

RESEARCH ARTICLE

Abundance estimates of eastern black rails in southeastern Colorado

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Abstract

The eastern black rail (*Laterallus jamaicensis jamaicensis*), a federally threatened subspecies, is cryptic and difficult to study. Once found across the eastern United States, eastern black rails currently occupy only a few interior regions and are largely limited to coastal marshes. Black rails elusive nature and patchy distributions have made abundance estimation difficult and occupancy modeling has been the primary method for monitoring population trajectory. In southeastern Colorado, one of the most prominent interior regions still occupied by eastern black rails, they are relatively common. We used detections from surveys conducted in 2019, 2020, 2022, and 2023 to estimate eastern black rail abundance along the Arkansas River in Colorado. Estimates were produced using a zero-inflated N-mixture model in a Bayesian framework. Our study confirmed predictors from previous work on black rail occupancy and abundance also predict detection, occupancy, and abundance of black rails in southeastern Colorado, though the relationships differ for predictors relative to other parts of the range. We found detection probability increased later in the season and later at night but decreased with ambient noise. We found occupancy increased with residual vegetation height and detection of Virginia rails (*Rallus limicola*). We found abundance increased with the height of live emergent vegetation and surrounding wetland cover but decreased

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with distance to a large wetland. We estimated 129 to 180 (\bar{x} = 160) eastern black rails at our surveyed point locations along the Arkansas River. Our results indicated that southeastern Colorado is hosting high numbers of eastern black rails at survey locations. The results of our work will inform future monitoring efforts and will allow for an improved understanding of management priorities for eastern black rails in southeastern Colorado.

KEYWORDS

abundance, call-broadcast surveys, eastern black rail, *Laterallus jamaicensis jamaicensis*, population monitoring, threatened and endangered species

Identification of effective monitoring methods for cryptic species is critical in detecting declining populations before they reach a point where meaningful recovery efforts can be implemented (Conway and Gibbs 2005, Willacy et al. 2015). However, cryptic traits, such as nocturnal and secretive behaviors can make traditional population monitoring techniques difficult. Traditional methods like capture-mark-recapture can be ineffective for species that are hard to capture or observe (Royle 2004). However, statistical advances have increased our ability to estimate the abundance of rare species while accounting for imperfect detection, including situations with unmarked individuals (Royle 2004). Advances in estimation methods have led to the successful estimation of abundance in small or cryptic populations (Vanausdall et al. 2022). However, estimation approaches have also been shown to result in imprecise estimates in some cases, highlighting the need for species-specific considerations (Couturier et al. 2013, Ward et al. 2017).

The eastern black rail (*Laterallus jamaicensis jamaicensis*; hereafter black rail) is a cryptic subspecies once found throughout most of the eastern United States but is now only known to occur in a few coastal wetlands and inland areas (U.S. Fish and Wildlife Service 2019). The smallest rail in North America, black rails inhabit wetlands with dense vegetation and are rarely observed flying (U.S. Fish and Wildlife Service 2019). Due to the black rail's elusive traits, visual observations of the species are uncommon, and detections are almost exclusively auditory (Runde et al. 1990). The inability to directly observe black rails makes them among the most understudied birds in North America (U.S. Fish and Wildlife Service 2019). Recent research efforts have identified range-wide population declines and loss, which ultimately resulted in listing the black rail as federally threatened (Watts 2016, Fish and Service 2020).

In 2018, Colorado Parks and Wildlife (CPW) began monitoring breeding black rails in southeastern Colorado. Unlike in coastal systems where black rail occupancy estimates range from 0.06 to 0.26, surveys in Colorado have found occupancy of about 0.7 in available habitat near the lower Arkansas River (Tolliver et al. 2019, Watts et al. 2021, L. Rossi and J. Runge, Colorado Parks and Wildlife, unpublished report). When nearly all surveyed properties are occupied, abundance becomes a more useful metric than occupancy for population monitoring (Couturier et al. 2013, Ward et al. 2017).

Few studies have attempted to estimate black rail abundance, and past efforts have had varying success. Abundance estimates of the California black rail (*Laterallus jamaicensis cortuniculus*) have been attempted by using distance sampling, density conversions, and relative abundance counts (Evens et al. 1991, Spautz et al. 2005, Conway and Sulzman 2007, Hinojosa-Huerta et al. 2013). In Texas, abundance estimates based on N-mixture models averaged 0.98 to 1.13 black rails/point (Tolliver et al. 2019). However, based on low detection probabilities (0.19 ± 0.02), the authors suggested their abundance estimates may be biased high (Tolliver et al. 2019). In the Chesapeake Bay, abundance estimates from N-mixture models averaged of 0.26 ± 0.02 black rails/point in 2014, which the authors suggest may be inflated due to the structure of detections (Watts et al. 2021).

We set out to facilitate conservation and management efforts for black rails in southeastern Colorado by 1) identifying an effective approach for abundance estimation and, 2) using this abundance estimation approach to examine habitat-based predictors of black rail abundance exploring characteristics that have been found to be important elsewhere in the species range. Our results will help inform future monitoring efforts and will provide valuable information to management decisions in southeastern Colorado.

STUDY AREA

Twelve survey properties on public land were identified using data from the National Wetlands Inventory and Colorado Natural Heritage Program along with public-lands data and local knowledge. We included all emergent freshwater wetland classes: PEM1A (temporarily flooded), PEM1B (saturated), PEM1C (seasonally flooded), PEM1F (semi-permanently flooded), PEM1G (intermittently exposed), PEM1H (permanently flooded), and PSS (shrub-dominated wetlands), but not forested wetlands (PFO). Although initial efforts were focused on public lands, we gained access to one private property and began surveying additional points in 2022. Habitat on the private property met the same criteria as the initial sampling frame selection.

Surveys were conducted from 2019 to 2020 and 2022 to 2023. All 13 properties were within a 20-km buffer around the Arkansas River in southeastern Colorado. In a 2018 pilot study 12 properties were surveyed, identified using the above criteria. From 2019 to 2022, Colorado Parks and Wildlife limited surveys to properties that were occupied in 2018, excluding the private property added in 2022. Survey points within the 13 properties mentioned above were not limited to occupied survey points. In 2023 we surveyed properties that were unoccupied in 2018, but which contained potential black rail habitat. As a result, we surveyed 9 properties in all 4 years, one property was only surveyed in 2022 and 2023, and 3 properties were only surveyed in 2023. The selected properties were within Bent ($n = 5$), Otero ($n = 4$), and Prowers ($n = 4$) counties (Figure 1). All the properties in Bent County were surveyed for 4 years. In Otero County, 3 properties were surveyed for 4 years, 1 property for 1 year. In Prowers County 2 properties were surveyed for 1 year, 1 property was surveyed for 2 years, and 1 property was surveyed for 4 years.

The Lower Arkansas River, associated water storage reservoirs, and surrounding agricultural irrigation systems feed most freshwater emergent wetlands in our study area. The entire system is fed by snowpack run-off that is managed for irrigation. Wetlands typically did not have water control structures and water levels varied throughout the season. Water-level variation differed depending on wetland size and proximity to larger bodies of water, and we were unable to measure water-level fluctuation throughout the season. The wetlands on each property varied from <1 to 426 ha, and most wetlands (83%) were <30 ha. The predominant emergent vegetation was cattail (*Typha* spp.) and hardstem bulrush (*Schoenoplectus acutus*). The average water depth at surveyed points was 8.93 cm (95% CI = 6.42–11.44 cm; Table 1). The surrounding land in the 3 surveyed counties was predominantly privately owned (73%) and was dominated by cropland and grasslands (U.S. Geological Survey Gap Analysis Project [USGSGAP] 2022). In the 3 surveyed counties, the selected properties accounted for 12% of all mapped freshwater emergent wetlands and 29% of the state and federally owned freshwater emergent wetlands (USGSGAP 2022, U.S. Fish and Wildlife Service 2023). Over the last 10 years (2013 to 2023) between May and August, the study counties experienced an average temperature of 22°C and an average precipitation of 24.13 cm (National Center for Environmental Information 2023).

METHODS

Black rail surveys

At all 13 properties, we placed the first survey point based on an access point and subsequent survey points were placed systematically along the edge of the wetland where cattail or bulrush began (Figure 2). All survey

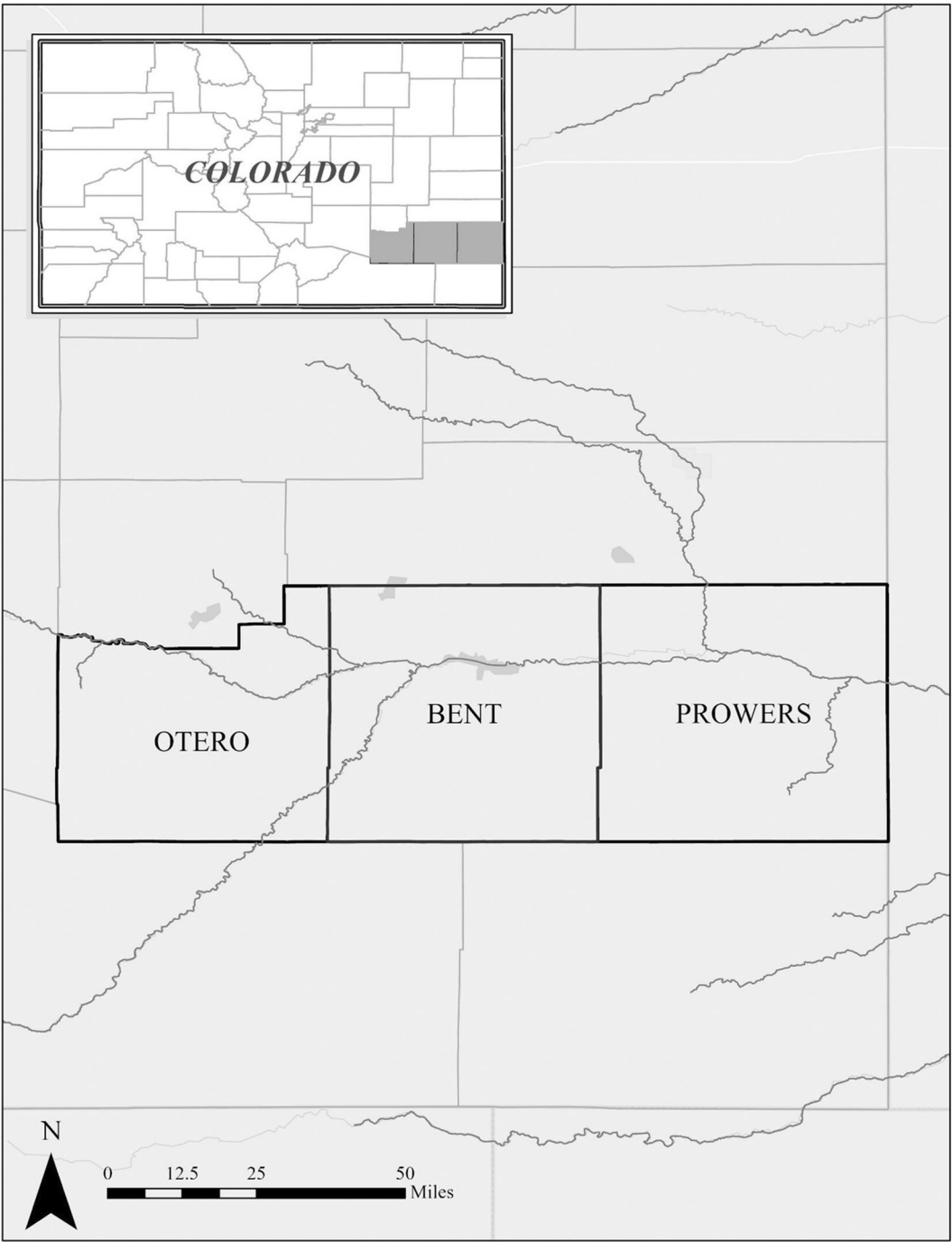


FIGURE 1 Counties where we surveyed properties for eastern black rails (*Laterallus jamaicensis jamaicensis*) between April 15 and June 15 in 2019, 2020, 2022, and 2023. Thirteen properties were surveyed across the counties but are not shown to protect local black rail populations. Dark gray polygons represent large bodies of water.

TABLE 1 Summary statistics of each predictor variable collected within wetlands surveyed for eastern black rail (*Laterallus jamaicensis jamaicensis*) near the Arkansas River in southeastern Colorado, 2019 to 2023.

	Mean	Median	Minimum	Maximum	SD
Water depth (cm)	8.93	1.67	0.00	88.00	15.59
Live emergent vegetation (cm)	181.37	181.83	0.00	331.67	59.12
Residual vegetation (cm)	49.91	49.5	0.00	150.67	36.90
Wetland cover (ha within 200 m)	3	2.77	0.2	12	2
Distance to a large wetland (km)	10.89	1.46	0.00	42.46	15.37
Hours since sunset	1.12	1.01	-2.52	6.98	1.98
Noise	1.18	1	0.00	4.00	0.95
Moon phase	7.50	8	0.00	15.00	4.47

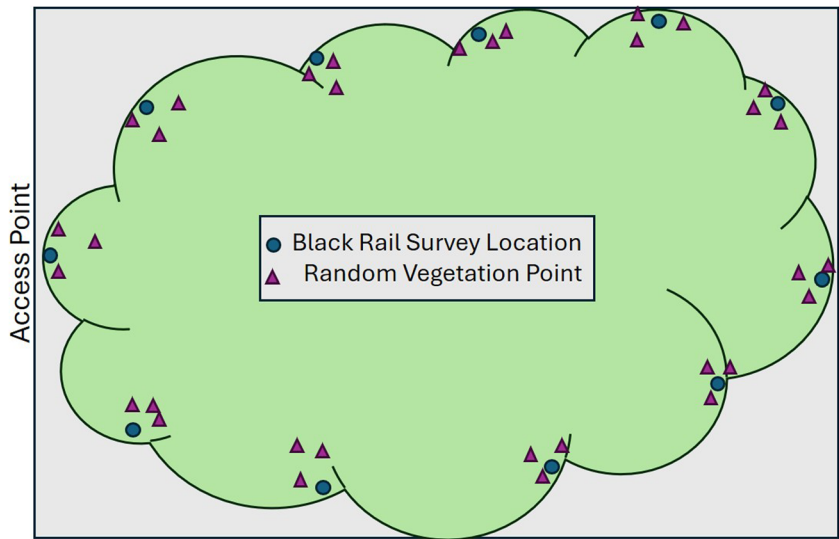


FIGURE 2 An example wetland, not drawn to scale, demonstrating the layout of locations surveyed for eastern black rails (*Laterallus jamaicensis jamaicensis*; blue circle) around the edge of the wetland (the green shape in the middle of the gray property rectangle), each survey location is paired with 3 random vegetation points (purple triangles).

points were separated by at least 400 m to reduce the chance of double counting individuals at multiple survey points (Conway 2011). Survey points were placed to maximize both accessibility and survey coverage. The number of survey points at each property ranged from 1 to 15 with a mean of 8 points per property. In small wetlands our survey points covered up to 100% of the wetland. In larger wetlands, our surveys covered less than the entire wetland area (e.g., ~1% of the largest wetland). Peak calling activity of marsh birds occurs during the courtship and egg-laying period in spring and early summer, and the ideal survey window for southeast Colorado is 15 April to 31 May (Conway 2011). We extended survey efforts to include 1 June to 15 June, totaling 4 15-day survey windows: 15 April to 30 April, 1 May to 15 May, 16 May to 31 May, and 1 June to 15 June. One

survey was completed at each survey point during each 15-day period and repeat surveys were separated by ≥ 10 days. Multiple surveys were conducted at each point across the season because black rails have a low detection rate, and multiple surveys help confirm presence (Conway et al. 2004, Tolliver et al. 2019). Surveys were conducted between 2 hours before sunset and 7 hours after sunset. Surveys were limited to evening and night periods based on preliminary surveys that demonstrated increased detection during that time relative to morning (L. Rossi and J. Runge, Colorado Parks and Wildlife, unpublished report). Surveys were not conducted if winds exceeded 20 km/hr (12 mph) or in heavy rain or fog (Conway 2011). To reduce temporal bias, we conducted successive surveys during different times of the night and, whenever possible, routes were reversed between surveys (Hunt et al. 2012).

The surveys started with 5 minutes of passive listening, followed by 4 minutes of active broadcast calling periods and a final passive minute. Black rail detections may increase with both conspecific and heterospecific calls therefore, black rail, Virginia rail (*Rallus limicola*), and sora (*Porzana carolina*) calls were included in our broadcast sequence (Conway et al. 2004, Conway and Nadeau 2010, Conway 2011). We completed the entire 10-minute survey sequence at each point (including the first passive listening period, the active broadcast calling period, and the final passive listening period). The recordings were broadcast using a FOXPRO NX4 speaker (FOXPRO Inc., Lewistown, PA, USA), and the speaker was not rotated during the survey. We standardized the speaker volume to 80 to 90 dB 1 m from the speaker using an Extech Sound Level Meter (Nashua, NH, USA; Conway 2011). During the survey, observers recorded individual black rail and Virginia rail detections within an unlimited radius, including a distance category for each observation (observed at 0 to 50 m, 51 to 100 m, 101 to 150 m, and >150 m). Detections were removed from analysis in cases where an observer identified an individual as having been recorded at a previous point.

Observers recorded the date, time, moon phase, and background noise level for each survey. Moon phase was measured on a 15-point scale: 0 representing new moon, 15 representing a full moon (Tolliver et al. 2019). Background noise level was measured on a 4-point scale: 0 representing no noise, 4 representing instances when observers could not hear some birds beyond 25 m (Conway 2011).

Habitat measurements

In 2022 and 2023, we collected habitat measurements at every survey point after the last survey was completed (after 15 June). We collected measurements at 3 random points within a 50-m radius of each survey point (Figure 2). We determined random points by generating a random bearing (0 to 360°) and distance (0 to 50 m), restricting our bearings to those in the direction of the wetland. If a randomly-generated bearing was not in the direction of the wetland, another random bearing was generated. If the bearing pointed into the wetland, but the distance took us past wetland habitat and into the upland, we shortened the distance to keep the random point 2 m within the wetland edge. Although the majority of detections were within 51 to 100 m from the survey point, we chose the smaller radius to reduce wetland disturbance and because our observations suggested placing our vegetation plots within 50 m of the survey point adequately quantified the broader habitat conditions associated with that point. At each random point, we recorded water depth (cm), height of live emergent vegetation (cm), and height (cm) of residual vegetation (dead vegetation from previous growing seasons). Water depth was measured without pressing through the substrate. Height of live emergent vegetation was measured at the droop height of emergent vegetation. The height of residual vegetation was measured as the height at which dead emergent vegetation lay at greater than 45 degrees. The measurements from the 3 random points were averaged to generate one measurement for each survey point. We measured wetland cover by digitizing wetland boundaries using ArcGIS Pro. We measured the hectares of wetland cover within a 200-m radius circular plot of each survey point. We also used ArcGIS Pro to measure the distance (km) from each survey point to the nearest wetland >30 ha in size (hereafter large wetland).

Data analysis

We estimated abundance using a zero-inflated Poisson N-mixture model using a Bayesian framework, which included estimation of point-level abundance (λ), individual-level detection probability (r), and point-level occupancy (Ψ ; Wenger and Freeman 2008). In addition to being able to handle the excess zeros common for rare and elusive species such as black rails, our approach allowed us to directly model predictors of both abundance and occupancy (i.e., rather than treating occupancy as a derived parameter in the analysis) in addition to detection probability (Wenger and Freeman 2008). We used data across all years in the analysis, and we accounted for repeat sampling of survey points among years by using survey point ID as a random intercept on occupancy.

Average live emergent vegetation height and average residual vegetation height were correlated with one another (Pearson's pairwise $R^2 = 0.49$), so we did not include both in the occupancy or abundance estimation (Butler et al. 2023). Based on confidence interval bounds and parameter significance in preliminary model runs, we retained residual vegetation height in the occupancy modeling and live emergent vegetation in the abundance modeling. For occupancy, we included covariates of year, Virginia rail detection, water depth, wetland cover, distance to a large wetland (km), and residual vegetation height (cm).

For abundance, we included year, wetland cover, distance to a large wetland (km), and live emergent vegetation height (cm) as covariates. The predictors of black rail abundance are less well known across the bird's range, and we selected these specific metrics based on expert opinions on black rail ecology.

Detection was modeled as a logit-linear function of survey date, noise level, moon phase, and survey time. Survey date was treated as a binary covariate, either conducted in the first (on or before 15 May) or second half of the survey season (after 15 May). We chose to turn this into a binary covariate instead of using each survey period (4 levels) individually based on our observations in the field that vocalization rates differed before and after May 15th. Noise level and moon phase were standardized, and the time of the survey was converted to hours since sunset. We selected noise level based on previous marsh bird survey work (Conway 2011), and we selected moon phase based on work in the Chesapeake Bay and Texas (Tolliver et al. 2019, Watts et al. 2021). We chose hours since sunset based on experience in our study area suggesting that black rails were more likely to vocalize after sunset, which differs from other parts of their range. Data were standardized across all years in the dataset [$x^* = (x - \bar{x})/sd(x)$]. For categorical variables, each level was assigned an increasing number (level 1 is 1, level 2 is 2), and those numbers were used to calculate the standardized values. We chose to standardize noise level even though it had a relatively small number of levels (4) to keep it consistent with the other standardized variables.

Occupancy was modeled as a logit-linear function of year, water depth, Virginia rail detection, residual vegetation height, standardized wetland cover, and distance to a large wetland. Year was treated as a continuous value. Eastern black rails are wetland-associated birds, and we hypothesized proximity to larger wetlands would increase occupancy of neighboring wetlands. Eastern black rails are known to respond to wetland structure and water depth in other parts of their range, which is why we included water depth, wetland cover, and residual vegetation height (Legare and Eddleman 2001, Tolliver et al. 2019, Butler et al. 2023). Virginia rail detection and water depth were included as binary covariates, with water depth either ≤ 10 cm or > 10 cm, as black rails are known to be limited to sites with < 6 cm water (U.S. Fish and Wildlife Service 2019). We increased the cutoff to 10 cm to accommodate potential fluctuation during the survey period. Virginia rails rather than sora were used as a covariate because Virginia rails breed locally and sora migrate farther north to breed, and Virginia rails have been found to have positive co-occurrence with black rails in smaller wetlands (Richmond et al. 2010). Abundance was modeled as a log-linear function of year, live emergent vegetation height, standardized wetland cover, and distance to a large wetland. Year was included as a continuous value. Wetland cover was standardized using the standardization equation above.

Covariates were collected in all years, but water depth, live emergent vegetation height, and residual vegetation height were not collected in 2019 or 2020; values for these variables were missing from 4 sites sampled in 2022 or 2023. Rather than fit separate models for all 4 years, we chose to impute the median value of the covariate for

cases with missing covariates (Nakagawa and Freckleton 2011). Ultimately, our approach is somewhat conservative with respect to detecting relationships between occupancy or abundance and the covariates (i.e., it essentially relies on the information present in 2022 and 2023 to drive any relationships) but does take advantage of the larger dataset for making inferences about occupancy, abundance, and detection. Given that our goal was to make inferences on the relative strength of a small set of predictor variables that we determined *a priori*, we fit a single global model with all covariates of interest (Hooten and Hobbs 2015, Bolker 2024). We used coefficient point estimates and whether 95% credible intervals overlapped zero to make inferences about covariate importance. If a covariate credible interval overlapped zero, we inferred that it was not a strong predictor.

In addition to examining covariate influence on abundance, we estimated total abundance of black rails as a derived parameter. Abundance was estimated across 68 survey points and points that were only surveyed one year were excluded from abundance estimation. Single-year survey points were excluded because we lacked information about year-to-year variation at these points and abundance could be over- or under-inflated.

We fit the single, global model to 2 different subsets of the entire dataset. The first considered all 10 minutes of the survey, including both the passive and broadcast periods. The second considered only the passive period (first 5 minutes) of the survey. We fit the passive-period-only model to ensure that including the active broadcast periods, which could potentially draw individuals from outside our sampling unit, did not unreasonably inflate abundance estimates or change our conclusions about covariate effects (Conway 2011). We placed vague priors on all covariates for the first 2 models because our study was performed in a new area and black rail behavior has been shown to vary across the range (Reynard 1974, Legare et al. 1999, Tolliver et al. 2019, Watts et al. 2021, Butler et al. 2023). All priors for occupancy and detection probability parameters were normally distributed around 0 with a standard deviation of 1.92 (precision of 0.27), which is appropriately vague on the logit scale (Northrup and Gerber 2018). Priors for abundance parameters were normally distributed around 0 with a standard deviation of 10 (precision of 0.01), which is vague on the log scale. We fit a third model using detections made during the entire 10-minute segment but used informative priors for covariates when we felt we had sufficient information from previous studies. Covariate estimates and abundance estimates from the second and third models were similar to those from the model that incorporated all 10 minutes and vague priors. However, the precision of estimates from the first model was much better when compared to the model that only included the first 5 minutes. We therefore present the results from the model that includes all 10 minutes and vague priors below. We have provided the JAGS model and estimates from the second and third model as well as a description of the informative priors (see Tables S1–S6, Figure S1, available in Supporting Information).

We fit all models using jagsUI (Kellner et al. 2021) in Rstudio (R v. 4.3.1, R Core Team 2023). We used the Gelman Rubin statistic and traceplots to diagnose convergence. R-hat values less than 1.01 were considered to indicate model convergence (Gelman and Rubin 1992). We diagnosed our model's goodness of fit by applying posterior predictive assessments. Bayesian *P*-values around 0.5 indicate good model fit using a chi-square statistic (Gelman et al. 1996). Our model was run using 3 Monte Carlo Markov Chains of 150,000 iterations, resulting in 21,000 samples after a 10,000 burn-in period and a thinning rate every 20 samples.

RESULTS

In all, we conducted surveys at 80 unique survey points over the 4 years. The number of survey points varied by year and ranged from a minimum of 47 in 2019 to a maximum of 80 in 2023 (Table 2). Black rail surveys were repeated 2 to 4 times at each survey point (Table 2). In total, we conducted 873 surveys and detected 590 black rails across all surveys. We heard a maximum of 7 black rails in a single survey (\bar{x} = 0.69, SD = 1.2).

On average, survey points were <11 km away from a large wetland, had ≤10 cm of water, relatively tall live and residual vegetation (181.37 cm, 49.91 cm respectively), and less than 5 ha wetland cover within a 200 m radius

(Table 1). On average, surveys took place <2 hours after sunset, with low noise, and with either a first-quarter or third-quarter moon (Table 1). Virginia rails were detected at 40% of the survey points.

We estimated an average individual detection probability of 0.30 (SD = 0.03, 95% CI = 0.23–0.36). Detection was affected by survey period, hours since sunset, and noise (Table 3). When only the passive minutes of surveys were analyzed, the effects for survey period, hours since sunset, and noise were similar, but moon phase had a negative effect on detection (Table S3, available in Supporting Information). Detection increased 6.6 times after 15 May (i.e., odds ratio = 6.6; Table 3, Figure 3). The odds ratio for hours since sunset meant that detection increased 1.4 times for every hour increase after sunset. Detection decreased 1.7 times with each standard deviation increase in noise (Table 3, Figure 3).

We estimated an average occupancy of 0.73 (SD = 0.03, 95% CI = 0.68–0.79). Occupancy increased with detection of Virginia rail and residual vegetation height. We did not find an effect for year, water depth, wetland cover, or distance to a large wetland (Table 4). Occupancy increased 30.9 times when a Virginia rail was detected (Table 4, Figure 4). Occupancy increased 1.04 times with each centimeter increase in residual vegetation height.

We estimated an average of 2.26 birds/point (SD = 0.25, 95% CI = 1.90–2.86). The total number of birds across points ranged from a low of 129 (CI = 101–175) in 2023 to a high of 180 (CI = 151–227) in 2020 (Figure 5). Abundance was affected by live emergent vegetation height, wetland cover, and distance to a large wetland (Table 5). We did not find an effect of year. Abundance was 1.5 times greater with each meter increase in live emergent vegetation, 1.14 times greater with each standard deviation increase in wetland cover, and 1.02 times lower with each kilometer increase away from a large wetland (Table 5, Figure 6). All parameter estimates showed strong convergence (R-hat values ≤ 1.001). Additionally, our posterior predictive assessment showed strong goodness-of-fit (Bayesian P -value = 0.44), meaning simulated and observed data showed similar deviance.

TABLE 2 Counts of number of survey points, and the number of survey points with 2, 3, or 4 replicate surveys for eastern black rails (*Laterallus jamaicensis jamaicensis*) in southeastern Colorado, 2019 to 2023.

Year	Number of survey points	Survey points with 2 replicate surveys	Survey points with 3 replicate surveys	Survey points with 4 replicate surveys
2019	47	13	34	0
2020	59	1	58	0
2022	68	9	2	57
2023	80	0	3	77

TABLE 3 Mean, standard deviation, and 95% credible interval of the posterior distribution for coefficient estimates of detection probability of eastern black rails (*Laterallus jamaicensis jamaicensis*) in southeastern Colorado, 2019 to 2023. Noise and moon phase were standardized prior to analysis.

Covariate	Mean	SD	95% Credible Interval
Survey period (before or after May 15)	1.89	0.29	1.36–2.50
Hours since sunset	0.31	0.06	0.20–0.44
Noise	–0.55	0.12	–0.81––0.32
Moon phase	–0.01	0.02	–0.06–0.04

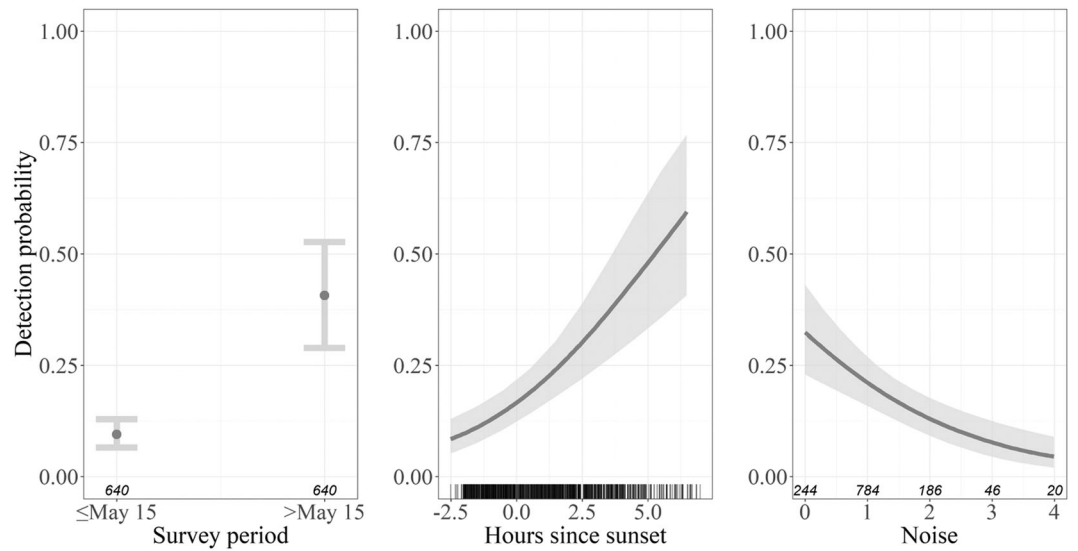


FIGURE 3 Effect of survey period, hours since sunset, and noise on detection probability of individual eastern black rails (*Laterallus jamaicensis jamaicensis*) in southeastern Colorado, 2019 to 2023. The 95% credible intervals are provided as error bars and in the shaded area. The number of raw measurements is shown near the x-axis in panels 1 and 3, while tick marks in panel 2 represent raw measurement values. Estimates for individual covariates were made using the median values for all other covariates (survey period, hours since sunset, noise, and moon).

TABLE 4 Occupancy coefficient estimates for eastern black rails (*Laterallus jamaicensis jamaicensis*) in southeastern Colorado, 2019 to 2023. Wetland cover was standardized prior to analysis.

Covariate	Mean	SD	95% Credible Interval
Residual vegetation height (cm)	0.04	0.01	0.02–0.07
Year	−0.53	0.43	−1.41–0.30
Detection of Virginia rail	3.43	0.87	1.81–5.25
Water depth (cm)	−0.28	0.98	−2.22–1.65
Wetland cover (ha within 200 m)	0.88	0.69	−0.35–2.34
Distance to a large wetland (km)	−0.01	0.04	−0.09–0.06

DISCUSSION

Our study confirmed predictors from previous work on black rails also predict detection, occupancy, and abundance of black rails in southeastern Colorado, though the relationships differed for some predictors relative to other parts of the range. Our model convergence and goodness of fit demonstrated that the zero-inflated Poisson N-mixture model is a reasonable method for black rail population estimation in southeastern Colorado. The insights into the habitat characteristics associated with higher black rail abundance will help inform management priorities. Additionally, the successful application of the zero-inflated Poisson N-mixture model in Colorado will inform future monitoring efforts and could potentially be applied to monitoring across the range.

We found individual detection probability in Colorado to be higher than estimates found in Texas and the Chesapeake Bay (Tolliver et al. 2019, Watts et al. 2021). We also found that detection was greater in the second half

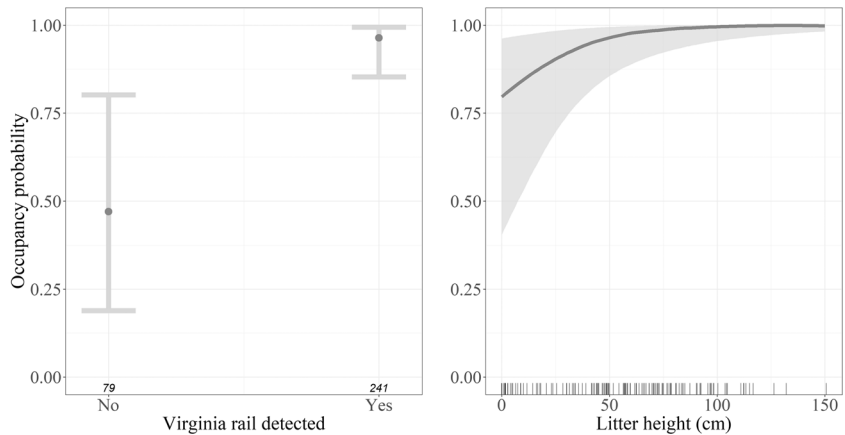


FIGURE 4 Effect of Virginia rail (*Rallus limicola*) detection and residual vegetation height (cm) on occupancy probability of eastern black rails (*Laterallus jamaicensis jamaicensis*) in southeastern Colorado, 2019 to 2023. The 95% credible intervals are provided as error bars and the shaded area. Positive or negative Virginia rail detection and litter height raw measurements are provided on the x-axis. Estimates for individual covariates were made in the presence of Virginia rails and using median values for all other covariates (year, residual vegetation height, water depth, wetland coverage, and distance to a large wetland).

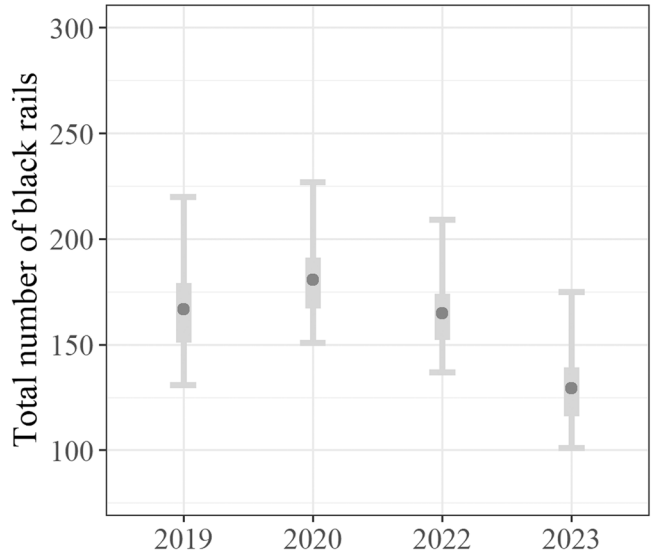


FIGURE 5 The estimated number of eastern black rails (*Laterallus jamaicensis jamaicensis*) at 68 surveyed locations in southeastern Colorado, 2019 to 2023. Survey points that were only surveyed one year were excluded from this estimate. Abundance ranged from 129 in 2023 to 180 in 2020. 95% and 50% credible intervals are provided as error bars.

of the season, later in the night, and in situations with less noise. Our results were consistent with findings in Texas, where detection increases later in the survey season, from dusk to night hours, and in surveys with less noise (Tolliver et al. 2019, Butler et al. 2023). However, our results are different from findings in the Chesapeake Bay, where black rail detection probability decreases later in the season (Watts et al. 2021), and in Florida where black rails were observed calling most often within 30 minutes of sunset (Legare et al. 1999). Our findings indicated variation in

TABLE 5 Abundance coefficient estimates for eastern black rails (*Laterallus jamaicensis jamaicensis*) in southeastern Colorado, 2019 to 2023. Wetland cover was standardized prior to analysis.

Covariate	Mean	SD	95% Credible Interval
Live emergent vegetation height (cm)	0.005	0.002	0.001–0.01
Year	−0.07	0.07	−0.20–0.07
Wetland cover (ha within 200 m)	0.13	0.07	0.003–0.26
Distance to a large wetland (km)	−0.02	0.01	−0.03–−0.01

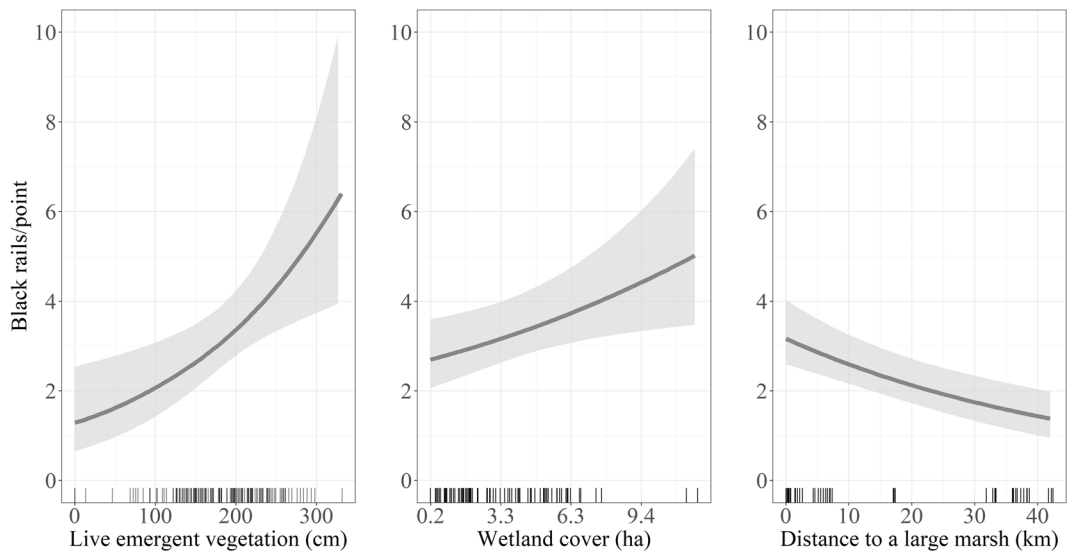


FIGURE 6 Effect of live emergent vegetation (cm), wetland cover (ha), and distance to a large wetland (km) on eastern black rail (*Laterallus jamaicensis jamaicensis*) abundance in southeastern Colorado, 2019 to 2023. The 95% credible intervals are provided in the shaded area. Raw measurements are provided on the x-axis. Estimates for individual covariates were made using the median values for all other covariates (year, live emergent vegetation height, wetland coverage, and distance to a large wetland).

detection patterns across the range and suggest that surveys in southeastern Colorado are most effective when conducted in the second half of the survey season and in nighttime hours as opposed to close to sunset.

We found a non-significant effect of moon phases on black rail detection, though the point estimate suggested a negative effect of later moon phases, and the use of broadcast calls can override that effect by elucidating response calls. Reduced detection when the moon is closer to full may indicate black rails are less likely to call during periods of increased moonlight when predation risk could be higher. Decreased calling during increased moonlight has been found in other bird and mammal species (Prugh and Golden 2014, Clink et al. 2021). Similar to variable detection patterns based on time, the effect of moon varies across the range, showing a positive effect in Texas and a negative effect in the Chesapeake Bay (Tolliver et al. 2019, Watts et al. 2021). Further investigation across the range is important to better understand the effect the moon plays on black rail detection. Understanding this relationship would increase monitoring efficiency.

Occupancy rates in our study were higher than estimates elsewhere in the range, and occupancy at our study sites remained relatively stable through time (Tolliver et al. 2019, Watts et al. 2021, Butler et al. 2023). It is worth

noting that our study design precluded detecting increases in occupancy over time. Because the original surveys were limited to occupied properties, we would be more likely to find decreasing occupancy over the years (Fournier et al. 2019). The fact that year did not conclusively show a negative effect may indicate that black rail occupancy in our sampled sites was stable or increasing.

Black rails were much more likely to be heard when Virginia rails were also detected. Similar results from California may indicate that both species are responding to similar environmental factors (Richmond et al. 2010). Griesse et al. (1980) found Virginia rails in Colorado associated with sites dominated by tall and dense cattail and shallow flooding, which is comparable to our finding that black rail occupancy increased with tall vegetation at survey locations with mean water level <10 cm. Another explanation could be heterospecific attraction between Virginia rails and black rails, a phenomenon that can be found in other wetland bird species (Ward et al. 2010, Brewer 2023). Either reasoning indicates that Virginia rails could potentially act as a good surrogate species for identifying suitable black rail habitat for future restoration efforts, and that Virginia rails can be used as an informative predictor variable when modeling occupancy of black rails.

Black rails nest and forage on the ground, so water depth is known to be a limiting factor for the species (Runde et al. 1990). However, we did not find an effect of water depth on occupancy. Our lack of effect of water depth on occupancy may be because active water management is rare, and most wetlands are fed from agricultural runoff, snowmelt, or rainfall leading to homogeneously shallow water levels across emergent freshwater wetlands in southeastern Colorado. The lack of effect of water depth on occupancy may also indicate that black rails in southeastern Colorado were able to compensate for variable water levels associated with snowmelt runoff by using matted residual vegetation as refuge or a nest substrate. Additional reasons for the lack of observed effect may be the timing of our water measurements occurring after the survey period and that our measurements were limited to 2 of the 4 years of sampling. Additionally, imputing the median value for missing water-level values in 2019 and 2020 may have limited our ability to detect a relationship. The Great Plains are predicted to have more frequent droughts and increased temperature (Ojima et al. 2021). If droughts become more frequent, southeastern Colorado may become more arid, and wetlands may not be able to hold sufficient moisture. In south Florida, extinction rates for black rails were higher when sites dried between years and occupancy was higher in sites with saturated soils (Hines et al. 2023). So, although we did not find an effect of water depth, past work confirms the importance of some inundation for black rails. Results from past work and climate predictions for increased drought in this region indicated that more effort should be put into strategies to maintain water availability on the landscape.

We found black rail occupancy was positively associated with the height of residual vegetation and abundance was positively associated with the height of live emergent vegetation. The relationships we found between residual vegetation height and abundance are confirmatory and do not exclude the other correlated variable from having an impact on the other variable (e.g., we cannot say live emergent vegetation is not associated with residual vegetation).

Our positive relationships between occupancy and abundance and relatively tall vegetation differ from findings elsewhere in the species' range. For example, in Texas a vegetation ceiling height greater than 23 cm was found to decrease occupancy (Butler et al. 2023). Similarly, black rails and black rail nests in Kansas, Texas, and Florida were primarily found in wetlands with emergent vegetation that remained below 1 m (Legare and Eddleman 2001, Kane 2011, Tolliver et al. 2019). Notably, although the height of vegetation in our study differs from that along the coast, the structure formed by the vegetation is similar. Along the coast, and in areas where black rails are found in shorter vegetation, the dominant vegetation is typically bunch forming species such as *Spartina* spp. and *Eleocharis* spp., (Legare and Eddleman 2001, Kane 2011, Tolliver et al. 2019, Butler et al. 2023). *Spartina* spp. and *Eleocharis* spp. form dense overhead cover but leave openings on the ground that can be used as travel corridors for black rails. The same structure, dense overhead coverage with openings underneath, is what we observed in Colorado. Our observations of similar vegetation structure in Colorado and elsewhere in the black rail's range indicate that even though black rails show a different relationship with tall residual and live vegetation in Colorado as compared to the coast, the structure created by either tall live or residual vegetation may be more important than the height

itself. California black rails also inhabit wetlands with tall emergent vegetation characterized by *Typha* spp., where structure may be more important than height (Tsao et al. 2015).

Surrounding wetland cover and distance to a large wetland were not found to affect occupancy, however, they did affect abundance. While larger wetlands can hold more birds than smaller wetlands, larger wetlands may also be less prone to drastic water level changes. We have observed that small wetlands in the area dry quickly, especially when they are isolated from larger wetlands or wetland complexes. Space, as well as unstable water levels, may be the reason for fewer birds in smaller, isolated wetlands. Additionally, we found occupancy was not affected by distance to a large wetland, which may be explained by our limited sample area. All properties were within 20 km of the Arkansas River, and the mean distance to a large wetland was approximately 10 km, meaning there was not much variation in distance to a large wetland. Connectivity and distance were found to be important predictor variables for colonization and occupancy for California black rail (Hall et al. 2018), suggesting that efforts to maintain or create large wetlands or wetland complexes may be more beneficial for black rails in Colorado than restoring isolated wetlands.

Our abundance estimate of 2.26 birds/point was higher than estimates from 2015 and 2016 in Texas along the Gulf of Mexico and 2014 in the Chesapeake Bay, where researchers estimated 0.98 to 1.13 birds/point and 0.26 birds/point, respectively. (Tolliver et al. 2019, Watts et al. 2021). Our estimate is similar to the estimated 1.98 birds/point in the Chesapeake Bay, which was calculated using 50 survey points during the 1990s (Watts et al. 2021). Although we did not observe a consistent decline in abundance across years, we did observe a noticeable drop in abundance estimates in 2023. More than 20% of Colorado was in a severe drought or greater from the spring of 2020 until the fall of 2022, and it is possible we are seeing effects from this drought (National Drought Mitigation Center 2024). As drought is predicted to become more frequent in the Great Plains, consistent monitoring is important to detect potential population declines (Ojima et al. 2021). The quick decline of black rails across their range illustrates that even though Colorado currently hosts a good number of black rails, strong conservation actions may be necessary in Colorado to maintain this population.

MANAGEMENT IMPLICATIONS

Our results demonstrated higher numbers of black rails at sampling locations than in other parts of the range, suggesting that southeastern Colorado is an important region when considering range-wide conservation and management of black rails. More work is needed, however, to extrapolate abundance at our survey sites to an estimate of the larger regional population size. We found the zero-inflated Poisson N-mixture model created reasonable abundance estimates in southeastern Colorado. Future research should investigate the reliability of our estimation technique in areas where black rails are rarer. Our results also demonstrate that surveys should be conducted during situations with less noise, and whenever possible, survey points should be placed strategically to avoid areas with frequent noise interference. We found higher detection later in the survey season and later in the night, indicating that surveys should be prioritized later at night and after 15 May. Variable results from across the range reiterate the regional differences in black rail behavior and show that region-specific studies are important. Our occupancy and abundance results demonstrate that management in southeastern Colorado should focus on maintaining large wetlands that are in close proximity to one another, instead of smaller isolated wetlands. We have also shown that tall and dense vegetation, whether from live emergent vegetation or residual vegetation, is important for black rail occupancy and abundance, suggesting that maintaining dense vegetative cover is important to sustain the black rail habitat in southeastern Colorado.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ETHICS STATEMENT

This research was completed in compliance with a Colorado Parks and Wildlife and U.S. Fish and Wildlife Service Cooperative Agreement under Section 6 of the Endangered Species Act.

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SUPPORTING INFORMATION

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