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SITE-OCCUPANCY MONITORING OF AN ECOSYSTEM INDICATOR: LINKING CHARACTERISTICS OF RIPARIAN VEGETATION TO BEAVER OCCURRENCE

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ABSTRACT.—Establishment of sampling frameworks to monitor the occurrence of ecological indicators and to identify the covariates that influence occurrence is a high-priority need for natural resource restoration and management efforts. We utilized occupancy modeling to identify patterns of beaver occurrence and factors influencing these patterns (i.e., type and amount of vegetation cover) in the Grand Canyon of the Colorado River ecosystem. We used rafts and kayaks to access a stratified random sample of sites (i.e., 100-m-long sections of riverbank) and used repeated sampling procedures to sample for beaver sign (i.e., lodges, cuttings, tracks, and beaver sightings). We quantified the type and amount of vegetation cover at each sampled section by using a GIS database of remotely sensed information on the riparian vegetation in the Grand Canyon. We first modeled occurrence of beaver sign as a function of the total amount of vegetation cover (summed across classes) and then determined the relative importance score for each of the 7 vegetation classes. Detection probability (p) was 2 times higher when observers traveled in kayaks (0.61) than when they traveled in rafts (0.29). Occurrence of beaver sign (ψ) in sampled transects was widespread throughout the Grand Canyon (ψ = 0.74, SE = 0.06) and positively associated with total vegetation. The relative importance scores for *Tamarix* and *Pluchea* vegetation classes were 1.5–2.5 times larger than those for all other vegetation classes, indicating that occurrence of beaver sign was most strongly associated with the cover of these 2 vegetation classes. Our results imply that quantifying the amount of riparian vegetation in close proximity to a river helps determine the occurrence of an important ecological indicator in riparian systems. The results also demonstrate a useful and cost-effective method for monitoring riverine species' usage patterns by explicitly accounting for detectability.

RESUMEN.—El establecimiento de infraestructura de muestreo, para controlar la existencia de indicadores geológicos y para identificar las covariables que influencian dicha existencia, es una necesidad de alta prioridad para la restauración de los recursos naturales y los esfuerzos de gestión. Utilizamos el modelado de ocupación para identificar los patrones de la existencia de castores y los factores que influencian estos patrones, (es decir, el tipo y la cantidad de cubierta de vegetación) en el ecosistema del Gran Cañón del Río Colorado. Utilizamos balsas y kayaks para tener acceso a una muestra aleatoria y estratificada de emplazamientos (es decir, secciones de 100 m de largo de las márgenes del río), y utilizamos procedimientos de muestreo repetidos para tomar muestras de indicios de castores (es decir, refugios, cortezas, huellas y avistamiento de castores). Medimos el tipo y la cantidad de cubierta de vegetación en cada sección muestreada utilizando una base de datos del Sistema de Información Geográfica (Geographic Information System, GIS), de información detectada en forma remota, sobre la vegetación ribereña del Gran Cañón. Primero modelamos los indicios de la existencia de castores como una función de la cantidad total de cubierta de vegetación (sumado entre las clases), y luego determinamos la calificación de importancia relativa para cada una de las 7 clases de vegetación. La probabilidad de detección (p) fue 2 veces más elevada cuando los observadores se trasladaban en kayaks (0.61) que cuando se trasladaban en balsas (0.29). Los indicios de existencia de castores (ψ) en transectos muestreados fueron extensos a lo largo del Gran Cañón (ψ = 0.74, SE = 0.06) y relacionados en forma positiva con la vegetación total. La calificación de importancia relativa para las clases de vegetación *Tamarix* y *Pluchea* fue de 1.5 a 2.5 veces mayor que todas las otras clases de vegetación, lo que indica que los indicios de la existencia de castores estaba relacionada de forma más contundente con la cubierta de estas 2 clases de vegetación. Nuestros resultados sugieren que el medir la cantidad de vegetación ribereña en proximidad cercana a un río ayuda a determinar la existencia de un indicador ecológico importante en sistemas ribereños. Los resultados también demuestran un método útil y rentable para realizar el control del uso de las especies ribereñas, al dar cuenta explícitamente de la detección.

Rivers support a vast array of aquatic and terrestrial biodiversity (Ward et al. 1999, 2002), particularly in arid ecosystems (Knopf et al. 1988). Altering the natural flow regime of rivers can impact plant and animal populations and ecological processes important in the functioning of riverine ecosystems (Dynesius and Nilsson 1994, Poff et al. 1997, Ward 1998,

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Andersen and Cooper 2000). Restoration and management of regulated rivers can be difficult because of competing demands for water and differences in dynamics between systems (Schmidt et al. 1998). However, one commonality to all restoration and management projects is the need to accurately monitor key species associated with riverine processes (Ward et al. 2001).

The beaver (*Castor canadensis*) is a keystone ecological indicator of a suite of riparian conditions and processes. It exhibits high ecological interaction strength in both small-order streams and large-order regulated rivers (Johnston and Naiman 1990, Breck et al. 2003, Rosell et al. 2005). Numerous studies have established the pervasive effects of beaver activity, foraging, and dams on hydrology and groundwater flow (Westbrook et al. 2006), fluvial geomorphology (Johnston and Naiman 1987), soil composition and moisture, forest structure, wetland development, and entire ecological assemblages (Andersen and Cooper 2000, Breck et al. 2003).

Likewise, components of riparian ecosystems, such as river geomorphology and riparian vegetation structure, influence beaver occurrence and abundance. For instance, in the Grand Canyon, the beaver population has likely increased since the construction of Glen Canyon Dam, putatively because controlled flows from the dam beginning in 1963 led to higher primary and secondary production in riparian ecosystems (Turner and Karpiscak 1980, Kearsley et al. 2006). Numerous studies have shown that riparian vegetation has increased in the Grand Canyon since flow regulation primarily because of the elimination of annual flood events that scoured shorelines (Turner and Karpiscak 1980, Stevens et al. 1995, Ralston et al. 2008). For instance, the area of riparian vegetation has increased by more than 50% and continues to expand (Ralston et al. 2008), and marsh communities have expanded throughout the corridor (Stevens et al. 1995). Mortenson et al. (2008) found that after accounting for river geomorphology, beaver presence in the Grand Canyon was more likely in areas with higher coverage of a particular type of plant (i.e., *Tamarix*).

Due to its ecological impact and associations with riparian conditions (e.g., utilization of vegetation and dependency and impact on hydrology), the beaver is a high-priority species for restoration and management programs (Rosell et al. 2005, Anderson et al. 2009). The monitoring of beaver occurrence with a cost-effective sampling framework has utility for such efforts. To address this need, we used an occupancy modeling framework (MacKenzie et al. 2006) that explicitly incorporated the probability of detecting beaver sign (i.e., lodges, cuttings, tracks, and beaver sightings) to estimate the occurrence of beavers in the Grand Canyon. We evaluated whether the abundance and composition of riparian vegetation classes could explain the occurrence of beaver sign. Employing a space-for-time substitution across sampling locations that varied in vegetation abundance (Likens 1989), we applied our results to inform hypotheses about increased abundance of beavers in the Grand Canyon due to flow regulation. In particular, an association between beaver use of an area and the amount and type of vegetation would be consistent with the hypothesis that an increase in riparian productivity has strongly influenced beaver abundance in the region.

METHODS

We based our sampling on the distribution and coverage of dominant riparian vegetation classes occurring in the Colorado River ecosystem between Glen Canyon Dam and the western boundary of Grand Canyon National Park (Fig. 1). Specifically, our sampling range of inference comprised 7 classes of vegetation patches (≥ 0.19 m^2) occurring on the bank of the 226 cubic meters per second (cms) shoreline between river miles 0 and 221 (see Stevens 1990 for description of river miles in the Grand Canyon). We utilized Ralston et al.'s (2008) riparian vegetation database, which was originally created to enable fine-scale detection of vegetation changes and establish sampling designs for terrestrial inventory efforts. This vegetation database resulted from (1) a ground survey effort to identify dominant vegetation classes; (2) acquisition of a 0.44-m-resolution, 4-band image (ISTAR Americas) during May 2002; and (3) application of a supervised classification procedure on the imagery. Vegetation was classified into 7 classes, following the National Vegetation Classification Standard (Federal Geographic Data Committee 2008), based on cover dominance: (1) sparse shrub, (2) *Pluchea*, (3) *Tamarix*, (4) wetland,

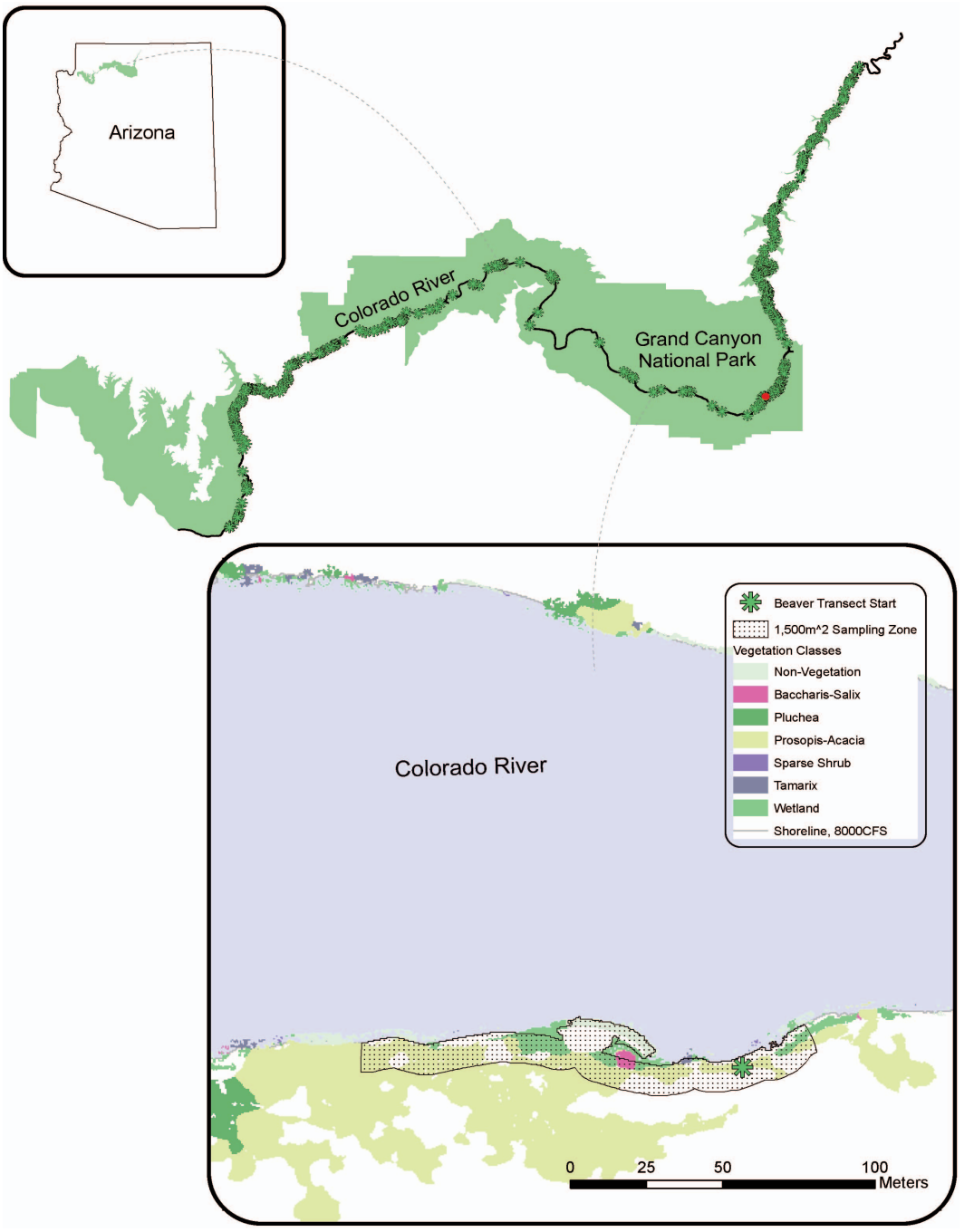

Fig. 1. Beaver-occupancy sampling locations along the Colorado River in Grand Canyon National Park, Arizona, USA. Lower inset is an example of transect locations relative to bank vegetation, which was derived from a high-resolution, riparian vegetation database (Ralston et al. 2008).

(5) *Prosopis-Acacia,* (6) *Baccharis-Salix,* and (7) nonvegetation. To conduct accuracy assessments of the classification procedure, vegetation classes in ground-truthing plots (acquired in 2003 and 2004) were compared with classified polygons at a 0.01-ha scale and at the scale of Federal mapping standards (0.5-ha). Accuracy assessment of the supervised classification varied 49%–90% among the 7 classes at the finer scale (0.01 ha), and was >80% at the broader scale (0.5 ha). In general, the vegetation composition follows a moisture gradient, with marsh species and obligate riparian species situated adjacent to the shoreline and facultative riparian and xerophytic species located farther upslope (Ralston et al. 2008). Further details regarding geomorphology and riparian vegetation can be found in Schmidt and Graf (1990), Stevens et al. (1995), Ralston et al. (2008), and Mortenson et al. (2008).

Beaver Occupancy Sampling

We sampled beaver occupancy from 11 September to 28 September 2008. Discharge was maintained at 12,000 cfs for the duration of the sampling period. Our beaver-sampling units were individual 100-m-long shoreline transects that consisted of mixed-composition riparian vegetation. To ensure adequate representation of riparian vegetation classes among sampling units, we used a stratified random sample and geographic information systems (GIS) to select 50 patches ($\geq$25 m^2) of each of the 7 vegetation classes mapped by Ralston et al. (2008). We derived coordinates for the centroid of each patch and used this location to delineate the starting location of each transect.

We used a handheld GPS unit to navigate to the upstream starting location of each transect and then searched for beaver sign along the shoreline and 100 m downstream. We excluded transects from sampling if they overlapped, were too close to rapids, or could not be surveyed due to low GPS accuracy (ca. >25 m), which resulted in 135 transects being surveyed. We sampled beaver sign by making observations from both rafts and kayaks, using multiple observers who recorded observations independently. Each transect was sampled by 2–5 observers (1–3 observers in rafts and 1–3 kayakers). During surveys, rafts stayed in the thalweg, resulting in surveys being conducted 10–25 m from shore, whereas kayaks paddled within 1–3 m of the shore. In rafts, observers used binoculars to scan the shoreline, whereas kayakers sampled the shoreline for beaver sign without visual aid. To maintain independence, observers in rafts did not communicate until each transect was completed, and observers in kayaks staggered their timing. Observers recorded presence but not quantity of beaver sign, including (1) presumed tracks or trails of beavers leading from the water; (2) sign of foraging, such as clipped vegetation; (3) bank dens; and (4) direct observations of beavers. We eliminated transects from subsequent analyses if transects were incompletely surveyed due to logistical difficulties, river conditions, or poor GPS accuracy (ca. >25 m).

Quantifying Vegetation

We did not sample vegetation on each transect; instead, we created a vegetation zone and used GIS to quantify the area coverage (m^2) of each of the 7 vegetation classes within each zone (Fig. 1). Each zone consisted of all riparian vegetation patches within a 150 × 10-m area: 25 m upstream and downstream of the 100-m beaver-sampling transect and 10 m inland from the shoreline (Fig. 1). We choose 10 m inland because this distance generally reflects the foraging distance of beavers from water (Jenkins 1980). These zones extended farther upstream and downstream of the 100-m beaver-sampling transects because we had to account for spatial error (ca. 5–25 m) of nondifferential GPS signals that we used to locate transect starting points. In addition, due to variability in shoreline complexity, the actual area of shoreline vegetation zones considered was ultimately slightly larger and more variable than 1500 m^2 ($\bar{x}$ = 1715, 95% CI 1688–1742).

Statistical Analysis

We used the program MARK (White and Burnham 1999) and the occupancy model option to analyze our data. We pooled observations of different beaver sign (i.e., tracks and trails, cuttings, bank dens, and beaver sightings) together because sample sizes for some types of sign (e.g., bank dens [n = 4] and visual observation of beavers [n = 3]) were small and because the different types of sign were correlated. We initially constrained occupancy (ψ, unitless) as a constant and modeled detection (p, unitless) as a function of type of craft (raft or kayak) and amount of cover of

TABLE 1. Available vegetation (m^2) averaged across transects for 7 vegetation classes within a 1500-m^2 sampling area (150 m × 10 m) of land adjacent to the Colorado River in Grand Canyon. Overall mean is the averaged values across all transects for each vegetation class. Standard errors are given in parentheses. The table can be read from left to right; for example, we started 19 surveys in the wetland vegetation class, and the mean area and SE for each vegetation class is shown through the row. Gray-shaded cells represent the highest values for each vegetation class.

		Mean area (m^2) of vegetation class (SE in parentheses)						
Habitat in which survey started	Number of transects	Wetland	*Tamarix*	Sparse shrub	*Prosopis-Acacia*	*Pluchea*	Non-vegetation	*Baccharis-Salix*
Wetland	19	200.5 (32.1)	125.0 (60.5)	33.1 (12.0)	18.1 (13.9)	123.8 (44.0)	166.5 (36.7)	12.4 (4.5)
Tamarix	19	72.5 (20.6)	248.0 (62.0)	39.1 (30.0)	22.3 (11.6)	77.4 (28.5)	46.9 (13.4)	28.6 (11.9)
Sparse shrub	23	22.2 (5.5)	51.5 (21.2)	118.9 (21.0)	2.4 (1.1)	138.6 (41.9)	76.1 (24.6)	3.3 (1.8)
Prosopis-Acacia	16	59.6 (15.5)	59.7 (26.5)	9.3 (7.3)	358.8 (94.8)	122.8 (51.8)	128.2 (35.0)	20.7 (10.6)
Pluchea	22	63.2 (23.2)	123.1 (60.1)	75.0 (28.4)	32.6 (15.9)	233.2 (45.5)	107.5 (28.5)	16.5 (5.1)
Nonvegetation	19	9.8 (2.8)	38.2 (19.0)	49.1 (17.0)	13.3 (7.5)	101.4 (36.6)	174.7 (45.2)	4.3 (2.0)
Baccharis-Salix	17	92.6 (24.9)	172.9 (54.3)	19.2 (9.1)	20.0 (12.6)	95.8 (35.2)	64.6 (19.4)	98.5 (16.6)
OVERALL MEAN	135	72.6	115.6	53.1	58.3	130.8	108.4	24.5

each vegetation class. At both vegetation scales, we found that detection probability was not dependent on the amount of vegetation cover but was dependent on the type of craft from which observations were made (see Results), and thus, for all subsequent efforts to model ψ, we included craft as a covariate for the detection parameter.

Our objective was to determine whether vegetation classes and cover influenced beaver occurrence. We first normalized vegetation cover data using the following equation:

$$Z = \frac{X - \bar{x}}{\mathrm{SD}} \quad ,$$

where X was the value to be normalized, and $\bar{x}$ and SD were the arithmetic mean and standard deviation, respectively, of all coverage values across transects for a particular vegetation class. We normalized the vegetation cover data because values for particular vegetation classes at a site often differed by an order of magnitude and we wanted to ensure that the numerical optimization algorithm in Program MARK was able to find correct parameter estimates (Help Files in program MARK, White and Burnham 1999). We then determined whether a simple vegetation parameter could help us effectively model beaver occurrence. We summed the total vegetation (TotVeg) across the 7 normalized vegetation parameters for each transect and then used this value as a covariate to model ψ. We used the small sample size correction of Akaike's information criterion (AIC_c) to evaluate this model relative to a model without total vegetation as a covariate. In addition to reporting model selection results, we also report the β parameter and 95% confidence interval for the TotVeg covariate. We evaluated whether or not the 95% confidence interval overlapped zero to assess the significance of TotVeg in models predicting occurrence of beaver sign.

Because we found a strong association between TotVeg and occurrence of beaver sign, we then asked whether particular classes of vegetation could model beaver sign occurrence. We had limited knowledge about the effect of vegetation classes on occurrence of beavers, thus we selected a strategy of multimodel inference using model averaging and the output of "relative importance values" to make inferences from our data (Burnham and Anderson 2002). Because "importance value" is a standard term in plant community ecology with a different meaning than used by Burnham and Anderson (2002), we therefore use the term "relative importance score" to reduce confusion. We evaluated the extent to which vegetation influenced beaver occurrence based on the relative importance score of each vegetation class. We used the variance inflation factor (i.e., median c-hat procedure in MARK)

TABLE 2. Results of occupancy analysis to test if total vegetation coverage (TotVeg) helped explain patterns of beaver occupancy along the Colorado River in Grand Canyon. The variable p is probability of detection, ψ is occupancy, (kraft) is a covariate influencing p, and TotVeg is a covariate representing the total vegetation coverage of 7 vegetation classes.

Model	$QAIC_c$	$QAIC_c$ weight	# Para.	Deviance
p (kraft); ψ (TotVeg)	514.9	0.93	4	506.6
p (kraft); ψ (.)	520.3	0.07	3	514.1

and small sample size correction of Akaike's information criterion ($QAIC_c$). We modeled all possible combinations of the 7 vegetation classes (no interaction terms) as a balanced model set (2^7 = 128 models) and calculated the relative importance score of variable x as the sum of all model weights in which variable x appears, or $w_+(x)$ (Burnham and Anderson 2002). We calculated model-averaged β parameters for each vegetation class by multiplying the β values and model weight from each model (including zeros when a parameter was not included in the model) and averaging across all models, as recommended by Burnham and Anderson (2002). To assess the importance of a β parameter, we also calculated 95% confidence intervals for the model-averaged β parameters (i.e., 7 vegetation class β parameters) using nonconditional standard errors that incorporated model selection uncertainty.

RESULTS

We surveyed a total of 135 transects, with roughly equal numbers (16–22) of transects beginning in each of the 7 vegetation classes (Table 1). The amount (m^2) of each vegetation class among transects was variable (Table 1). Vegetation classes targeted for sampling always had the highest value (see gray-shaded cells in Table 1), except for the class sparse shrub, in which *Pluchea* was the most common. Averaged across all transects, *Pluchea* had the highest mean coverage and *Baccharis-Salix* had the lowest coverage (Table 1).

The percentage of transects with evidence of beavers varied by type of sign (tracks = 46.7%, cuttings = 37.0%, lodges = 3.0%, beavers seen = 2.2%). We found no evidence that detection probability of beaver sign varied by vegetation class (AIC_c weight = 0 for all models that included vegetation classes), but we did find strong support for using craft to model detection probability (AIC_c weight = 1 for the model including craft). Specifically, the use of kayaks doubled the probability of detection (kayak p = 0.61, raft p = 0.29).

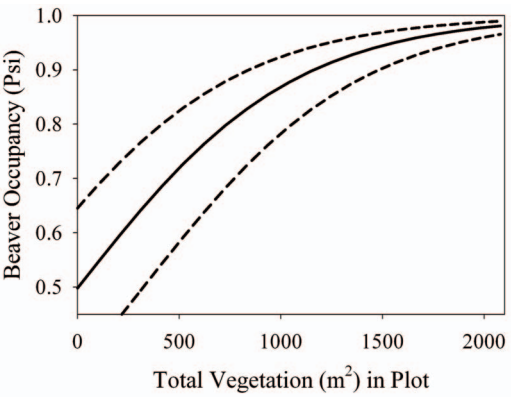

Fig. 2. The predicted relationship (solid line; dashed lines show 95% confidence interval) between use of a site (occupancy) by beavers and coverage (m^2) of total vegetation comprising 7 vegetation classes along the Colorado River, Grand Canyon. Size of sampling plot was 1715 ± 27 m^2.

We found support for using TotVeg to model occurrence of beaver sign in that the model including TotVeg as a covariate for occupancy ranked higher than the model without TotVeg ($QAIC_c$ weight = 0.93, Table 2). Furthermore, the β parameter for TotVeg had a 95% confidence interval that did not overlap zero (β value = 0.72, 95% CI = 0.11–1.32), indicating that beaver sign occurrence increased as the amount of total vegetation increased (Fig. 2). Overall occurrence of beaver sign was 0.74 (SE = 0.06), indicating that beaver sign occurred in about 75% of sampled areas within the Grand Canyon. Our analysis to determine whether any of the 7 vegetation classes were more important for occurrence of beaver sign indicated that *Tamarix* and *Pluchea* had relative importance scores that were 1.2–2.5 times greater than wetland, sparse shrub, *Prosopis-Acacia*, nonvegetation, and *Baccharis-Salix* (Fig. 3). Wetland had a relative importance score that was 1.2–1.4 times greater than the 4 vegetation classes with the lowest relative importance scores (Fig. 3). The 95% confidence intervals overlapped zero for the model-averaged β values of the 7 vegetation class covariates (Fig. 3).

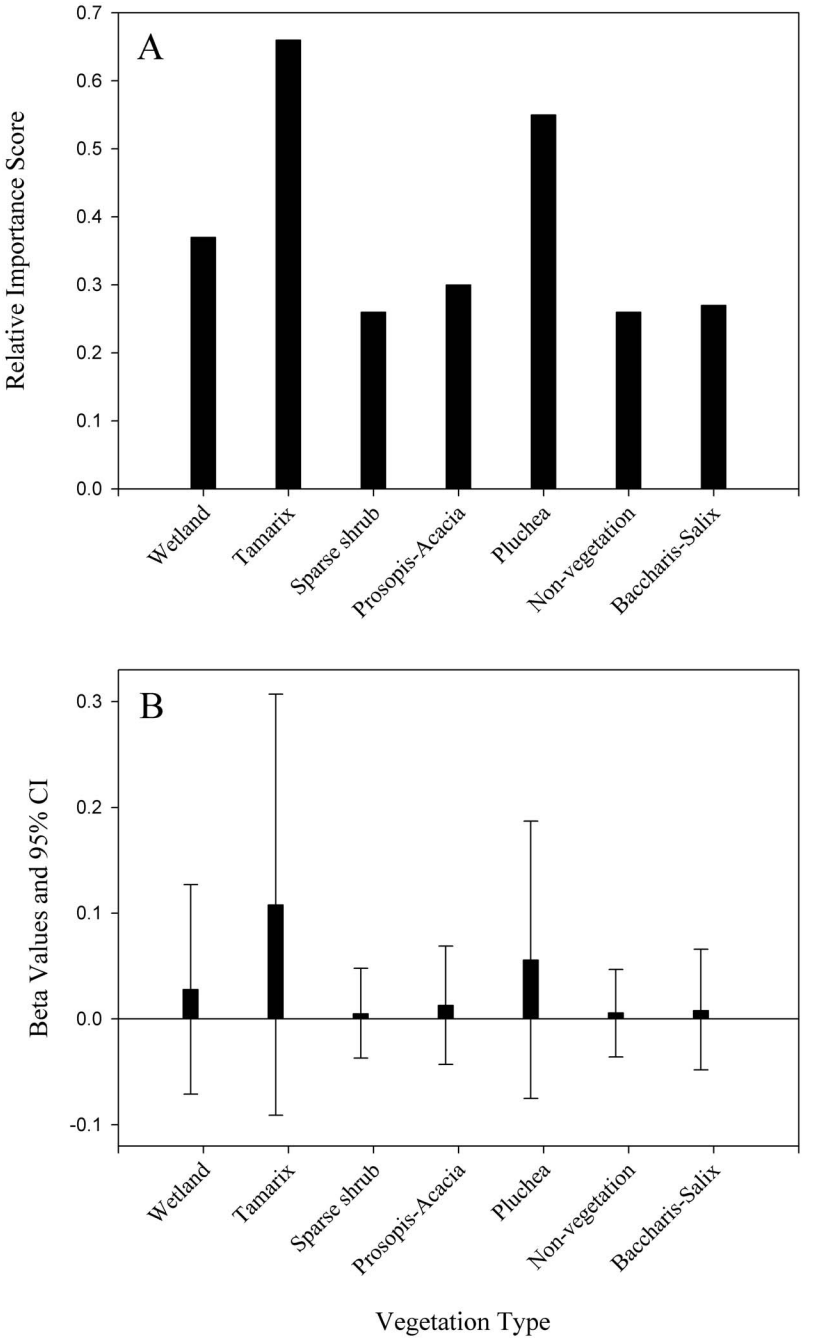

Fig. 3. (A) Relative importance scores and (B) model-averaged β estimates (unconditional SE) and 95% confidence intervals for the β estimates for the 7 vegetation predictors of beaver (*Castor canadensis*) use of sites along the Colorado River in Grand Canyon. Relative importance scores and β estimates were calculated by running all possible models generated from the inclusion of 7 vegetation classes (see methods for details).

DISCUSSION

Our estimate of occurrence indicated that beaver activity was common (74% of sampled sites) throughout the Grand Canyon and was more likely with greater riparian vegetation cover (Fig. 2). This robust association between beaver occurrence and total vegetation cover indicated that a gross measurement of the total vegetation within 10 m of shore was a useful indicator of beaver sign occurrence on the Colorado River. This indicator is likely accurate in other systems, particularly in systems that have heterogeneous amounts of vegetation cover within the river system. Breck et al. (2001) found that beaver densities were nearly twice as high on the flow-regulated Green River than on the comparable free-flowing Yampa River. In this system, the Yampa River had greater amounts of riparian plant cover, but, during much of the year, it was unavailable for use by beavers because of the creation of large sandbars during low water that inhibited beaver activity. The result was that beaver territories on the Yampa were interspersed with areas of nonuse, resulting in lower density.

Because the amount of riparian vegetation and its availability to beavers have increased in the Grand Canyon due to flow regulation (Turner and Karpiscak 1980, Stevens et al. 1995, Ralston et al. 2008), it is likely that beaver density has also increased. However, our results neither support nor refute this hypothesis, primarily because occurrence of beaver sign as we measured it cannot be used as a surrogate for beaver density. A more meaningful focus to more directly address this question would be lodge-site occurrence because beavers practice central-place foraging (Hood and Bayley 2008). Therefore, lodge-site location is more closely tied to habitat use, longer-term distribution, and animal fitness and demographics. Information about lodge-site selection could not only improve understanding of the use of riparian corridors, but could also be useful for monitoring changes in populations. Lodges occurred along only 3.0% of transects, and because of these low sample sizes, we were unable to analyze lodges separately from other types of beaver sign. For future efforts, sampling units larger than we employed, combined with an increase in the number of sampling events, would putatively address naturally low occurrence and low detection, thus increasing the utility of lodge sites for monitoring efforts. We note that beavers in this system may be bank-dwelling and that the few lodges we detected were cryptic and unlike "typical" lodges encountered in beaver ponds. The best time to survey may be during lower-flow periods when the river is not at bank-full depth.

Our results indicated that *Tamarix*, *Pluchea*, and, to a lesser degree, wetland vegetation classes were potentially higher-quality areas for beavers in the Grand Canyon (Fig. 2). *Tamarix* is not known to be preferred forage for beavers, and thus we speculate the relationship between beaver occurrence and *Tamarix* was more likely because *Tamarix* can form dense stands that tend to stabilize river banks. These stands probably created good cover and areas suitable for bank dens. Indeed, the few observations of beaver and beaver dens were all anecdotally associated with thick stands of *Tamarix*. The reason for the relatively strong relationship between *Pluchea* and beaver occurrence is unknown. *Pluchea sericea* is a rhizomatous evergreen shrub that can form dense thickets along riparian areas of deserts in the southwestern United States. *Pluchea* can be important forage for burros and mule deer (Hanley and Brady 1977, Marshal et al. 2004) but, to our knowledge, has not been documented as an important food species for beavers. *Pluchea* is fairly abundant in the riparian zone of the Grand Canyon (Ralston et al. 2008), and because of its ability to form dense thickets, it is possible that like *Tamarix*, *Pluchea* also provides good cover for beavers and good areas to create bank dens. We also detected a relatively weak association between occurrence of beaver sign and wetland vegetation. The wetland plant association may provide important food sources for beavers in the form of herbaceous plant species (Svendsen 1980, Roberts and Arner 1984). Little research has considered the importance of herbaceous plants in supporting beaver populations, but in a system like the Grand Canyon, with no over-winter ice cover and a longer growing season, herbaceous plant material may form a bigger part of beaver's diet.

Discussion on the importance of various vegetation classes must be tempered by 2 important limitations of this study. First, even though we found stronger associations for 2 or 3 vegetation classes, the 95% confidence intervals

around the β estimates for these vegetation classes still overlapped zero, indicating a weak association and/or a great deal of variability around the β parameters. Second, we sampled vegetation coverage based on foraging patterns of beavers (i.e., 10 m inland from the water's edge), partially implying that forage was the primary reason beavers selected various vegetation types. But, as our results indicate, it is possible that beavers were not responding to amount of vegetation cover 10 m inland, but to other characteristics such as bank stability, forage quality, or the number of predators along sections of each reach. Because we pooled all types of beaver sign together, we likely diluted any patterns of foraging use based on the amount of vegetation cover. We treated tracks equal with more direct evidence of habitat use (i.e., foraging, dens). Tracks, however, may not reflect selection for vegetation and could result from dispersal, territoriality, or movement for reasons unrelated to foraging; therefore, tracks may have a weak link to vegetation.

Our results indicated that beaver were distributed widely in the Grand Canyon Colorado River corridor and were positively associated with total vegetation cover, *Tamarix,* and *Pluchea.* More broadly, we showed success at using agile crafts (i.e., kayaks) to increase detection probability and double naïve estimates of beaver occurrence. We developed our methods for estimating occurrence of beavers in a canyon setting, and similar methodology could be applied to riverine systems in non-canyon areas. Furthermore, aspects of our methodology, such as staggering the start of independent surveyors, provide valuable guidance in improving occupancy-sampling designs for cost-effective monitoring of a wide variety of riverine biota on remote rivers with difficult access.

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