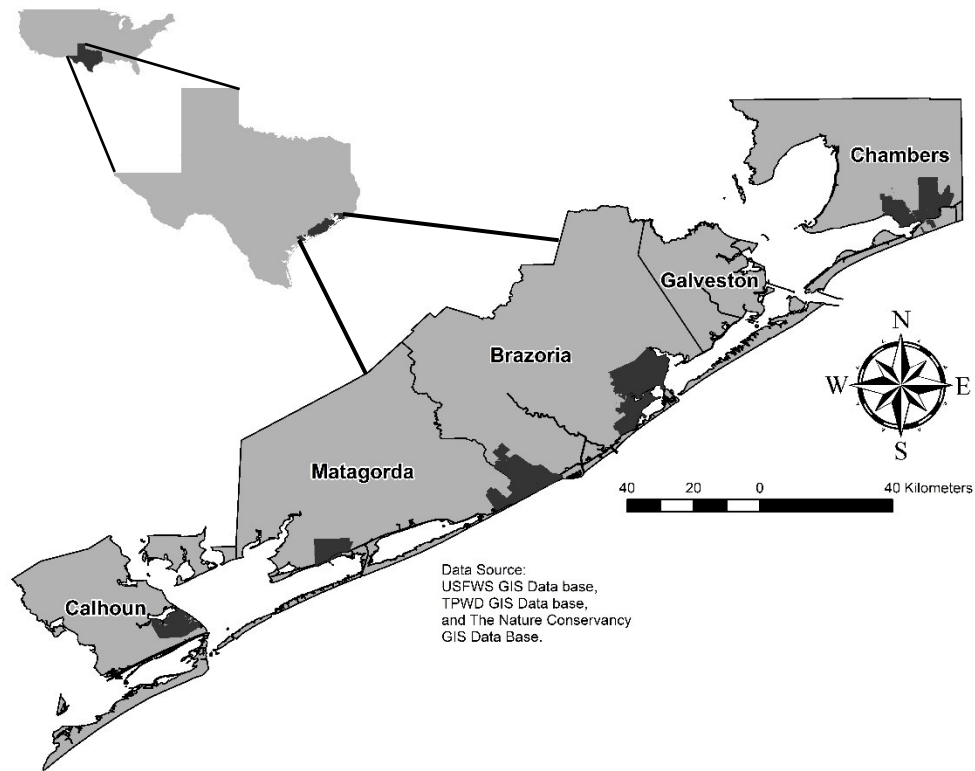| Parameter	Estimate	SE	*P*
$\hat{\lambda}_{b0}$	- 0.770	0.325	0.018
$\hat{\lambda}_{Herb.}$	1.048	0.382	0.006
$\hat{\lambda}_{Spartina}$	1.804	0.378	< 0.001
$\hat{\lambda}_{Woody}$	0.387	0.192	0.044
$\hat{\lambda}_{INTM}$	0.547	0.144	< 0.001
$\hat{\gamma}_{b0}$	- 1.550	0.367	< 0.001
$\hat{\gamma}_{burned}$	1.970	0.380	< 0.001
$\hat{\omega}_{b0}$	- 0.304	0.441	0.491
$\hat{r}_{b0}$	- 2.643	0.292	< 0.001
$\hat{r}_{Wind}$	- 0.455	0.093	< 0.001
$\hat{r}_{Temp.}$	0.172	0.079	0.029
$\hat{r}_{Lunar}$	0.208	0.079	0.008
$\hat{r}_{Noise}$	- 0.455	0.084	0.050
$\hat{\alpha}$	0.073	0.420	0.863

Figure 1. Black rail (*Laterallus jamaicensis*) study sites. Shown are the 6 study sites surveyed for black rails with point count stations from mid-March to the end of May (2015 and 2016). Dark gray indicates areas selected for study and light gray indicates contextual area. From northeast to southwest are Anahuac National Wildlife Refuge (NWR), Brazoria NWR, San Bernard NWR, Mad Island Wildlife Management Area and Clive Runnells Family Mad Island Marsh Preserve (shown in the same polygon), and Powderhorn Ranch Preserve.
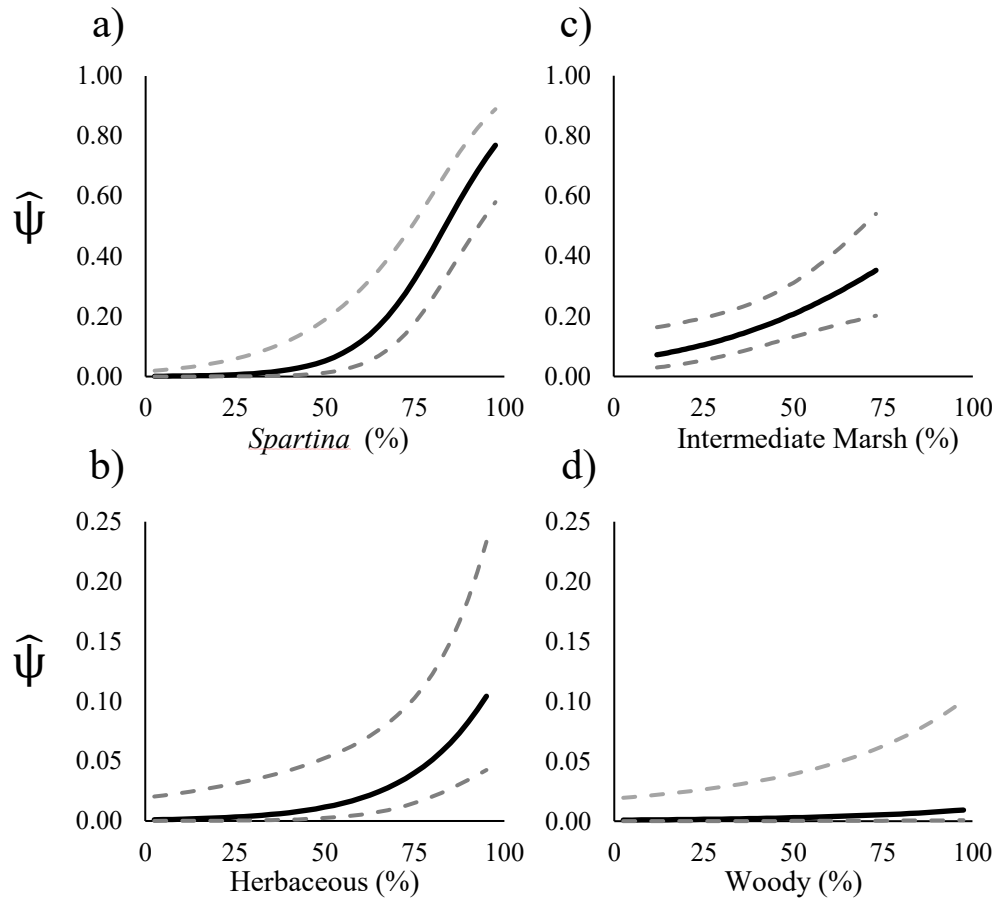
Figure 2. Estimated habitat relationships with black rail (*Laterallus jamaicensis*) occupancy. Shown are the estimated relationships (solid black lines), and 95% confidence intervals (broken gray lines), of multiscale covariates influencing black rail occupancy ($\widehat{\psi}$) at 6 sites across the Texas coast. Covariates were a) cordgrass species (*Spartina* spp. %) cover, b) non-*Spatina* herbaceous species cover, c) intermediate marsh cover, and d) woody species cover. a), b), and d) are at the scale of a survey point while c) is at the scale of a survey site.
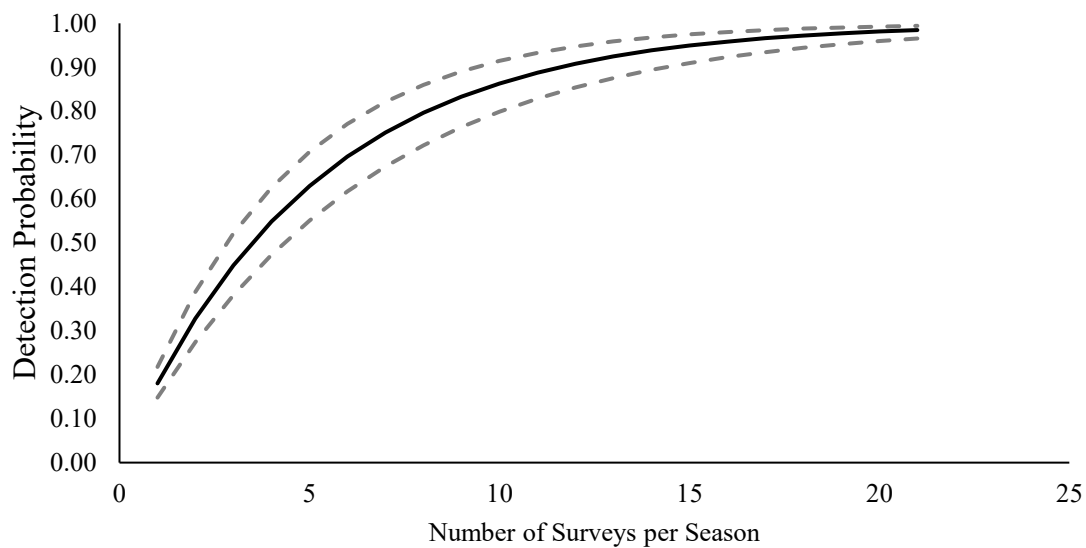
Figure 3. Survey effort required to establish presence of black rails (*Laterallus jamaicensis*). Shown is the estimated relationship between black rail detection (solid black line), and 95% confidence intervals (broken gray lines), and number of surveys of a site per season at 6 study sites across the Texas coast.
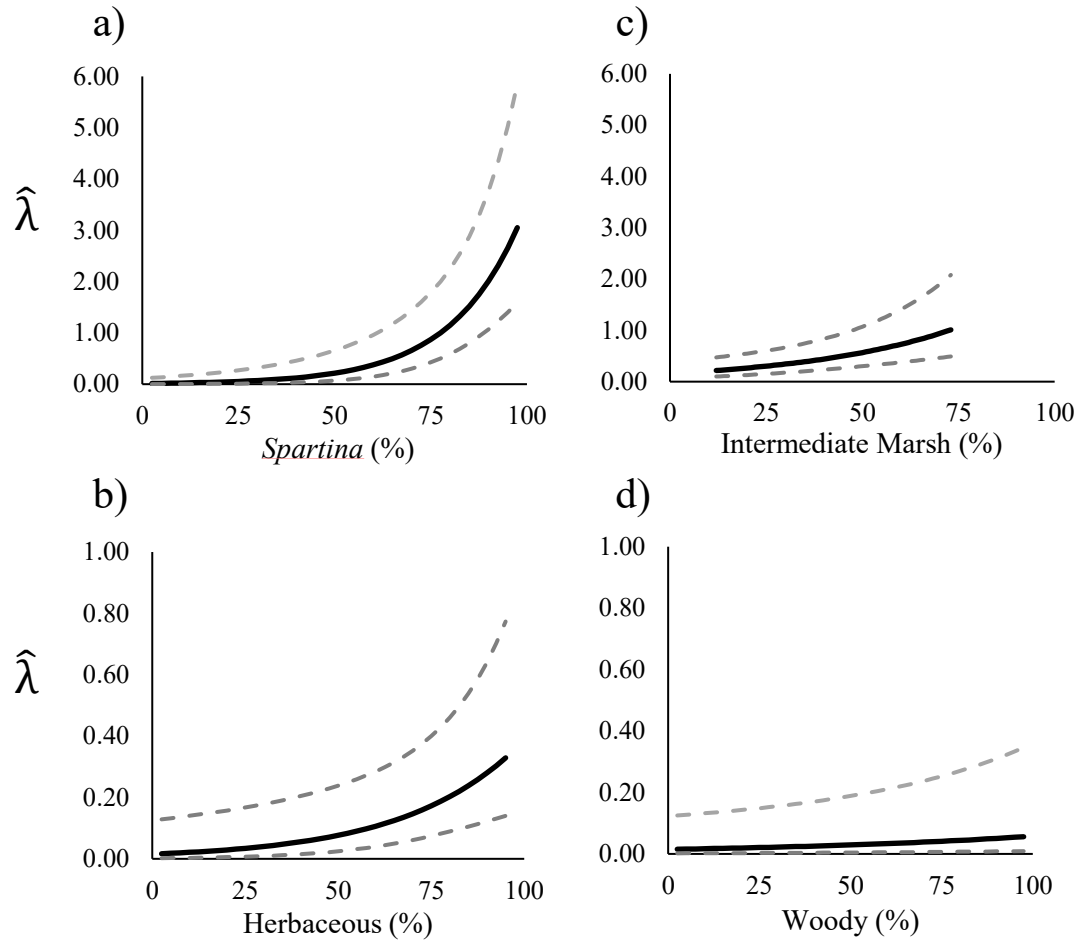
Figure 4. Estimated habitat relationships with black rail (*Laterallus jamaicensis*) abundance. Shown are estimated relationships (solid black lines), and 95% confidence intervals (broken gray lines), of multi-scale covariates influencing black rail abundance ($\hat{\lambda}$) at 6 sites across the Texas coast. Covariates were a) cordgrass (*Spartina*) cover, b) non-*Spatina* herbaceous cover, c) intermediate marsh cover, and d) woody spp. cover. a), b), and d) are at the scale of a survey point while c) is at the scale of a survey site.

APPENDIX SECTION

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APPENDIX A

Below are the results from preliminary analyses on influences of detecting one or more

black rails. Analysis was conducted on survey data from 4,023 surveys performed at 375

points from mid-March to the end of May (2015 and 2016) at 6 study sites across the

Texas coast. Sample sizes were larger for these preliminary analyses as points were not

excluded when they lacked vegetation data or were only sampled in one year. Figure A1

was estimated from the final occupancy model and therefore has the same sample sizes as

described in the text.

Table A1. Black rail (*Laterallus jamaicensis*) detection model selection analysis for single covariate models. Covariates were selected when all covariate parameter estimates had an absolute Z-score ≥ 1.41. Covariates included in the models were change in barometric pressure (PB), Julian date (JD), lunar phase (Lunar), cloud cover (Sky), average survey temperature (Temp.), Time after dawn survey start time (TSS), time of day (diel), whether black rail calls or clapper rail calls were played first (CO), ambient noise (Noise), and wind speed (Wind). The table includes: model statements (Model), influences on detection (covariate), covariate parameter estimates (parameter estimate), Z-scores for estimates (Z-score) and t-scores for estimates (t-score). Models selected to be used in AIC$_C$ model selection were wind, Lunar, Noise, CO, and Temp.

Model	Covariate	Parameter Estimate	Z-score	t-score
$\widehat{\psi}(.), \hat{p}(\text{Wind})$	Wind	- 0.37	- 4.49	5.1
$\widehat{\psi}(.), \hat{p}(\text{Lunar})$	Lunar	0.34	4.29	92.9
$\widehat{\psi}(.), \hat{p}(\text{Noise})$	Noise	- 0.19	- 2.56	24.4
$\widehat{\psi}(.), \hat{p}(\text{CO})$	CO	- 0.36	- 2.32	26.8
$\widehat{\psi}(.), \hat{p}(\text{Temp.})$	Temp.	0.13	1.66	66.6
$\widehat{\psi}(.), \hat{p}(\text{Sky})$	Clear Sky	0.35	2.00	70.0
	Variable Sky	- 0.15	- 0.77	42.3
	Overcast	- 9.27	- 0.01	49.9
	Fog	- 0.89	- 1.19	38.1
	Drizzle	0.05	0.06	50.6
	Showers	- 9.07	- 0.08	49.2
$\widehat{\psi}(.), \hat{p}(\text{TSS})$	TSS	0.07	0.97	59.7
$\widehat{\psi}(.), \hat{p}(\text{Diel})$	Diel	0.10	0.70	57.0
$\widehat{\psi}(.), \hat{p}(\text{JD})$	JD	0.02	0.29	52.9
$\widehat{\psi}(.), \hat{p}(\text{PB})$	PB	0.02	0.10	51.0

Table A2. Model selection analysis for single-season occupancy models of black rail (*Laterallus jamaicensis*) detection. Included were all possible combinations of the covariates wind speed (Wind), lunar phase (Lunar), ambient noise (Noise), whether black rail calls or clapper rail calls were played first (CO), and average survey temperature. Included in the table are model statements (Model), number of parameters (K), the difference between the top ranked model AIC_C and model$_i$'s AIC_C (ΔAIC_C), and the model deviance (deviance). Three models were ranked as competing (within 2 ΔAIC_C); the model including wind, average survey temperature, and lunar phase was selected from these competing model because it was the most parsimonious model of the three.

| Model	K	ΔAIC_C	Deviance
$\widehat{\psi}(.), \hat{p}$(Wind + Temp + Noise + Lunar)	6	0.00	1,572.77
$\widehat{\psi}(.), \hat{p}$(Wind + Temp + Lunar)	5	1.33	1,576.34
$\widehat{\psi}(.), \hat{p}$(Global)	7	1.59	1,572.08
$\widehat{\psi}(.), \hat{p}$(Wind + Lunar)	4	8.84	1,586.03
$\widehat{\psi}(.), \hat{p}$(Wind + Noise + Lunar)	5	8.90	1,583.91
$\widehat{\psi}(.), \hat{p}$(Wind + Lunar + Call Order)	5	10.59	1,585.59
$\widehat{\psi}(.), \hat{p}$(Temp. + Noise + Lunar)	5	15.67	1,590.67
$\widehat{\psi}(.), \hat{p}$(Wind + Temp. + Noise + Call Order)	6	15.79	1,588.56
$\widehat{\psi}(.), \hat{p}$(Wind + Temp. + Call Order)	5	15.82	1,590.82
$\widehat{\psi}(.), \hat{p}$(Temp. + Noise + Lunar + Call Order)	6	16.22	1,588.99
$\widehat{\psi}(.), \hat{p}$(Wind + Temp. + Noise)	5	16.46	1,591.46
$\widehat{\psi}(.), \hat{p}$(Wind + Temp.)	4	16.92	1,594.11
$\widehat{\psi}(.), \hat{p}$(Noise + Lunar)	4	21.17	1,598.36
$\widehat{\psi}(.), \hat{p}$(Noise + Lunar + Call Order)	5	22.39	1,597.39
$\widehat{\psi}(.), \hat{p}$(Wind + Call Order)	4	22.51	1,599.71
$\widehat{\psi}(.), \hat{p}$(Wind)	3	22.81	1,602.16
$\widehat{\psi}(.), \hat{p}$(Wind + Noise)	4	23.41	1,600.60
$\widehat{\psi}(.), \hat{p}$(Temp. + Lunar)	4	23.93	1,601.12
$\widehat{\psi}(.), \hat{p}$(Lunar)	3	26.67	1,606.01
$\widehat{\psi}(.), \hat{p}$(Lunar + Call Order)	4	27.01	1,604.20
$\widehat{\psi}(.), \hat{p}$(Temp. + Noise + Call Order)	5	33.15	1,608.15
$\widehat{\psi}(.), \hat{p}$(Temp. + Noise)	4	36.21	1,613.40
$\widehat{\psi}(.), \hat{p}$(Noise + Call Order)	4	37.09	1,614.29
$\widehat{\psi}(.), \hat{p}$(Temp. + Call Order)	4	38.35	1,615.54
$\widehat{\psi}(.), \hat{p}$(Noise)	3	39.03	1,618.38
$\widehat{\psi}(.), \hat{p}$(Call Order)	3	40.28	1,619.63
$\widehat{\psi}(.), \hat{p}$(Temp.)	3	42.96	1,622.30
$\widehat{\psi}(.), \hat{p}(.)$	2	43.73	1,625.18
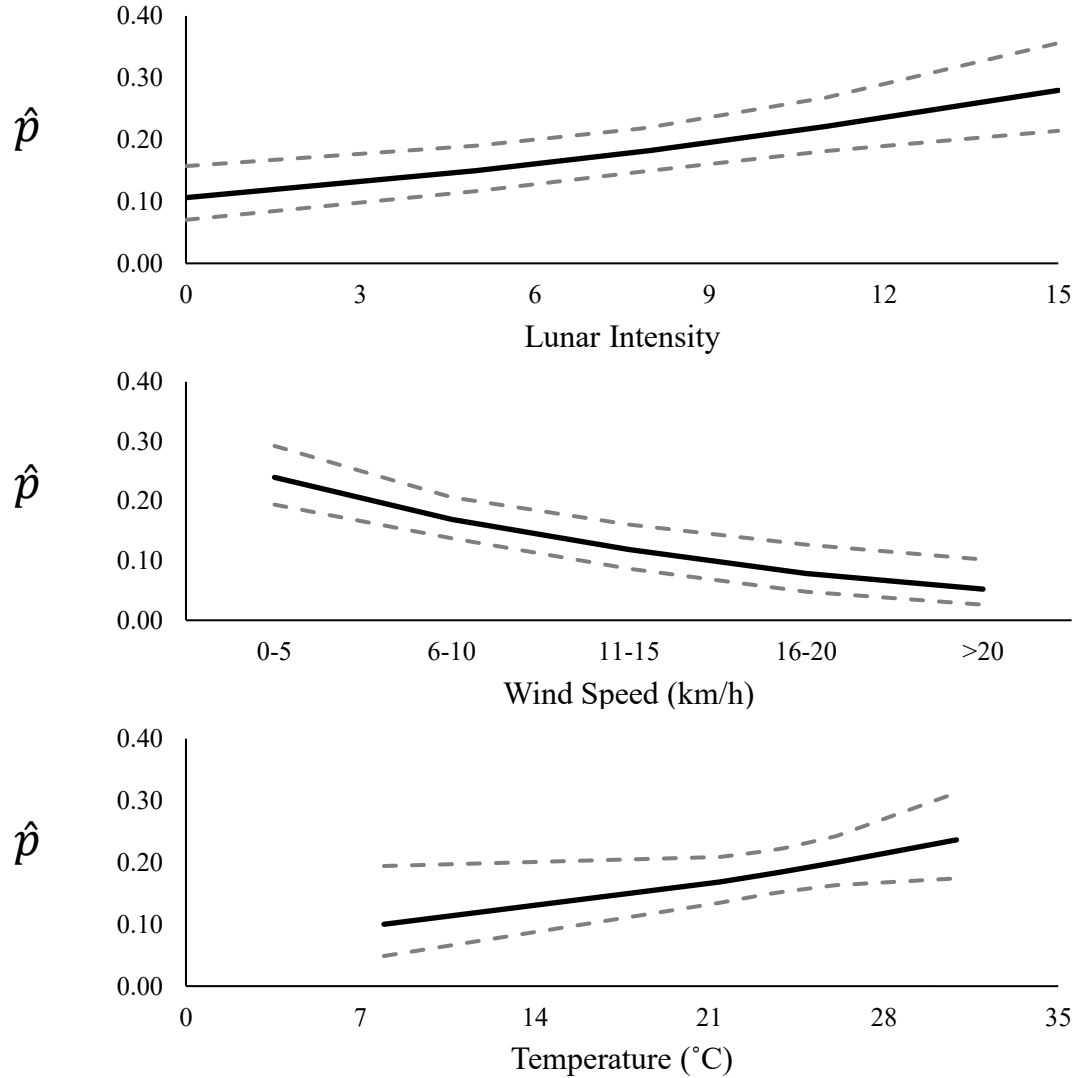
Figure A1. Estimated influences on black rail (*Laterallus jamaicensis*) species detection. Shown are the estimated relationships (solid black lines), and 95% confidence intervals (broken gray lines), of covariates influencing detection of one or more black rails ($\hat{p}$) at 6 sites across the Texas coast. Covariates were moon phase (lunar intensity) that ranged from no moon (0) to full moon (15) (top), wind speed in five continuous discrete ranges of wind speed (middle), and the continuous random factor of temperature (bottom).

Below are the results of preliminary analyses of influences on individual black rail detection. Analyses were conducted on survey data from 4,023 surveys performed at 375 points from mid-March to the end of May (2015 and 2016) at 6 study sites across the Texas coast. Reported Sample sizes are larger than those in the text because points were not excluded when they had no vegetation data or were only sampled in one year. Figure B1 was estimated with the final negative binomial model and therefore has the same sample sizes as reported in the text.

Table B1. Individual black rail (*Laterallus jamaicensis*) detection model selection analysis for single covariate models. Covariates were selected when all covariate parameter estimates had an absolute Z-score ≥ 1.41. Covariates included in the models were change in barometric pressure (PB), Julian date (JD), lunar phase (Lunar), cloud cover (Sky), average survey temperature (Temp.), Time after dawn survey start time (TSS), time of day (diel), whether black rail calls or clapper rail calls were played first (CO), ambient noise (Noise), and wind speed (Wind). The table includes: model statements (Model), influences on detection (covariate), covariate parameter estimates (parameter estimate), Z-scores for estimates (Z-score) and t-scores for estimates (t-score).

Model	Covariate	Parameter Estimate	Z-score	t-score
$\hat{\lambda}(.), \hat{r}(\text{Wind})$	Wind	- 0.41	- 5.47	- 4.7
$\hat{\lambda}(.), \hat{r}(\text{Lunar})$	Lunar Phase	0.27	3.99	89.9
$\hat{\lambda}(.), \hat{r}(\text{Noise})$	Noise	- 0.23	- 3.36	16.4
$\hat{\lambda}(.), \hat{r}(\text{CO})$	CO	- 0.39	- 2.86	21.4
$\hat{\lambda}(.), \hat{r}(\text{Temp.})$	Temp.	0.11	1.68	66.8
$\hat{\lambda}(.), \hat{r}(\text{Sky})$	Clear Sky	0.21	1.38	63.8
	Variable Sky	- 0.25	- 1.51	34.9
	Overcast	- 8.57	- 0.02	49.8
	Fog	- 1.10	- 1.50	35.0
	Drizzle	- 0.41	- 0.55	44.5
	Showers	- 8.10	- 0.15	48.6
$\hat{\lambda}(.), \hat{r}(\text{Diel})$	Diel	0.16	1.27	62.7
$\hat{\lambda}(.), \hat{r}(\text{TSS})$	TSS	0.08	1.24	62.4
$\hat{\lambda}(.), \hat{r}(\text{Baro})$	Baro.	0.60	1.17	61.7
$\hat{\lambda}(.), \hat{r}(\text{JD})$	JD	0.03	0.47	54.7

Table B2. Model selection analysis for single-season Poisson *N*-mixture models of individual black rail (*Laterallus jamaicensis*) detection. Included were all possible combinations of the covariates wind speed (Wind), lunar phase (Lunar), ambient noise (Noise), whether black rail calls or clapper rail calls were played first (CO), and average survey temperature. Included in the table are model statements (Model), number of parameters (*K*), the difference between the top ranked model AIC and model$_i$'s AIC (ΔAIC), and the model deviance (deviance). Three models were ranked as competing (within 2 ΔAIC); the model including wind, average survey temperature, and lunar phase was selected from these competing models because it was the most parsimonious model of the three.

| Model	*K*	ΔAIC	Deviance
$\hat{\lambda}(.)$, $\hat{r}$(Wind + Temp + Noise + Lunar)	6	0.00	1,926.12
$\hat{\lambda}(.)$, $\hat{r}$(Global)	7	1.16	1,925.00
$\hat{\lambda}(.)$, $\hat{r}$(Wind + Temp + Lunar)	5	3.85	1,932.20
$\hat{\lambda}(.)$, $\hat{r}$(Wind + Temp. + Noise + Call Order)	6	10.12	1,936.24
$\hat{\lambda}(.)$, $\hat{r}$(Wind + Noise + Lunar)	5	11.12	1,939.47
$\hat{\lambda}(.)$, $\hat{r}$(Wind + Temp. + Noise)	5	11.31	1,939.66
$\hat{\lambda}(.)$, $\hat{r}$(Wind + Temp. + Call Order)	5	12.53	1,940.88
$\hat{\lambda}(.)$, $\hat{r}$(Wind + Lunar)	4	12.92	1,943.46
$\hat{\lambda}(.)$, $\hat{r}$(Wind + Temp.)	4	14.22	1,944.76
$\hat{\lambda}(.)$, $\hat{r}$(Wind + Lunar + Call Order)	5	14.35	1,942.70
$\hat{\lambda}(.)$, $\hat{r}$(Wind + Noise)	4	21.18	1,951.73
$\hat{\lambda}(.)$, $\hat{r}$(Wind + Call Order)	4	21.67	1,952.22
$\hat{\lambda}(.)$, $\hat{r}$(Wind)	3	22.33	1,955.02
$\hat{\lambda}(.)$, $\hat{r}$(Temp. + Noise + Lunar + Call Order)	6	23.15	1,949.27
$\hat{\lambda}(.)$, $\hat{r}$(Temp. + Noise + Lunar)	5	24.23	1,952.58
$\hat{\lambda}(.)$, $\hat{r}$(Noise + Lunar)	4	30.38	1,960.93
$\hat{\lambda}(.)$, $\hat{r}$(Noise + Lunar + Call Order)	5	30.45	1,958.80
$\hat{\lambda}(.)$, $\hat{r}$(Temp. + Noise + Call Order)	5	35.61	1,963.96
$\hat{\lambda}(.)$, $\hat{r}$(Temp. + Lunar)	4	38.28	1,968.82
$\hat{\lambda}(.)$, $\hat{r}$(Lunar + Call Order)	4	39.49	1,970.03
$\hat{\lambda}(.)$, $\hat{r}$(Lunar)	3	40.87	1,973.57
$\hat{\lambda}(.)$, $\hat{r}$(Noise + Call Order)	4	41.19	1,971.73
$\hat{\lambda}(.)$, $\hat{r}$(Temp. + Noise)	4	41.56	1,972.11
$\hat{\lambda}(.)$, $\hat{r}$(Noise)	3	45.28	1,977.98
$\hat{\lambda}(.)$, $\hat{r}$(Temp. + Call Order)	4	46.25	1,976.79
$\hat{\lambda}(.)$, $\hat{r}$(Call Order)	3	48.78	1,981.48
$\hat{\lambda}(.)$, $\hat{r}$(Temp.)	3	54.36	1,987.05
$\hat{\lambda}(.)$, $\hat{r}(.)$	2	55.17	1,989.98
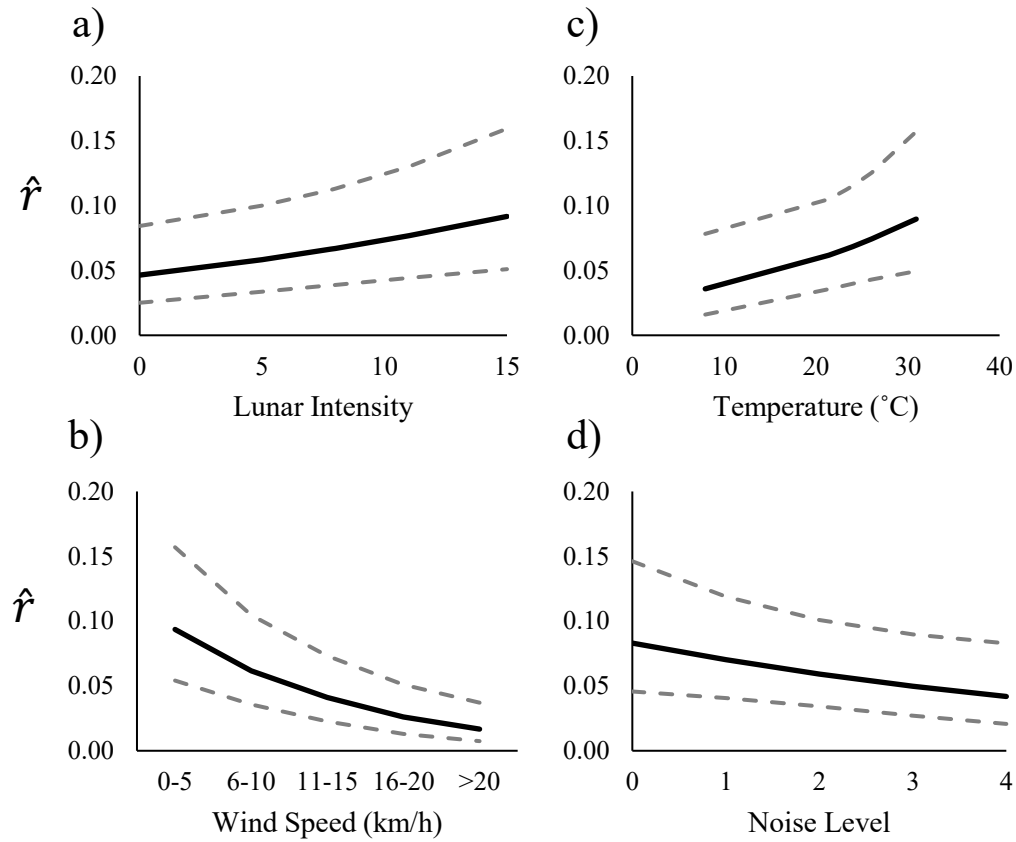
Figure B1. Estimated influences on individual black rail (*Laterallus jamaicensis*) detection. Shown are the estimated relationships (solid black lines), and 95% confidence intervals (broken gray lines), of covariates influencing detection of individual black rails ($\hat{r}$) at 6 sites across the Texas coast. Covariates were a) moon phase (lunar intensity) that ranged from no moon (0) to full moon (15), b) wind speed in five continuous discrete ranges of wind speed, c) the continuous random factor of temperature, and the discrete random variable ambient noise (noise level) which ranged from no ambient little ambient noise (1) to intense ambient noise (5).

APPENDIX C

Below are the results of a model selection analysis on zero-inflated Poisson abundance

models estimated with the data reported in the text.

Table C1. Model selection analysis for multi-season zero-inflated Poisson *N*-mixture models of black rail (*Laterallus jamaicensis*) abundance. Primary periods were 2015 and 2016 and secondary periods were 3 to 8 repeated call broadcast surveys from March to May (2015 and 2016). Included were combinations of multiscale abundance ($\hat{\lambda}$) covariates (point level and site level), a binomial recruitment ($\hat{\gamma}$) influence, constant apparent survival ($\hat{\omega}$), and individual detection probability ($\hat{r}$) influences. Point level covariates were: percent cover of non-*Spartina* herbaceous species (herb.), *Spartina* species (*spartina*), and woody species (woody); and if points were grazed (grazed). Site level covariates were: percent cover of intermediate marsh (INTM) and open water. Recruitment was influenced by a binomial covariate where unburned was the reference category. Influences on $\hat{r}$ were wind speed (wind), lunar phase (lunar), average survey temperature (temp.), and ambient noise (noise). The zero-inflated parameter ($\hat{\delta}$) was used to fit each model. Included in the table are model statements (Model), number of parameters (*K*), and the difference between the top ranked model AIC and model$_i$'s AIC (ΔAIC), the model deviance (deviance), and each model's estimated Nagelkerke's R^2 (R^2).

Model	*K*	ΔAIC	Deviance	R^2
$\hat{\lambda}$(herb. + spartina + woody + graze + INTM + open water), $\hat{\gamma}$(burned), $\hat{\omega}$(.), $\hat{r}$(wind + temp. + lunar + noise), $\hat{\delta}$	16	0.00	1,466.98	0.36
$\hat{\lambda}$(herb. + spartina + woody + INTM), $\hat{\gamma}$(burned), $\hat{\omega}$(.), $\hat{r}$(wind + temp. + lunar + noise), $\hat{\delta}$	14	1.98	1,472.96	0.35
$\hat{\lambda}$(herb. + spartina + INTM), $\hat{\gamma}$(burned), $\hat{\omega}$(.), $\hat{r}$(wind + temp. + lunar + noise) $\hat{\delta}$	13	4.54	1,477.53	0.34
$\hat{\lambda}$(spartina + woody + graze + INTM + open water), $\hat{\gamma}$(burned), $\hat{\omega}$(.), $\hat{r}$(wind + temp. + lunar + noise) $\hat{\delta}$	15	5.22	1,474.20	0.35
$\hat{\lambda}$(spartina + INTM), $\hat{\gamma}$(burned), $\hat{\omega}$(.), $\hat{r}$(wind + temp. + lunar + noise) $\hat{\delta}$	12	8.21	1,483.20	0.33

Table C1 continued.

Model	K	ΔAIC	Deviance	R^2
$\hat\lambda$(spartina + woody + INTM), $\hat\gamma$(burned), $\hat{w}$(.), $\hat{r}$(wind + temp. + lunar + noise) $\hat{\hat\delta}$	13	9.37	1,482.35	0.33
$\hat\lambda$(herb. + spartina), $\hat\gamma$(burned), $\hat{w}$(.), $\hat{r}$(wind + temp. + lunar + noise) $\hat{\hat\delta}$	12	14.66	1,489.64	0.31
$\hat\lambda$(herb + spartina + woody + graze), $\hat\gamma$(burned), $\hat{w}$(.), $\hat{r}$(wind + temp. + lunar + noise) $\hat{\hat\delta}$	14	16.67	1,487.66	0.32
$\hat\lambda$(herb. + woody + graze + INTM + open water), $\hat\gamma$(burned), $\hat{w}$(.), $\hat{r}$(wind + temp. + lunar + noise) $\hat{\hat\delta}$	15	26.01	1,494.98	0.30
$\hat\lambda$(spartina), $\hat\gamma$(burned), $\hat{w}$(.), $\hat{r}$(wind + temp. + lunar + noise) $\hat{\hat\delta}$	11	26.20	1,503.15	0.28
$\hat\lambda$(herb. + woody + INTM), $\hat\gamma$(burned), $\hat{w}$(.), $\hat{r}$(wind + temp. + lunar + noise) $\hat{\delta}$	13	36.20	1,509.18	0.27
$\hat\lambda$(INTM + open water), $\hat\gamma$(burned), $\hat{w}$(.), $\hat{r}$(wind + temp. + lunar + noise) $\hat{\hat\delta}$	12	43.70	1,518.70	0.25
$\hat\lambda$ (INTM), $\hat\gamma$(burned), $\hat{w}$(.), $\hat{r}$(wind + temp. + lunar + noise) $\hat{\hat\delta}$	11	52.20	1,529.17	0.22
$\hat\lambda$(open water), $\hat\gamma$(burned), $\hat{w}$(.), $\hat{r}$(wind + temp. + lunar + noise) $\hat{\delta}$	11	58.30	1,535.33	0.20
$\hat\lambda$(herb.), $\hat\gamma$(burned), $\hat{w}$(.), $\hat{r}$(wind + temp. + lunar + noise) $\hat{\delta}$	11	59.10	1,536.07	0.20
$\hat\lambda$(woody), $\hat\gamma$(burned), $\hat{w}$(.), $\hat{r}$(wind + temp. + lunar + noise) $\hat{\hat\delta}$	11	61.60	1,538.611	0.19

Table C1 continued.

Model	K	ΔAIC	Deviance	R^2
$\hat{\lambda}$(graze), $\hat{\gamma}$(burned), $\hat{w}$(.), $\hat{r}$ (wind + temp. + lunar + noise) $\hat{\delta}$	11	68.90	1,545.86	0.18
$\hat{\lambda}$(.), $\hat{\gamma}$(burned), $\hat{w}$(.), $\hat{r}$(wind + temp. + lunar + noise) $\hat{\delta}$	9	79.00	1,559.99	0.14
$\hat{\lambda}$(.),$\hat{\gamma}$(.), $\hat{w}$(.),$\hat{r}$(.),$\hat{\delta}$	5	115.99	1,604.97	0.00

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