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Investigating the dispersal routes used by an invasive amphibian, *Lithobates catesbeianus*, in human-dominated landscapes

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Abstract Clarifying how species move across and utilize human-modified landscapes is key to the conservation of declining populations, as well as to the management and control of invasive species. The North American bullfrog (*Lithobates catesbeianus*) is a globally distributed invasive amphibian that has been implicated in the decline of native amphibians across its invasive range and may also act as a transport vector for a number of deadly amphibian pathogens. Identifying the landscape-level features that facilitate or hinder this species as it moves across an ever-changing landscape is necessary to inform control efforts and limit this species' impact on already declining amphibian populations. We conducted surveys of 243 wetlands across the Colorado Front Range and used an information-theoretic approach to evaluate the contribution of wetland-specific characteristics and landscape-level factors in determining the detection of bullfrog populations and breeding bullfrog populations. Specifically, our goal was to determine whether features related to overland dispersal or to the connectivity of wetlands were better predictors of bullfrog occurrence. Our results indicated that landscape-level factors that may either hinder or facilitate overland movement, such as topographic complexity and the density of wetlands, were the best predictors of bullfrog occurrence at the scale of our analysis, rather than characteristics relating to the connectivity of wetlands to lotic waterway systems. We suggest that when considering the control or eradication of this species, efforts should be directed at reducing hydroperiod of wetlands and should target regions with a high density of wetlands and/or low topographic relief.

Keywords Biological invasions · Bullfrog · *Lithobates catesbeianus* · Landscape ecology · Dispersal · Habitat alteration

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Introduction

Anthropogenic activity can have differential impacts on species. While many species respond negatively to anthropogenic influence, others have increased in range as a result of human activities (McKinney and Lockwood 1999). Humans can facilitate this range expansion through at least two major processes: by directly introducing invasive species into new systems, and by modifying the habitat in such a way that favors invasion (McKinney and Lockwood 1999; Rahel 2002). While often relatively benign, invasive species can occasionally have catastrophic negative

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impacts on native species, and thus are considered one of the leading factors contributing to biodiversity loss globally (McKinney and Lockwood 1999; Sala et al. 2000; Rahel 2002). Managing invasive populations is often of concern when considering the conservation of declining populations, emphasizing the importance of understanding how invasive species spread across the landscape to inform eradication efforts or to reduce their spread into new habitats.

Aquatic communities are among the most threatened and highly invaded systems on the planet (Dudgeon et al. 2006; Sala et al. 2000), and large-scale habitat alteration can further facilitate invasion into these systems (e.g. Havel et al. 2005; Johnson et al. 2008; Rahel 2002, 2007). Landscape-level human modification can increase connectivity of aquatic systems across the landscape, which is known to facilitate the dispersal and invasion of highly aquatic species such as fish (e.g. Hohausova et al. 2010; Rahel 2002, 2007). However, fragmentation of the landscape is also known to inhibit movement of more terrestrial invasive species (With 2002). In order to better understand how invasive species move across human-dominated landscapes, studies of animal movement should attempt to capture the complexity of an animal's environment. Often times, straight-line distance measures may not capture the reality an animal faces as it moves across a landscape (Murphey et al. 2010). Including measures such as topography or barriers to dispersal may provide a more accurate picture of how species, especially those that can move either overland or via aquatic systems, disperse in human-dominated landscapes.

Amphibians present an interesting challenge with regard to studying dispersal because they can uniquely use both terrestrial and aquatic systems and are often physiologically constrained to specific habitat types. Additionally, amphibian populations often undergo patterns of localized extinction and re-colonization (Ray et al. 2002; Semlitsch 2008; Smith and Green 2005), making them especially sensitive to anthropogenic habitat alteration, which may disrupt or facilitate these processes (Ficetola and De Bernardi 2004). The North American bullfrog (*Lithobates catesbeianus,* hereafter referred to as bullfrog) is a nearly globally distributed invasive amphibian that is originally native to the Eastern United States and has been associated with declines in native amphibian populations across their invasive range (Adams 2000; Casper and Hendricks 2000). Studies examining how bullfrogs disperse between aquatic habitats remain limited, and have mostly focused on movement distances of individuals (e.g. Ingram and Raney 1943; Willis et al. 1956). Studies that address a more complex suite of landscape-level features that may promote this species' dispersal and establishment remain lacking, but are of importance given the widespread and potentially detrimental nature of invasive bullfrog populations.

In arid regions such as the western United States, two major types of aquatic habitat alteration can potentially influence the spread of bullfrogs, and include the alteration of the hydroperiod of standing water bodies, as well as alteration to flowing water systems (Nilsson et al. 2005; Smith et al. 2002; Weiner et al. 2008), (Fig. 1). The goal of our study was to clarify which of these two types of habitat modification may be most important for facilitating the dispersal of bullfrogs. We concentrated our efforts on bullfrog populations in the Front Range region of Colorado, as this is the most densely populated region of the state, and consists of a heterogeneous patchwork of protected grasslands, urban development and agriculture (Fig. 2). Over the last 30 years, human population growth and suburbanization in the Colorado Front Range has exceeded most other parts of the US and increases of up to 51 % are projected for the next 25 years (Fishman and Roberts 2001). The suburbanized landscapes have led to the creation of many artificially permanent water bodies, primarily in the form of retention ponds, ornamental community ponds, and hazard ponds on golf course properties (Hammerson 1999; Wright 1914; Wiener et al. 2008). Bullfrog tadpoles require two years to complete their development prior to metamorphosis, and thus require permanent wetlands for breeding and for developing tadpoles to over-winter (Wright 1914). The increase in number of permanent wetlands may facilitate bullfrog persistence by creating stepping-stones of hospitable habitat (Maret et al. 2006) that can aid in the dispersal of invasive species into new landscapes (Havel et al. 2005). Additionally, in Colorado, as in much of the west, flowing waterway systems have been highly modified (Nilsson et al. 2005; Wiener et al. 2008). Such modification is known to facilitate the movement of other aquatic invaders such as fish (Hohausova et al. 2010) and reduction in the variability of water flow is known to favor bullfrog presence (Fuller et al. 2011). Man-made ditches and stream diversions may

Fig. 1 **a** A permanent wetland occupied by bullfrogs, the surrounding habitat is typical of much of the land-use found across the Colorado Front Range. **b** A ditch system in our study area, also typical of those found across our study region [photo credit: VJ McKenzie (**a**), AC Peterson (**b**)]

facilitate bullfrog movement by increasing connectivity of wetlands with areas of hospitable habitat.

In our study, we combined wetland survey information, GIS landscape analysis, and a model selection approach to examine whether landscape features that may relate to overland dispersal of bullfrogs, waterway dispersal of bullfrogs, within-wetland site characteristics, or a combination of these factors are the strongest predictors of detection of invasive bullfrog presence and bullfrog breeding presence. We sought to include measures that would address the complexity of the landscape in the Colorado Front Range, with the goal of illuminating features that may facilitate or hinder the dispersal of bullfrogs into new landscapes. Such information can inform management and control strategies of invasive bullfrog populations, can inform niche modeling integral to predicting regions most vulnerable to bullfrog invasion, and can provide a broader understanding of how semi-aquatic invasive species move across human-modified terrestrial and aquatic habitats.

Methods

Wetland surveys

To determine the distribution of bullfrog populations in wetlands across the Colorado Front Range, we combined information from wetland surveys of 243 wetlands from eight counties (Fig. 2). These wetlands occur in urban, grassland, forest, and agricultural areas and are found on both public and private lands. We haphazardly selected sites across different land use types to encompass a variety of land-use practices with varying degrees of wetland and lotic water body density, although practicality and accessibility were considered when selecting wetlands to include in this study. We sampled all wetlands during the months of May-August during the years 2007–2011. All wetlands surveyed were below 2,000 m in elevation, as bullfrogs are known to inhabit mostly lowland habitats, and are rarely found above this elevation (Hammerson 1999; Moyle 1973). A 3–4 person field crew sampled all wetlands utilizing the same sampling protocol in all years (as per Johnson et al. 2011). Upon arriving at a wetland, we conducted a visual encounter survey (VES) to establish the presence of adult and recently metamorphosed amphibians. During the VES, we walked the perimeter of each wetland and recorded the number and species of all amphibians seen or heard within 3 m of shoreline and also noted the presence of other vertebrate activity. We conducted dip-net sweeps by pulling a 1.4-mm mesh size dip net rapidly through the water in a 1.5-m line perpendicular to the shore. These sweeps were conducted every 15 m around the circumference of the pond. We placed the contents of each sweep into a plastic tray and recorded the number and identity of all larval and adult amphibians captured. The only non-native amphibian we encountered in this study was the North American bullfrog (*Lithobates catesbeianus*), while the native amphibian species we encountered included: Western chorus frog (*Pseudacris triseriata*), Northern leopard frog (*Lithobates pipiens*), Woodhouse's toad (*Anaxyrus woodhousii*), and the tiger salamander (*Ambystoma tigrinum*). Whenever possible, we completed 2–4 seine net hauls, with a net of

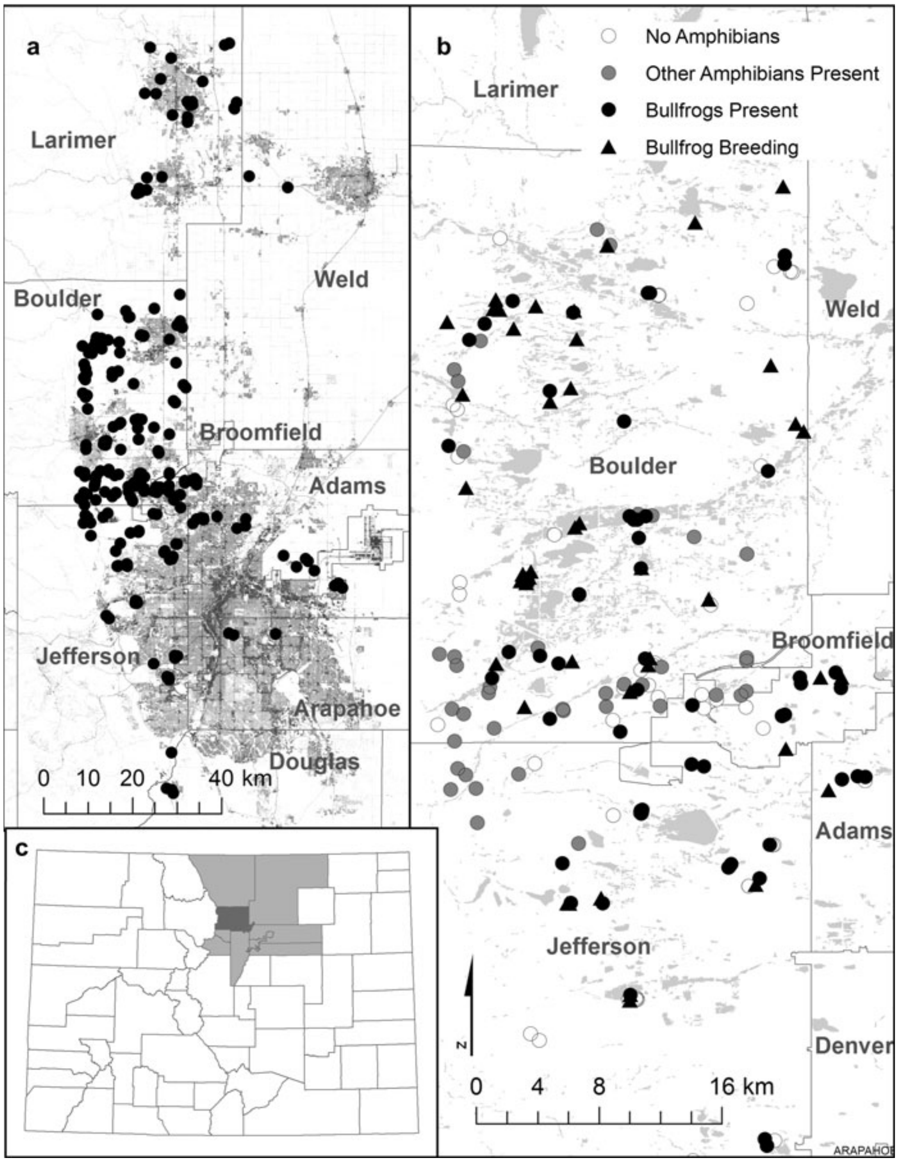

Fig. 2 **a** This map shows the distribution of all 243 wetlands (the *black dots*) surveyed from 2007 to 2011 in the Front Range of Colorado (*light gray* counties in **c**), density of urban development is represented by the impervious surfaces layer (*light-dark gray pixels*). **b** This map represents sites sampled in Boulder County, CO (*dark grey* county in **c**) from 2007 to 2011, including bullfrog breeding sites (*black triangles*), bullfrog present sites (*black circles*), other amphibians present (*gray circles*), and amphibians absent (*white circles*) with density of wetlands represented by the USGS Hydrography layer (*gray polygons*). **c** *Inset* of Colorado, showing the 8 counties sampled and represented in **a** (*light grey* counties) and Boulder County (*dark grey* county), which had the highest density of sampling and is represented in **b**

0.8 m × 2 m by stretching the net between two people, and dragging it a distance of 3–8 m. We recorded the number and identity of all amphibians captured in each seine net haul. After completion of sampling at each pond, we decontaminated all waders, nets and other equipment with a 10 % bleach solution and sun-dried the gear in order to reduce the risk of spreading material and pathogens between wetlands.

Hypothesis and model building

We used an information theoretic approach (Burnham and Anderson 2002) to create and select among competing models to determine the within-wetland characteristics and landscape-level features that are most important for predicting the detection of bullfrogs at a wetland (bullfrog occurrence), as well as the bullfrog breeding presence at a wetland (bullfrog breeding). If we detected any bullfrogs, including adults, sub-adults, recently metamorphosed individuals or larval stages, we considered the wetland a bullfrog occupied site. If we detected the presence of larval bullfrogs or bullfrog egg masses at a wetland, it was considered a bullfrog-breeding site. We created three categories of variables to determine the combination of wetland-specific characteristics and landscape level factors important for predicting bullfrog occurrence and bullfrog breeding across the landscape. Specifically, our three categories of variables included the following: (1) within-wetland characteristics, which included variables that describe the individual wetlands, (2) overland dispersal, which included variables hypothesized to either facilitate or impede overland movement of bullfrogs, and (3) waterway connectivity, which included variables that relate to the connectivity of a wetland with lotic systems (see Table 1 for an outline of all models). The rationale and variables associated with each of the three categories of variables is further elaborated upon below.

Within-wetland characteristics

We hypothesized that the within wetland characteristics area and hydroperiod may influence bullfrog occupancy, as bullfrog tadpoles require permanent wetlands to complete their lifecycle (Wright 1914), and because larger wetlands are more likely to contain amphibian predators, such as fish, which may influence bullfrog presence (Adams 2000, Adams et al. 2003). We used a hand-held Garmin GPS model 60CSx (Garmin International, Olathe, Kansas) to determine the coordinates of each wetland and to calculate surface area when sampling each wetland. We determined the hydroperiod (categorized as either permanent or temporary) of each wetland by pairing on the ground observations with Google Earth™ imaging. In the Front Range Region of Colorado there are many Google Earth™ image layers available which allowed us to view satellite images of each wetland in summer, fall and winter seasons. We categorized a wetland as temporary if it was dry during any season, or at any time during field sampling. We categorized all other wetlands as permanent wetlands.

Overland dispersal

We quantified geographic characteristics within a 1-km radial buffer of each wetland surveyed. While bullfrogs are known to move greater than 1-km in

Table 1 Summary of variables included in our 16 candidate models predicting bullfrog occupancy and bullfrog breeding utilizing all Colorado wetlands (n = 243)

Model number	Model type	Within wetland characteristics		Overland dispersal				Waterway connectivity	
		Area	Hydroperiod	Wetland (%)	Distance nearest lake	Topographic complexity	Impervious surfaces	Summed waterway amount	Distance to nearest waterway
1	Global	1	1	1	1	1	1	1	1
2	Single variable	0	0	0	0	0	0	0	0
3	Single variable	1	0	0	0	0	0	0	0
4	Single variable	0	1	0	0	0	0	0	0
5	Single variable	0	0	1	0	0	0	0	0
6	Single variable	0	0	0	1	0	0	0	0
7	Single variable	0	0	0	0	1	0	0	0
8	Single variable	0	0	0	0	0	1	0	0
9	Single variable	0	0	0	0	0	0	1	0
10	Single variable	0	0	0	0	0	0	0	1
11	Wetland	1	1	0	0	0	0	0	0
12	Overland	0	0	1	1	1	1	0	0
13	Waterway	0	0	0	0	0	0	1	1
14	Wetland + Overland	1	1	1	1	1	1	0	0
15	Wetland + Waterway	1	1	0	0	0	0	1	1
16	Overland + Waterway	0	0	1	1	1	1	1	1

These are the simple additive models that did not include any interaction terms distance (e.g. Willis et al. 1956), such long distance dispersal is not typical of most individuals, and thus a spatial extent of 1 km is likely an appropriate scale when determining landscape features relevant to amphibians (Semlitsch 2008). If bullfrog dispersal is mostly via overland movement, we hypothesized that the average percentage of wetland area within a 1-km radial buffer zone may positively associate with bullfrog presence, as marshy, wet areas may facilitate the overland movement of this highly aquatic species. Reservoirs are known to act as source populations for a number of aquatic invaders (Johnson et al. 2008), and thus we hypothesized that wetlands nearer to lakes or reservoirs may more often associate with bullfrog presence. We also hypothesized that the average percentage of impervious surfaces and topographic complexity may represent barriers to amphibian overland movement (Fahrig et al. 1995; Murphy et al. 2010) and therefore associate negatively with bullfrog occupancy and breeding presence.

To calculate the variables included in our overland dispersal category, we utilized the United States Geologic Survey (USGS) National Land Cover Dataset to quantify the percentage of wetland area and the average percentage of impervious surfaces within a 1-km buffer zone of each wetland. We used the USGS National Hydrography dataset to quantify the straight-line distance of each wetland surveyed to the nearest lake (defined as any water body >10,000 m^2 in area). Topographic complexity represents the maximum elevation change within each 1-km buffer, calculated from the National Elevation Dataset (USGS). All spatial analyses were conducted in ArcGIS 10 (ESRI).

Waterway connectivity

If bullfrog dispersal occurs primarily via waterways, we hypothesized that the distance of a wetland to the nearest waterway and the amount of waterway present in the 1-km buffer zone may facilitate movement of bullfrogs, and thus we included these variables as predictors in our waterway connectivity category. To calculate these variables, we used the National Hydrography Dataset (1:24,000 USGS) layer to sum the lengths of all streams, rivers, ditches and canals within the 1-km buffer zone of each wetland and to calculate the straight line distance of each wetland to the nearest waterway of any type.

Analysis

We transformed predictor variables with a logarithm or square root transformation, and checked all predictor variables for collinearity. None was found ($r < 0.4$ in all cases), so all predictor variables were included in our analyses. We used generalized linear modeling (GLM) as we were predicting a binomial response. We fitted a GLM with all predictor variables from all categories, and checked the residuals of this global model for spatial autocorrelation utilizing a Monte Carlo (random) Moran's I, in which we completed 999 random simulations and compared the Moran's I value of our global model to the null Moran's I values produced by the random simulations. The results of this analysis suggested no spatial-autocorrelation in the residuals of the global model (Moran's I statistics $= -0.0042$, $p = 0.933$), and thus we utilized non-spatial models for the remainder of our analyses.

We created three categories of variables according to our hypotheses (within-wetland characteristics, overland dispersal, waterway connectivity), and created 33 candidate models to predict bullfrog occurrence and bullfrog breeding presence. Sixteen of those did not include interaction terms. Those models consisted of: a single global model that included all predictor variables, 6 models that consisted of all combinations of the local, overland and waterway categories, 8 single variable models, and one null intercept model (Table 1). Due to the known association of bullfrog breeding populations with permanent wetlands, we also included the select interaction terms: hydroperiod × wetland %, hydroperiod × distance to lake, hydroperiod × topographic complexity, hydroperiod × distance to waterway and hydroperiod × amount of waterway into a set of models predicting bullfrog breeding and bullfrog occupancy. Seventeen of our models included these interaction terms in a factorial design.

Before proceeding with an analysis of all wetland sites, we examined whether the variable 'distance to nearest occupied site' was an important predictor variable. 'Distance to nearest occupied site' is a straight-line measure of each site to the next nearest site that is occupied with the species in question, which can sometimes be an important predictor of amphibian occupancy (e.g. Ficetola and De Bernardi 2004; Fuller et al. 2011; Knutson et al. 1999). Our sampling efforts were not complete in all areas across the scope of the region primarily due to access restrictions, so we avoided conflating 'distance to nearest occupied site' with the spatial gaps in our surveys by analyzing the region with the best sampling coverage. Therefore, we included the variable 'distance to nearest occupied site' as an a priori predictor in every model in an analysis of only wetlands in Boulder County ($n = 121$), where sampling was more thorough across the landscape. We used logistic regression to determine the variables, or categories of variables, that best predict bullfrog presence and bullfrog breeding presence and ranked the models according to their second order Akaike Information Criterion (AIC_c) with the AICcmodavg package in R (Burnham and Anderson 2002; R Development Core Team 2000). We used the AIC_c due to our small sample size in comparison to the number of parameters used in our models (Burnham and Anderson 2002).

We ranked all models according to their AIC_c, and the model with the lowest AIC_c was considered the best-supported model relative to all other models considered in our analysis. All models that were within 2 ΔAIC_c of the best-supported model were also considered well-supported predictors of bullfrog presence or bullfrog breeding presence relative to all other models included in our analysis (Burnham and Anderson 2002), (Table 2). We transformed the continuous probabilities predicted by each model to a binary variable by categorizing all predicted probabilities <0.5 as a 0, and all predicted probabilities >0.5 as a 1 for each wetland, and then calculated the Cohen's kappa value for all of the well-supported models (Table 2), (Fielding and Bell 1997). As there were a number of well-supported models for each response variable, we used multi-model averaging to calculate the model averaged coefficients, standard errors, confidence intervals and Akaike weights (which provide a measure of the relative importance of the predictor variables included in the best-supported models) using the package MuMIn in R (Table 3). Individual predictor variables that had an Akaike weight > 0.8 or model averaged confidence intervals that did not include 0 were considered well supported by our data and are included in Table 3, (Burnham and Anderson 2002).

The variable 'distance to nearest occupied site' was not considered well supported by our data, and thus we removed this variable from all models and re-ran all analyses with the full Colorado wetland dataset ($n = 243$). All results shown are from the analyses utilizing the full wetland dataset. Additionally, none of the interaction terms were considered well supported by our data when predicting either bullfrog occurrence or bullfrog breeding, so for simplicity we removed all interaction terms from our analyses. All results shown are from the 16 candidate models that did not include interaction terms (see Table 1 for a summary of these 16 models).

Results

During the years of 2007–2011 we sampled 243 wetlands across 8 counties in the Front Range Region of Colorado (Fig. 2). Of those wetlands sampled, 198 were permanent wetlands and 45 were temporary wetlands. See Fig. 3 for a breakdown of the proportion of permanent and temporary wetlands that supported bullfrog occupancy and bullfrog breeding populations. Across all wetlands, 169 ($\sim$70 %) had the presence of some amphibian, while 122 ($\sim$72 %) of amphibian positive wetlands ($\sim$50 % of all wetlands) included the presence of bullfrogs. Fifty-five ($\sim$45 %) of the sites where bullfrogs were present supported breeding bullfrog populations. Native Colorado amphibians were found at 82 ($\sim$34 %) of the wetlands included in this study.

Bullfrog occurrence

Predictor variables in all three classes of variables were included in our well-supported models predicting bullfrog occurrence in the Colorado Front Range. Both of the well-supported models correctly predicted bullfrog occurrence at >60 % of the wetlands included in our study, and also correctly categorized >20 % more wetlands than a baseline null model predicting bullfrog occurrence across our full dataset (Cohen's Kappa > 0.2) (Table 2). The wetland-specific class of variables and the overland dispersal class of variables were included in all of our best-supported models, while the waterway connectivity class of variables was included in only one of our best-supported models (the global model). When considering wetland-specific characteristics, bullfrog occurrence was negatively associated with both temporary wetlands and with wetland area. The results of model-averaging show that both hydroperiod and area are well-supported predictors of bullfrog occurrence at scale of our study,

Table 2 Best supported models predicting bullfrog occurrence and breeding presence in Colorado Front Range wetlands (n = 243)

Response	Model[a]	K[a]	AIC_c^b	ΔAIC_c^b	AIC_c Wt[b]	Proportion correctly predicted[c]	Cohen's Kappa[d]
All Colorado wetlands							
Bullfrog occurrence	Wetland + Overland	7	318.02	0	0.51	0.62	0.23
	Global	9	318.46	0.44	0.41	0.68	0.36
Bullfrog breeding	Hydroperiod	2	250.46	0	0.43	0.77	0
	Wetland characteristics	3	251.21	0.74	0.29	0.77	0
	Local + Overland	7	251.95	1.49	0.2	0.77	0.03

[a] The categories of variables included in each model, see Table 1 for full description

[b] K is the number of parameters included in each model examined, AIC_c is the second order Akaike information criterion, ΔAIC_c is the difference in AIC_c units between the model with the lowest AIC_c value and the model examined, AIC_c Wt is the second order Akaike weight

[c] The proportion of wetlands in the dataset that are correctly categorized as either bullfrog occupied wetlands or bullfrog breeding wetlands by the model examined

[d] Cohen's Kappa is a measure of the proportion of wetlands correctly predicted by each model beyond chance expectation

Table 3 Model averaged coefficients, standard errors, confidence intervals and cumulative Akaike weight for variables predicting bullfrog presence and bullfrog breeding presence at all Colorado Front Range wetlands (n = 243)

Response	Predictor	Model-Averaged Coefficient	Adjusted SE	Lower CI	Upper CI	Cumulative Akaike Weight
All Colorado wetlands						
Bullfrog occurrence	Topographic complexity[b]	−0.0092	0.0040	−0.0170	−0.0014[c]	1.00
	Hydroperiod (temporary)[a]	−1.6200	0.4320	−2.4600	−0.7710[c]	1.00
	Wetland %[b]	0.0278	0.0139	0.0006	0.0551[c]	1.00
	Area[a]	−0.0245	0.0745	−0.1710	0.1220	1.00
	Distance to Lake[b]	0.0002	0.0002	−0.0001	0.0005	1.00
	Impervious surfaces[b]	−0.0115	0.0105	−0.0322	0.0091	1.00
Bullfrog breeding	Hydroperiod (temporary)[a]	−2.1100	0.7520	−3.5800	−0.6330[c]	1.00

[a] Variables included in the wetland-specific category of variables

[b] Variables included in the overland dispersal category of variables

[c] Variables with a 95 % confidence interval that do not include 0

as hydroperiod has a confidence interval that did not include 0 and a cumulative AIC weight > 0.8 while area had an AIC weight > 0.8 (Table 3). When considering landscape level variables, only variables relating to the overland dispersal of bullfrogs were well-supported predictors of bullfrog occurrence at the scale of our study. Areas with higher levels of topographic complexity and with higher levels of impervious surfaces within a 1-km radial buffer zone of the wetland were negatively associated with bullfrog occurrence. However, bullfrog occurrence was positively associated with wetlands surrounded by a high density of wetland area as well as the distance to the nearest lake (identified here as any water body >10,000 m^2 in area).

Bullfrog breeding

The within-wetland category of variables and the overland dispersal category of variables were included in our top selected models predicting bullfrog-breeding presence in Colorado Front Range wetlands. All of the well-supported models correctly predicted >75 % of bullfrog breeding wetlands; however, none of these

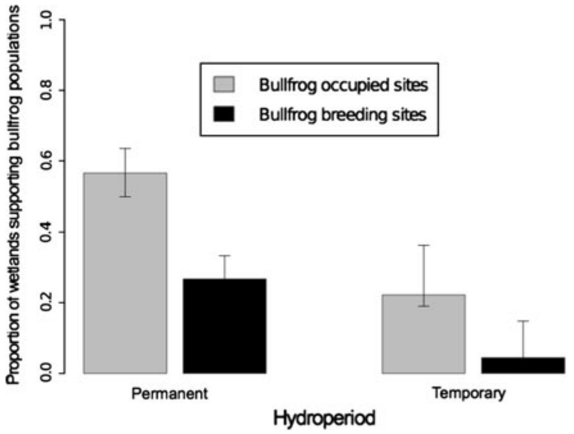

Fig. 3 Proportion of permanent wetlands (n = 198) and temporary wetlands (n = 45) that support bullfrog populations and breeding bullfrog populations in the Colorado Front Range. Bullfrog occupied sites represent all sites where bullfrogs were present, while bullfrog breeding sites represent the subset of bullfrog occupied sites that supported breeding populations of bullfrogs

models showed a predictive power beyond a baseline null model predicting the absence of breeding (the most frequent outcome in our dataset) at all wetlands (Cohen's Kappa = 0) (Table 2). This may be due to the relative rarity of bullfrog breeding presence in our dataset, as Cohen's Kappa is sensitive to sample size and can fail when number of successes (presence of bullfrog breeding populations, n = 55) is very low in comparison to the number of trials (number of wetlands sampled, n = 243) (Fielding and Bell 1997). After averaging across these top selected models, only the variable hydroperiod was considered a well-supported predictor of bullfrog breeding presence, with temporary wetlands negatively associated with bullfrog breeding populations.

Discussion

Aquatic freshwater systems are under intense pressure from human activities, especially in arid regions where these resources are limited (Dudgeon et al. 2006; Sala et al. 2000; Wiener et al. 2008). As a result, aquatic systems are especially vulnerable to invasion, and understanding how anthropogenic activities influence invasion processes beyond the initial introduction phase is key to eradicating invasive populations or limiting their spread into new habitats (Dudgeon et al. 2006; Rahel 2007).

In our study we paired extensive survey information with geographic data and used an information-theoretic approach to determine the categories of variables that most often associate with bullfrog detection and bullfrog breeding in the Colorado Front Range. We focused on categories of variables rather than individual predictor variables in order to examine the relative support for different hypotheses regarding the dispersal patterns of invasive bullfrogs. The Cohen's Kappa values from our best-supported models (see Table 2) are similar to those found in other ecological systems predicting presence or absence of species (Manel et al. 2001), indicating that we can have some confidence in extending inferences from these findings. While our best-supported models predicting bullfrog detection do offer improvement beyond a null model, the moderate values of Cohen's Kappa suggest that there may be other unconsidered variables that are also important to bullfrog detection in the Colorado Front Range.

In all, of the variables considered in our analysis, our results indicate that bullfrog populations are more often associated with features relating to overland dispersal than to features relating to the connectivity of a wetland to lotic waterway systems. Additionally, within these categories of variables, we can offer some indication of the relative importance of the different variables considered in our analysis. Below we highlight the specific within-wetland characteristics and landscape-level features that we included in our analysis that appear to more often relate to wetlands where we identified bullfrog occurrence and breeding presence in the Colorado Front Range.

Within-wetland characteristics

The within-wetland characteristic hydroperiod was included in all of our top-selected models, with the permanency of a wetland a consistent predictor of both bullfrog occupancy and bullfrog breeding populations in Colorado Front Range wetlands. Hydroperiod was the only well-supported predictor of breeding populations in our study system (Table 3). While the models predicting bullfrog breeding presence do not show predictive power beyond a null model, the patchy nature of amphibian breeding (e.g. Smith and Green 2005) as well as the overall low number of breeding sites found in our survey may make predicting amphibian breeding in our system especially difficult. However, our models do suggest that the permanence of a wetland is an important factor relating to bullfrog breeding presence, which is consistent with both the natural history of this species as well as with the results of other studies (Hammerson 1999; Maret et al. 2006; Boone et al. 2008; Fuller et al. 2011; Johnson et al. 2011). Unlike native Colorado anurans, bullfrogs require permanent wetlands to complete larval development (Hammerson 1999; Willis et al. 1956). Permanent wetlands are historically rare across the Colorado Front Range landscape (Hammerson 1999; Wiener et al. 2008) and our results suggest that human modification may have facilitated the invasion of bullfrogs by increasing the number of permanent wetlands that fill a critical niche characteristic of this species. Our results are consistent with other studies that have suggested that alteration of hydroperiod, namely reducing the permanency of lentic systems, is likely to be useful when considering the control of bullfrog populations (e.g. Boone et al. 2008; Fuller et al. 2011; Maret et al. 2006; Johnson et al. 2011). Reducing wetland hydroperiod will likely facilitate eradication of breeding populations, which appear to rely on these permanent wetlands. Additionally, it appears that in the Colorado Front Range mobile adult and sub-adult populations also utilize permanent wetlands. Reducing hydroperiod of these wetlands may also reduce more transient bullfrog populations consisting of individuals that are capable of long-distance dispersal and re-colonization.

Overland dispersal

To shed light on potential dispersal modes used by bullfrogs, our analyses included landscape-level features hypothesized to relate to either overland dispersal or to the connectivity of wetlands to waterway systems. It is not clear how these features relate to breeding bullfrog populations, as one of these landscape-level variables were considered well-supported predictors of bullfrog breeding populations. However, when considering bullfrog occurrence, models including the overland dispersal category of variables were consistently included in our top-selected models. We found that the distance of a wetland to the nearest lake, as well at the amount of wetland area within the 1-km buffer of a wetland, were positively associated with bullfrog presence (Fig. 4). Previous accounts have suggested that inadvertent introduction during lake fish stocking operations is one potential route of introduction of bullfrogs into the Colorado Front Range (Hammerson 1999) and man-made reservoirs and lakes have been identified as important introduction points for a number of other aquatic invaders (Havel et al. 2005; Johnson et al. 2008). In our study, we found a higher probability of observing bullfrogs at wetlands that are further from lakes. This is contrary to what might be expected if these lakes have acted as introduction points for bullfrogs in the past, suggesting that if any accidental introductions of bullfrogs into these lakes did occur, it was long enough ago or so infrequent that there no longer remains any signal of introduction into these systems. However, we did identify bullfrogs more often in wetlands that are surrounded by a high density of wetland area-which suggest that wetland area can reduce the distance that bullfrogs need to move overland between sites, and supports the hypothesis that wetland areas can act as stepping-stones, facilitating dispersal across the landscape.

In addition to straight-line distance measures, we also attempted to include features that would realistically capture the landscape-level complexity faced by an amphibian as it moves across the landscape. We calculated the topographic complexity, which is a measure of the maximum elevation change within a 1-km radial buffer of a wetland, as well as the amount of impervious surfaces within the 1-km radial buffer of a wetland. We found that both of these variables were negatively related to bullfrog occurrence at a wetland, suggesting these characteristics may act as barriers for overland movement of bullfrogs, as has been seen with other amphibian species (e.g. Fahrig et al. 1995; Murphy et al. 2010; Johnson et al. 2011), (Fig. 4). The impervious surfaces variable included in our analysis represents a measure of mostly artificial features such as parking lots, buildings and roadways. Wetlands surrounded by high levels of such surfaces may be unreachable by most amphibian species, including bullfrogs. However, other studies (e.g. Richter and Azous 2001) have suggested that urban wetlands are highly susceptible to bullfrog colonization. It is possible that the observed negative association with bullfrogs in these areas is a historical relict, as amphibian occurrence is also known to relate to wetland age (Birx-Raybuck et al. 2009). The age of the wetlands in our study was not known, and it is logical that developed areas in the Colorado Front Range may also hold more recently constructed wetlands, which

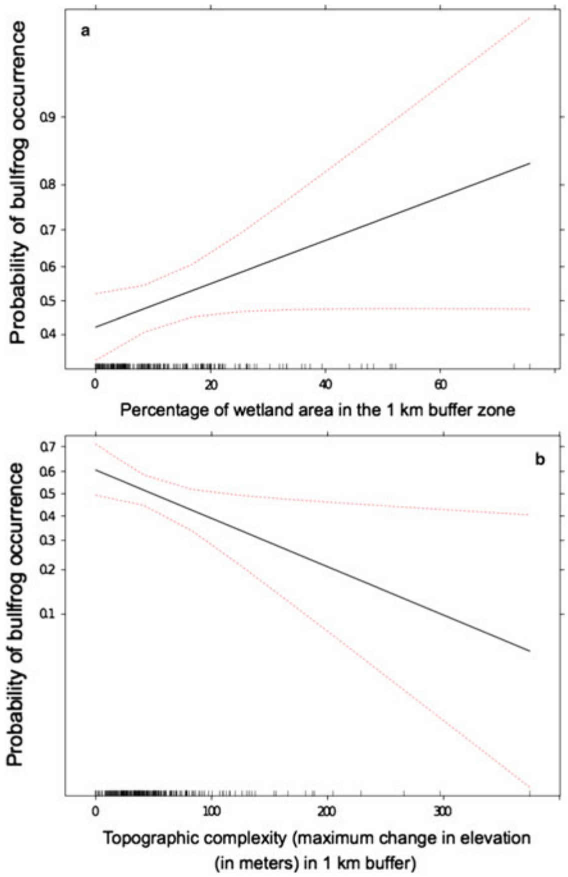

Fig. 4 The probability of bullfrog occurrence increases with increasing amount of wetland area within the 1-km radial buffer of a wetland (**a**) and decreases with the level of topographic complexity (measured as the maximum change in elevation in meters in the 1 km buffer zone). **b** Fitted values (*solid line*) versus observed values (*hash marks*) obtained from the best supported model predicting bullfrog occurrence (wetland characteristics + overland dispersal) in (Table 1). *Dashed lines* represent 95 % confidence intervals

bullfrogs may not yet have reached. Additional research should be conducted before determining the degree to which wetlands in urban areas can be considered potential bullfrog habitat.

Waterway connectivity

We found little support for the hypothesis that connectivity to waterways is an important predictor of bullfrog presence, suggesting that bullfrogs do not often use these waterway corridors in our system as they disperse across the landscape. However, studies of other aquatic invaders have found that these waterway systems may act as important corridors of movement (e.g. Hohausova et al. 2010; Rahel 2002, 2007). In the Colorado Front Range, as in other arid regions, many of the waterways connecting wetlands are ephemeral in nature, and it is possible that waterway corridors might be more often associated with bullfrogs if they are permanent. We currently do not have information about the hydroperiod of the waterway systems we included in our analyses, but this information may be useful for elucidating if and when bullfrogs do utilize waterway corridors for movement. Further study is necessary to determine the full extent to which bullfrogs may utilize these lotic waterway systems. Additionally, we observed bullfrogs at ~57 % of permanent wetlands, and breeding populations at ~26 % of permanent wetlands (Fig. 3). Amphibian populations are known to have variable recruitment across years (i.e. Skelly et al. 2003), making interpretation of these proportions difficult. However, it is possible that this relatively high proportion of occupied permanent sites represents saturation of bullfrog populations across the landscape (i.e. bullfrog populations have established at most of the wetlands that are suitable). If this is the case, then the relationship of bullfrogs to landscape-level variables, such as waterway connectivity, may be diluted if bullfrogs are no longer dispersal limited.

Implications and management suggestions

In our study, only the landscape-level features relating to overland dispersal of bullfrogs were found to be well-supported predictors of bullfrog occurrence, suggesting that in the Colorado Front Range bullfrogs may be more likely to move via overland routes than via lotic waterway systems. The moderate predictive power of our best-supported models (indicated by Cohen's Kappa, see Table 2) may also suggest that bullfrogs are no longer dispersal limited in our system and may be approaching saturation, as this is hypothesized to reduce the ability of landscape-level variables relating to dispersal routes to predict bullfrog occurrence. However, we did find a consistent relationship between bullfrog occurrence and characteristics relating to overland movement, emphasizing that these factors are likely important in influencing the distribution of bullfrog populations across the landscape. Studies of other aquatic invaders have highlighted the importance of waterway systems in facilitating their movement (Houhasova et al. 2010;

Rahel 2002, 2007) and our results suggest that a single strategy may not be effective in controlling populations of different invasive species, even if all species are mostly aquatic. Rather, efforts aimed at managing populations of invasive animal species, especially those that can move either overland or via waterways, should consider both overland and waterway routes as potential corridors of movement.

Our study also highlights specific landscape-level features that should be considered when developing control or eradication strategies targeted at bullfrogs, or when developing niche models aimed at predicting future spread of this species into novel habitats. As has been suggested by other studies (e.g. Johnson et al. 2011; Fuller et al. 2011), we recommend that reducing hydroperiod of a wetland will likely be effective at eradicating both breeding bullfrog populations as well as limiting populations of transient adult or sub-adult populations. Specifically, efforts concentrating on reducing hydroperiod of wetlands located in areas with a high density of permanent wetlands per unit land area, or in regions with low levels of topographic relief, will likely be most effective at limiting or eradicating bullfrog populations in our system. Controlling such populations is especially important in the light of recent amphibian declines, as amphibians are now considered the most threatened class of vertebrate on the planet, and habitat loss, invasive species, and disease are implicated as major factors contributing to these declines globally (Stuart et al. 2004). The North American bullfrog is a globally distributed invasive species that has been associated with declining amphibian populations across its invasive range (Casper and Hendricks 2000; Maret et al. 2006; Johnson et al. 2011), and this species has been implicated as a transport vector for a number of deadly amphibian pathogens (Schloegel et al. 2009; Schloegel et al. 2010). Clarifying the features that facilitate this species as it moves across an ever-changing landscape can aid in limiting the spread of this species into new regions and can limit its impact in the regions where it has already been established. Such actions may facilitate conservation of declining amphibian populations in Colorado, and can potentially facilitate management of this nearly globally distributed invasive species across its range.

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