BIRD ABUNDANCE AND RICHNESS IN A DESERT RIPARIAN AREA FOLLOWING BEAVER RE-INTRODUCTION

by

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ABSTRACT

I measured bird abundance and richness along the upper San Pedro River in 2005 and 2006 to investigate how beavers (*Castor canadensis*) may act as ecosystem engineers after reintroduction to a southwestern U.S. desert riparian area. In areas where beavers colonized, I found higher bird abundance and richness of bird groups such as all breeding birds, insectivorous birds, and riparian specialists, and higher relative abundance of many individual species—including several avian species of conservation concern. After accounting for environmental factors such as presence or persistence of surface water, and extent of Frémont cottonwood (*Populus fremontii*) and Goodding willow (*Salix gooddingii*), the relative influence of beaver activity was not as strong as these other environmental factors. However, there was still evidence of an association between beaver activity and bird abundance and richness, as models that included beaver-related variables better explained variation in bird abundance and richness for 71% of species groups 46% of individual species we built models for. Though the effect sizes associated with the beaver influence on the bird community were smaller than similar studies conducted in other regions, the biological significance of beaver activity within the upper San Pedro River riparian area will likely become even stronger with increasing time since the reintroduction.

INTRODUCTION

Interactions among organisms are often examined by ecologists to help understand dynamic processes affecting the distribution and persistence of species. For example, interactions can be trophic or chemical, competitive or mutualistic, intra- or inter-specific. The concept of ecosystem engineering is used to investigate interactions that arise when an organism physically creates or modifies its environment and thereby changes the availability of abiotic resources required by other organisms, which may result in direct, indirect, or cascading biotic effects (Jones et al. 1994, 1997, 2010, Berke 2010, Thomsen et al. 2010). The strength of ecosystem engineering and the effects it can exert on community dynamics can be explicitly parameterized to help generate testable hypotheses and predictions, as demonstrated in observational, experimental, and modeling studies investigating hundreds of species and ecological contexts (Badano and Cavieres 2006, Wright and Jones 2006, Hastings et al. 2007, Cuddington et al. 2007, Cuddington et al. 2009, Wright et al. 2003, Wright 2009, Jones et al. 2010). The concept focuses attention on 1) the *process* by which organisms may change the *physical structure* or other *abiotic* dimensions of their environment, and then 2) the *consequence(s)* physical changes may have on *biotic* elements in the community (Jones and Gutiérrez 2007, Jones et al. 2010). While there is some overlap with other terms (e.g., foundation species, dominants, habitat cascades, niche construction, facilitation, keystone species) ecosystem engineering is not synonymous with these concepts, for example because it is *not* dependent on disproportionate effects of a species or organism's biomass, trophic interactions, evolutionary consequences of habitat formation, or purely beneficial interactions (Jones et al. 1994, Wright and Jones 2006, Hastings et al. 2007, Berke 2010). When focusing on a specific organism, one could classify both "autogenic" ecosystem engineers that modulate abiotic resources through their physical structure alone (e.g., coral reefs, kelp beds, large trees) as well as "*allogenic*" engineers that can modify their environment through behavior (e.g., mammals burrowing in the earth or woodpeckers excavating cavities). However, since all organisms modify their environment to some degree, the question "is this species an engineer?" is not particularly informative. Rather, by focusing on the process when it is relevant, e.g., "how and when do ecosystem engineering activities of an organism exert influence on other organisms?" new insights can be gained regarding the direct or indirect interactions that influence community dynamics and structure (Jones et al. 2010).

The concept of ecosystem engineering is relevant and has proved useful in applied contexts where the goal is to conserve or restore populations or ecosystem function (Wright et al. 2002, Byers et al. 2006, Crain and Bertness 2006, Boogert 2006, Moore 2006, Laland and Boogert 2010, Griffiths et al. 2010). Beaver (*Castor canadensis*) are often cited as the quintessential ecosystem engineer, and have consistently been promoted by resource managers in North America and Europe as an inexpensive tool for restoring ecological function in riparian areas (Apple 1985, Olson and Hubert 1994, Fredlake 1997, Albert and Trimble 2000, Baker and Hill 2003, Rosell et al. 2005, Boyle and Owens 2007, Prettyman 2009). Throughout North America beavers historically had a profound impact on stream ecology and watershed function, and after extensive extirpation due to trapping in the 18^{th} and 19^{th} centuries, the species returned to portions of its former range during the 20^{th} century—both through natural re-colonization and human reintroduction (Naiman et al. 1988, Baker and Hill 2003, Rosell et al. 2005). Despite beavers' consumption of riparian vegetation and use of plant material to build dams, many land managers and restoration ecologists believe the benefits to the ecosystem as a whole outweigh any consequences of herbivory or felling of trees (Apple 1985, Olson and Hubert 1994, Fredlake 1997, Albert and Trimble 2000, Fouty 2002). Ostensibly, the potential benefits of beaver on ecosystems that are sought by managers are the same as the ecosystem engineering effects (described below), though this is not always explicitly stated as such.

A beaver's ecosystem engineering process begins with several abiotic effects on the environment. Beavers create dams that impound water, reduce water velocity, promote deposition and retention of sediments, organic matter, and dissolved nutrients, while reducing turbidity downstream. At larger scales, beaver dams can modulate high flow events and capture precipitation that is then released slowly into the groundwater and stream channel, which ultimately can alter erosion patterns, stream channel morphology and stream gradients (Naiman 1988, Gurnell 1998, Baker and Hill 2003). In addition to maintaining hydrologic stability, or even de-entrenching some down-cut stream channels (Albert and Trimble 2000), the totality of beaver influences typically make some resources more available such as water, organic matter and nutrients such as dissolved nitrogen and phosphorous (Naiman et al. 1988, Wright et al. 2003, Baker and Hill 2003). Additionally, through creation of canopy gaps due to tree felling, beaver activity can alter the temperature and moisture gradients in their terrestrial environment, and create a mosaic of disturbed and undisturbed patches with different levels abiotic conditions or resources required by other species (Wright et al. 2002, 2003).

Given such dramatic effects on the abiotic components of the environment, many studies have found biotic consequences associated with beaver activity, for example raised water tables and increased soil-water interface can facilitate germination, recruitment, and primary production of trees and shrubs and thus have a positive feedback on beavers, as well as other species dependent on riparian vegetation (Naiman et al 1988). Beaver activity has been associated with higher species richness and abundance of a broad range of taxa including plants, odontanate insects, aquatic invertebrates, fish, amphibians, reptiles, and small mammals (Wright et al. 1996, 2003, Baker and Hill 2003, and Rosell and Parker 2005, Rosell et al. 2005). Many anecdotal natural history accounts have noted that bird communities appear to thrive where beavers are found (Carr 1940, Muller-Schwarze 1992, Wilkinson 2003, Nijhuis 2011). The majority of rigorous (e.g., experimental) studies regarding the effects of beaver activity on birds have focused on waterfowl (Anatidiae), oftentimes demonstrating a positive effects of beaver ponds on habitat use and vital rates (Speake 1956, Arner 1963, Renouf 1972, Nummi 1989, 1992, Nummi and Poyosa 1997, Nummi and Hahtola 2008, Merendino 1995, Hartke and Hepp 2004, McKinstry et al. 2001). Observational studies on other groups of birds (e.g, songbirds), although fewer in number, have also consistently found that beaver activity is correlated with higher species richness and abundance in both mesic environments of eastern North America (Reese and Hair 1976, Edwards and Otis 1999, Grover and Baldassarre 1995, Bulluck and Rowe 2006, Aznar and Desrochers 2008) and in more arid regions in western North America (Brown and Parsons 1996, Medin and Clary 1990, Cooke and Zack 2008). Yet in these studies, explanations for these effects are typically correlative, invoking increases in riparian vegetation, open water, prey (e.g., insect) availability, and structural complexity at small and/or large scales.

Despite the presumed effects of beaver on birds, specific mechanisms by which beaver activity affects avian communities have only been studied for waterfowl. Past studies on the association between beaver and bird communities have usually assumed that observed differences between areas with beaver and surrounding environments could be attributed to the beaver activity. Beaver habitat selection may also explain some of these observed patterns, yet few studies have attempted to account for co-varying factors that could simultaneously influence the habitat selection of both birds and beavers (but see Cooke and Zach 2008, Chandler et al. 2009).

Beaver were once widespread in riparian areas in the southwestern U.S., although they were largely extirpated in the 19th century (Baker and Hill 2003, Webb et al. 2007). The gallery forests of cottonwood and willow in the Southwest support breeding bird communities known for being among the highest density and diversity in North America

(Carothers 1974, Hunter et al. 1987). In southeast Arizona, beavers were so common along the San Pedro River in the 1800's that James Ohio Pattie named it the "Beaver River" in 1825 (Webb et al. 2007), yet by the early 20th century this mammal was extirpated there.

In 1984 when the Bureau of Land Management (BLM) assumed stewardship of approximately 75 km of the upper San Pedro watershed and created the San Pedro Riparian National Conservation Area (SPRNCA), conservation of birds and other wildlife became a central management objective. In cooperation with Arizona Game and Fish and others, BLM personnel re-introduced beaver in the SPRNCA from 1999-2002, resulting in at least 40 individuals present in 13 different sites by 2005 (M. Fredlake, personal communication). Along with returning a potentially important native species to the ecosystem, goals of this program were to increase water retention, restore the structural heterogeneity of vegetation, and enhance conditions for wildlife (Fredlake 1997).

Similar to other locations where beaver activity exists in conjunction with a management priority on birds (e.g., Longcore et al. 2007), some have voiced concerns that beaver activity may jeopardize the riparian forests and the bird community of the SPRNCA (M. Fredlake, personal communication). For example, tree-felling by beaver could reduce canopy cover needed by some birds such as the Yellow-billed Cuckoo (*Coccyzus americanus*), a candidate for listing under the Endangered Species Act that is relatively common along the San Pedro compared to other river systems in the region

(Johnson et al. 2010). Conversely, reduced over-story canopy of cottonwood, an increase in early successional (i.e., shrub-form) growth of willows, and other components of beaver activity are associated with habitat for Willow Flycatcher (*Empidonax traillii extimus*; Finch et al. 2000, Sogge and Marshall 2000), which is listed as threatened in Arizona at both the state and federal level. Increases in habitat for the flycatcher in this area may contribute to recovery given the species' historical and contemporary nest records in the local area combined with the presence of large populations to the north along the lower reach of the San Pedro (Johnson and van Riper in prep). However, if beaver heavily utilized willow or cottonwood and caused net losses to either of these woody species, it could affect both of these bird species of conservation concern as well as many others that depend on riparian vegetation.

Within a few years after the reintroduction of beaver, the reduction in over-story canopy and/or construction of dams and retention of water were expected to be the potential pathways for abiotic influences of beaver activity—and thus initial components of the ecosystem engineering process. The primary abiotic driver for the majority of bird species on the upper San Pedro is the depth or availability of water, because this directly affects the extent and vigor of riparian vegetation, which in turn can affect vegetative and insect food availability, nesting substrate, cowbird parasitism, and nest predation (Brand et al. 2010a, 2010b, 2011). Previous studies along the San Pedro have empirically demonstrated how groundwater depth is the key driver of vegetation dynamics, especially determining the extent of cottonwood and willow in reaches with relatively shallow (available) groundwater versus reaches more dominated by tamarisk and/or mesquite in areas with deeper (less available) water (Stromberg et al.1998, Leenhouts et al. 2005, Stromberg and Tellman 2010). The extent and persistence of surface water is also affected by groundwater depth, and though surface water does not directly drive vegetation dynamics (Stromberg et al. 1998) it is crucial to water-dependent birds such as Mallard (*Anas platyrhynchos*) and others (Brand et al. 2010a).

I investigated the potential for activities of beaver to affect the riparian ecosystem and influence breeding bird communities along the upper San Pedro River. I hypothesized that if beavers were affecting the environment through the ecosystem engineering process, I would find that differences in the breeding bird communities along the river would be non-randomly associated with where beavers had settled. However, I recognized the possibility that any non-random association could result either from an ecosystem engineering process and its effects on water and riparian vegetation structure (i.e., increased shrub cover due to more water availability and/or through a direct reduction in canopy over-story cover due to tree-felling) or simply be the result of both beaver and certain bird species being drawn to the same environments. Depending on the length of time beaver had been in the system (3-6 years depending on the site and settlement date), bird community structure could be influenced more by water and vegetation dynamics than beaver activity.

To consider the full complement of environmental conditions present on the upper San Pedro I sampled throughout this portion of the watershed along a gradient of vegetative and hydrologic conditions, which included areas with and without beaver but that were otherwise similar. I specifically assessed three questions: 1) Were there differences in the number of breeding bird species and the abundance of individual species where beavers were present in the SPRNCA? 2) Were differences in these parameters attributable to environmental factors that were merely correlated with beaver habitat selection? Or alternatively, 3) was there evidence that observed differences could be attributed to beaver activity—either from tree felling and/or the creation of dams? Because the area is specifically managed for birds I wanted to assess if the distribution of birds—especially species of concern—and beaver were spatially related in any way, and thus whether beaver activity might lead to management concerns or opportunities in relation to the beaver reintroduction program. I extensively sampled birds and environmental attributes, and then modeled the potential relationships between the avian community and factors in their environment including vegetation, water, and beaver activity.

STUDY AREA

I studied interactions between bird communities and beaver in the lower riparian floodplain terrace and channel (and “channel shelf” and “floodplain bank”, especially when vegetated; Hupp and Osterkamp 1996) along 68.5 km of the upper San Pedro River, within the boundaries of the SPRNCA. The SPRNCA extends from the international border with Mexico north approximately 60 km to St. David, Arizona, and is managed by the Bureau of Land Management. Elevation ranged from 1,125 m at the northern-most portion of my study to 1,285 m at the southern-most point, 2.5 km north of the international border. Prior research conducted on the upper San Pedro River has described the interaction between groundwater, surface water, and vegetation community dynamics within and adjacent to the riparian areas (see Stromberg and Tellman 2010, and Webb et al. 2007 for reviews), providing the basis for the following summary. The upper San Pedro contains reaches with perennial, intermittent, and ephemeral surface water. Riparian vegetation consists primarily of Frémont cottonwood (*Populus fremontii*) and Goodding willow (*Salix gooddingii*) as the dominant over-story canopy, with seepwillow (*Baccharis salicifolia*) often present in the understory along wetter reaches. Mesquite (*Prosopis velutina*) occurs on higher floodplain terraces adjacent to the primary riparian vegetation. Mesquite and non-native tamarisk (i.e., saltcedar *Tamarix chinensis* and closely related species) are regular yet minor components of the vegetation throughout the length of the study area, and dominate along some of the drier, ephemeral reaches in the north of the study area where groundwater is deeper and less accessible. Tamarisk, especially, forms fairly homogenous stands in some areas in the northern section of the study area near the community of St. David, though there are scattered remnant or senescing cottonwood trees. Additional woody species present in the study area include velvet ash (*Fraxinus velutina*), Arizona walnut (*Juglans microcarpa* v. *major*), netleaf hackberry (*Celtis reticulata*), western soapberry (*Sapindus saponaria*), and desert willow (*Chilopsis linearis*). Emergent vegetation at sites with perennial, slow-moving water include bulrush (*Scirpus sp.*), cattail (*Typha domingensis*) and various species of sedge (*Carex sp.*).

In the early the 19th century the San Pedro River basin was documented as being swampy, with beaver dams, isolated patches of gallery cottonwood forest, and a high water table and extensive sacaton grasslands within the primary floodplain (Stromberg and Tellman 2010). Similar to much of the Southwest in the second half of the 19th century, channel incision and arroyo formation started to occur on the upper San Pedro, draining wetlands and resulting in a lower water table. Like previous arroyo-formation, channel widening, and fill-in cycles over the last 8,000 years, the documented entrenchment on the San Pedro and throughout the Southwest is correlated with a climate-flood cycle (Webb et al. 2007). However, in the 19th century anthropogenic factors (e.g., livestock grazing, removal of beaver dams, wood cutting, agriculture and ground-water use) may have contributed to the speed and severity of entrenchment. River down-cutting and channel widening continued through the 1930's, after which cottonwood and willow established itself more widely as the channel stabilized and secondary, lower floodplains formed adjacent to the main channel. Throughout the later 20th century riparian vegetation continued to expand in extent and height along the new, lowered floodplain of upper San Pedro, especially during the 1980's and early 1990's (Webb et al. 2007, Stromberg and Tellman 2010). The removal of cattle grazing in the 1990's probably contributed to increased riparian vegetation production and the dramatic increases in bird abundance in the SPRNCA documented by Krueper et al. (2003).

Due largely to the current extent of cottonwood-willow cover along the upper San Pedro, the area is recognized as a regionally important area for breeding and migrating birds, and has been the site of multiple avian studies (Skagen et al. 1998, Krueper 1999, Krueper et al. 2003, Brand et al. 2008, 2010a, 2011, McFarland et al. 2011). In a review, Brand et al. (2010b) found that breeding bird species richness estimates from the upper San Pedro were approximately twice as high as reported from other Southwestern rivers. The river is perhaps best known for its recreational bird-watching opportunities and for the near-certainty that local ground-water pumping is depleting the aquifer that supplies the river's surface water and supports the adjacent cottonwood-willow riparian forests (Stromberg and Tiller 1996, Stromberg et al. 1998, Rojo et al. 1999, Steiner et al. 2000, Davis 2004, Steinitz et al. 2005, Mac Nish et al. 2010).

METHODS

To estimate abundance of breeding birds, I used variable-radius point count surveys combined with distance sampling (Reynolds et al. 1980, Ralph et al. 1993, Buckland et al. 2001, Thomas et al. 2010) from 24 May to 24 July, 2005 and 2006. To quantify environmental conditions at point count stations, I documented the presence of surface water and its persistence through the dry season, canopy cover and basal area of all woody plants, and width of riparian vegetation areas along the river channel. To quantify the presence and intensity of use by beaver, I also utilized data on beaver activity and location collected by BLM staff from the time of initial release in late 1999 through spring 2005, and then documented all beaver activity at and near the survey stations in 2005 and 2006. I then used model selection techniques to evaluate the strength of associations between bird population and community parameters, beaver activity environmental factors.

Sampling Design

To achieve extensive spatial coverage across riparian vegetation areas targeted for sampling, I randomly chose a start point and placed survey points systematically throughout the SPRNCA. Survey stations (n = 240) were located every 250-285 m along the upper San Pedro River in riparian vegetation adjacent to the river on the lowest available floodplain terrace, which was typically just above (0.5-2 m) the river level. The initial stations were located randomly at 100, 200, or 300 meters from bridges or other access points along the river, and then additional stations were systematically placed within available riparian vegetation, utilizing Garmin 12XL and 12X GPS units to estimate distances between stations. The distance of a given station from the river's edge varied slightly depending on the perpendicular width of the riparian vegetation corridor, but was typically placed under canopy cover within 10 meters of the river-side edge of riparian vegetation. At some locations (less than 10%) with very wide riparian corridors and/or where floods had scoured vegetation, stations were placed 16-46 m from the edge of the river. Previous observations by BLM personnel indicated beaver were building dams in the San Pedro on or near larger (>5m) wash-inlets, so when beaver dams or wash inlets were encountered more than 100 meters from a previously established survey station, the station was replaced with a new station located 5-15 meters up-river of the dam or wash inlet.

Bird Surveys

I used modified point-count survey methods (Reynolds et al. 1980, Ralph et al. 1993) incorporating field procedures for distance sampling (Buckland et al. 2001, Thomas et al. 2010) to estimate bird abundance and breeding bird species richness. Seven-minute point count surveys were conducted from mid-May to early August, which represents the most active period of breeding bird activity in this riparian area. Though surveys were conducted from 15 May to 5 August, I only utilized surveys from 24 May to 24 July; lingering winter birds and/or late-spring migrants complicated detection of territorial singing birds earlier in May, and rain and flood events during late July and early August precluded consistent and/or safe sampling in the lower floodplain thereafter. After excluding these surveys (before May 24 and after July 24) for which detectability of breeding birds was compromised, total effort at each station over the two years ranged from 5 to 8 visits. Field personnel surveyed 8-15 stations per morning between 0500-0900 hrs. Throughout the survey period each year stations were visited at a variety of times during the day by randomizing start points of successive visits. For each bird detected the observer estimated the distance (to nearest m) visually or with Bushnell Yardage-Pro laser rangefinders, and also recorded the detection type (song, call, visual, moving/flying within riparian vegetation, or flyover) and whether birds were detected within the first five minutes or the last two minutes. Indications of breeding activity were documented at every opportunity during or between surveys, along with incidental sightings of rare species and those of conservation concern (Johnson and van Riper in press).

To account for variation in detection probabilities (e.g., due to bird behavior, observer skill, environmental factors, and because the adjacent upland environment generally had much fewer birds which were not as likely to be affected by beaver activity), I included only birds detected within 50 m of stations for analyses. I arrived at this distance cut-off point through several lines of evidence. A line fitted to a plot of the number of birds detected within 100 meters of the stations approached a horizontal asymptote at approximately 50 meters (Figure 1), due to the decreased detectability with increasing distance coupled with the proximity of the edge of the riparian corridor.

Histograms of detection distances from point count stations typically demonstrate an increasing number of detections within distance categories further away from the center point, due to the effect of increasing area of each successive distance-bin, and the point at which detectability drops significantly can be inferred by noting where the “shoulder” to the right of the peak is located (Emlen 1971, Buckland et al. 2001). I checked this assumption by evaluating the relationship between detectability-adjusted estimates of density and relative abundance.

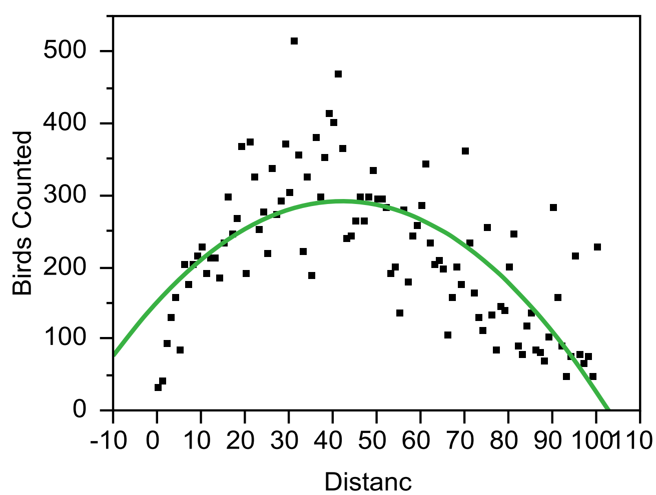

Figure 1. Number of birds counted (Y axis) within 1 meter Distance bins (X axis) along the upper San Pedro River, May-July 2005 and 2006; a total of 22,166 bird detections are represented.

I used the multiple covariate distance sampling approach within program DISTANCE (Marques et al. 2007, Thomas et al. 2010) to construct detection probabilities and density estimates per hectare for two of the more common species in the study, Yellow Warbler (*Setophaga petechia*) and Song Sparrow (*Melospiza melodia*).

These density estimates for each station were then compared to the maximum number of singing males detected per visit, median number of singing males detected across all visits, and relative abundance (total number of birds detected at each station divided by effort at the station, i.e., the average number of birds/visit) calculated from my raw data but truncated at 30, 50, 60, 80, and 100 meters. I used the 50-meter truncation distance for all bird species as it was most closely correlated to the program DISTANCE-derived density estimates (see Results). Though this obviously left out many detections (i.e., singing birds beyond 50 m), I felt this truncation distance was an appropriate balance of considerations related to detection probability, the extent of vegetation measurements (the majority of which were within 30 m), and inclusion of a representative sample of birds using the station-area.

I recorded all birds detected, including migrants and vagrants, yet for my analyses considered only species known to breed in the upper San Pedro River Valley (Krueper 1999, Krueper et al. 2003, Brand et al. 2008, 2010a). Birds were excluded if detected flying over the canopy at the station and not utilizing the surrounding riparian environment.

Avian Species Groups

In addition to considering only breeding bird species (using my own observations as well as those of Krueper 1999 and Brand et al. 2010a), I grouped some species that use similar environments or have similar foraging strategies. I used prior research (Hunter et al. 1987, Krueper 1999, Brand et al. 2010a) to determine: 1) which bird species are, or are not, associated with riparian environments in the southwestern U.S., and then 2) for each of the riparian-associated species whether they are considered riparian generalists or riparian obligates. I grouped species as a "riparian generalist" if known to utilize multiple riparian vegetation types (e.g., mesquite and tamarisk, either more often or in equal proportion to cottonwood/willow use), and I grouped species as a "riparian specialist" if either obligated or strongly associated with cottonwood-willow forests and/or surface water on the upper San Pedro according to Brand et al. (2010a), Krueper (1999), or Hunter et al. (1987). For all species detected, I also determined whether each was of conservation concern status if the species was indicated by Hunter et al. (1987) as "declining" in Southwestern broadleaf riparian forests, or if it was included in the "Birds of Conservation Concern" list of the U.S. Fish and Wildlife Service (2008).

Environmental Measurements

I quantified a range of environmental conditions at each survey station. To estimate canopy cover for each species of tree and shrub I added all percent cover estimates from nine different height strata measured (0-1 meter, 1-3m, 3-5m, 5-7m, 7-10m, 10-15m, 15-20 m, 20-25m, 25-30m) for each of five dominant woody species, i.e., cottonwood, willow, tamarisk, mesquite and seepwillow. To estimate upper levels of canopy cover for cottonwood, I also included "canopy cover from 20-30 m" to ensure I accounted for this potentially important variable. To measure standing tree density, I recorded diameter-at-breast-height (DBH) for all trees within 30 meters. To estimate relative abundances of different size classes of trees and shrubs I considered all woody stems within a 30-meter radius of the station center and used Biltmore sticks and/or DBH tapes to check sizes and recorded measurements to the nearest centimeter. I also recorded when trees had signs of beaver gnawing (these are reported with other living trees when reporting canopy cover and for most basal area measurements) and measured the diameter of all beaver stumps, beaver-created snags, or felled trees, measuring as close to 1.3 m from the ground to stem when possible, or as high as possible for stumps. To analyze tree mortality and canopy openings related to beaver within the 30-m vegetation plots, I combined beaver-created stumps, snags, and recently downed trees of willow and cottonwood into one grouping, because it was often difficult or impossible to distinguish between stumps of willow or cottonwood (especially after a year or two of weathering), and because there were few beaver-created snags or beaver-felled trees. For analyses, DBH measurements were transformed to individual tree basal areas (DBH^2* 0.00007854; Dunster and Dunster 1996) then all basal area measurements for each plot were summed for each species within each of 6 DBH size classes (size 1 = 1-4 cm dbh, 2 = 5-11 dbh, 3 = 12-18 dbh, 4 = 19-25 dbh, 5 = 26-52 dbh, 6 = >53 cm dbh) for five dominant species (cottonwood, willow, mesquite, tamarisk, and Baccharis) and for stumps. Due to colinearity between these classes, for analyses, I condensed the live woody stems into three classes (<12 cm DBH, 12-25 cm DBH, and >25 cm DBH) and beaver-created stumps, snags, and recently felled trees were condensed into one basal area class which was the sum of their values at each site. Because other woody species are relatively minor components of the canopy, I did not test for effects for all species.

For example, cottonwood, willow, mesquite, and tamarisk made up 95.3% (16,907) of all stem and stump diameters recorded (17,724), with seepwillow comprising another 2.3 % (418 stems). Basal area calculations are presented directly as measured then summarized (in m^2) for each 30-meter radius plot surrounding the station, or 2826 m^2 (0.2826 hectare) rather than extrapolated to a single, larger unit (hectare, squared km, etc.). An index of vegetation structure was created by allocating a “1” to each height strata level above 1 meter (all sites had some vegetation below 1 m) with vegetation cover, which were then summed to get a "Vegetation Height Diversity" at each site (scored from 1-7).

To categorize riparian vegetation and geomorphological influences at the stations outside 30 m, I measured the over-all width of riparian vegetation perpendicular to orientation of river, distance from the survey center point to edges of riparian vegetation, river bank, and other habitats farther away (e.g., grassland, mesquite savannah, or mesquite bosque), width and depth of river, and other vegetative and geomorphic factors such as vegetation community type(s) in each area and depth of entrenchment/terracing. During the analysis phase I reduced these variables considerably (from > 100 columns to less than 20), for example, reducing the canopy coverage classes to either the “average % cover” (all percent cover measurements within each height strata, divided by the number of strata with measurements), and by not including more than one of any two highly correlated variables in the final analysis. Table 1 summarizes environmental measurements used for analyses.

Beaver and Water Measurements

Immediately after each avian survey and while transiting along the river between survey stations I recorded beaver sign (dams, gnawed trees, stumps, downed trees) and condition of river (dry, recently dried, or water present, and if present whether shallow or deep, <0.2 m and >0.2m, respectively) at the stations. Water data were summarized to provide a measure of the persistence of surface water throughout the dry season before the late-summer monsoons. I considered three classes of surface water conditions as potentially important to birds: if a station was dry from May through June (unless a rain or flood event occurred, i.e., "ephemeral"), if a station had flowing water which persisted until at least late May (but later dried up at some sites) when many birds are setting up territories or have already settled into their breeding activities, and if a site contained perennial water which lasted throughout the summer (Table 1). I used indicator variables for the latter two classes (i.e., =1 if condition is true at the site) and sites without either of these water conditions were used as the reference levels (i.e., =0; Table 1).

Data were provided for beaver activity locations from late 1999 through early 2005 by BLM personnel, and I collected these data from 2005-2006, which I categorized by year according to an annual cycle which started after the majority of rains and flooding from the summer monsoon season had subsided (October 1) and extending for the following year. To determine beaver influence at each avian survey station I projected two circles of 50-m and 100-m radius around each station in Arc Map 9 (ERSI, 2009; displaying map at a 1:3,200 scale). For each year period, I projected all spatial beaver information around each station location and determined proximity of dams and sign within each 50-m or 100-m distance bin, or within 150 m downriver because downriver dam locations regularly had backwater up to 150 m upriver, and beavers use this water to travel and forage. If a dam or location coordinates appeared to span both sides of a distance-boundary (e.g., from 45-55 m), I included it within the closer category.

To model beaver activity as an explanatory (independent) variable at each avian survey station I included three variables in my analyses: presence/absence, number of years where a dam was present within 50 m, and an intensity scale which ranked sites according to beaver presence and both the distance to dams and the number of years dams were located in the vicinity of stations (see Tables1-3). Presence was inferred by beaver sign documented within 100 meters of the station (in any year), and included dams, gnawed trees, stumps, bank dens, and other signs of occupation. I counted the number of years in which a dam was present within 50 m or 100 m of a given station, or 150 meters if the dam was downriver, but used just the number of years stations had a dam within 50 m as the only continuous variable related to beaver activity. In order to rank the intensity of beaver use at sites I considered the results that the BLM and I documented (Tables 2 and 3) and created the following levels of indicator variables, with the reference level set to “beaver absence”: low-use sites which did not include sites with any dams but did include any other “beaver presence” sign such as bank dens and/or at least 10 gnawed/felled trees documented within 100 meters of the avian survey station ("beaver level 1"); moderate-use sites where no more than one dam was located within 50 m of a station, and/or where stations had less than 3 dams documented within 100 m of a station, in any year ("beaver level 2"); and high use sites where dams were located within 50 m of stations for two or more years, and/or where dams were located within 100 m for 3 or more years ("beaver level 3") (Table 1).

Statistical Analyses

To assess non-random associations between relative bird abundance or richness when comparing areas with and without beavers, I first categorized all 240 survey stations into two groups based on the documented presence of beaver (i.e., dams or any other sign within 100 m). I then conducted a two-tailed *t* test for the difference in mean relative abundance at stations with beaver activity versus those with no activity, both for species most commonly detected (n = 31) and species groups. Because bird abundance is affected by a complex of environmental conditions (not just beaver activity) at each station, non-random associations between bird abundance and beaver presence do not suggest mechanistic or causal relationships. Therefore, to further address the question of how beaver may conduct ecosystem engineering, I first explained variation in bird abundance due to environmental factors other than beaver. I used multiple linear regression to describe "habitat relationships" for species with a $\geq 50\%$ difference in abundance when comparing stations with and without beaver (for all species where the difference was significant at the $P \leq 0.05$ level and that had > 50 detections) , and similarly constructed "environmental correlate models" for the total number of breeding birds and riparian birds detected within 50 m of stations ("habitat" is species-specific so I do not use this term for groups of species).

I first screened for highly correlated variables by computing pairwise correlations (Pearson's correlation coefficients), and eliminated one variable of any pair where $r \geq 0.65$ (retaining the most biologically significant variable), yielding a set of 18 environmental covariates for potential inclusion in habitat/covariate models (Table 1). To choose a candidate model of environmental covariates for each species or species group, I fit all possible models because I had no a priori expectations. The stepwise variable selection platform in JMP was used to select an environmental habitat model (using "all possible models" option with "minimum BIC" as a stopping rule, fitting up to 8 parameters). Due to the possibility of potentially correlated variables (biologically if not statistically), and to guard against over-fitting models, I used Bayesian Information Criterion (BIC; Schwarz 1978) to rank support for each model:

$$-2\text{loglikelihood} + k \times \ln(n)$$

Where k is the number of parameters, and n is the sample size (i.e., the number of data points in the study; $n = 240$). I chose BIC over AIC for initial model selection because it applies a larger penalty for each additional model parameter that is dependent on the sample sizes (Ramsey and Schafer 2002); therefore models were much more parsimonious and less likely to include insignificant or redundant variables. Each model explained relative abundance, or richness, at all stations sampled.

After building models that attempted to account for variation attributable to habitat of each species, or for environmental correlates of the different species groups, I examined whether beaver-related variables explained additional variation over the habitat/covariate models alone, and the strength of the additional model parameters. The models were ranked and compared using AIC_c values, ΔAIC, and Akaike weights (w_i). AICc were used for initial ranking of models. Models with beaver-related variables in which ΔAIC ≤ 2 of the top ranked variable are reported (i.e., regression coefficients), though I give summary model statistics (R^2, AICc, delta AIC, Akaike weights) for all models ranked. I used Burnham and Anderson's (2004) "simple rules of thumb" to assess the relative merits of models in the set, where models having ΔAIC ≤ 2 have substantial support (evidence), those in which 4 ≤ ΔAIC ≤ 7 have considerably less support, and models having ΔAIC > 10 have essentially no support. Finally, I considered evidence that the top-ranked models (highest-ranked habitat/environment and beaver models) contained the most accurate model using w_i, which reflects the likelihood that a particular model was best among those considered (Burnham and Anderson 2004, Chandler et al 2009).

I used JMP 9.0.2 (SAS Institute, Inc., 2010) for all statistical analyses. To better meet assumptions, most continuous variables were log transformed ([X + 1] log 10) before regression analyses. Though this transformation did not always result in normal univariate distributions, residuals were checked after fitting final models to confirm approximate normality. For example, the distribution of variables with percent values were compared after arcsine and log transformations, and the log-transformed variables were retained after determining the distribution of the residuals were approximately normal (Ramsey and Schafer 2004). I used $P \leq 0.05$ as my accepted level of significance for all *t*-tests and inferences regarding individual regression estimates, and based the latter on the variables included within the ranked models (i.e., rather than using model averaging) since each beaver variable was entered in only one model.

RESULTS

Avian Survey Effort and Detections

A total of 1,480 survey visits (759 in 2005, 721 in 2006) were conducted at the 240 stations; > 90% of stations were surveyed 3 times per year. I found that relative abundance at stations after truncating detection data at 50 meters was most strongly correlated with the density calculated by program DISTANCE, for both Yellow Warbler ($r = 0.93$, $P < 0.0001$) and Song Sparrow ($r = 0.892$, $P < 0.0001$). After excluding birds detected > 50 m from stations, flyovers, wintering birds and obvious migrants, juveniles, or other birds for which detectability may have been compromised (e.g., vagrants), I analyzed 13,590 detections of 76 species known to breed in the upper San Pedro basin (Table 4). This included 42 species that are primarily associated with riparian vegetation and surface water in the region, and 34 species that more typically use upland vegetation and yet also visit adjacent riparian areas (Hunter et al. 1987, Krueper 1999, Brand et al. 2010a). Of the 42 riparian-associated species, 28 were riparian specialists, and 14 were riparian generalists. Additionally, 68% of species (52 of 76) were primarily insectivorous, and 25% were species of regional conservation concern (U.S. Fish and Wildlife Service 2008, Hunter et al. 1987). Of the 19 species of regional conservation concern, 14 were also riparian-associated species (Table 4), and 11 of these had sufficient detections to test for differences in relative abundance between sites with and without beaver.

Beaver Activity

Beaver census data yielded 2,943 observations of sign (bank dens, gnawed or felled trees) and at least 122 instances where dams were found on the upper San Pedro River from 2000-2006, allowing us to determine the number of years in which beaver may have influenced the environment at avian survey station locations. At 64% of stations (n = 154) beavers were apparently absent as no sign was documented, with the remaining 36% of stations (n = 86) divided between low-, moderate-, and high-use sites (14%, 14%, and 8% of stations, respectively). Beaver dams were located within the following distance categories from stations: within 50 m at 14% of stations (n = 33), within 51-100 m at 5% of stations (n = 13), and downstream 100-150 m from 3% of stations (n = 6) (see Table 2 for totals by year). Including all signs documented over the six year period at the 36% of stations that had some level of beaver activity within 100 m, 14% were stations (n = 34) where only presence was documented, whereas dams were documented at the 22% (n = 52) of stations (i.e., those categorized as moderate and high-use (Table 3).

Virtually all woody vegetation that beaver felled, gnawed, or consumed living materials from was either willow or cottonwood. No tamarisk, mesquite, or other woody species was observed gnawed more than a few times, although limbs of these species were occasionally seen in dam construction. The stem density (DBH) counts within 30 m of each station revealed that extant beaver stumps represented a maximum of 15%, 19%, and 20 % of total basal area of cottonwood/willow stems within beaver low-, moderate-, and high-use sites, respectively. However, the sites with the highest percentage of stump basal area within each level of beaver intensity all hosted a relatively low number of stems (e.g., total of 10 trees and/or stumps) and thus a few stumps could make up a large proportion of stems and thus basal area. Considering the summed basal area for cottonwood and willow (since the stumps of these two species were not always readily distinguished) across all sites within each of the low-, moderate, and high-use beaver intensity classes, extant beaver stumps represented a total of 1.9%, 2.2%, and 1.6% of total cottonwood/willow basal area within each class, respectively (Figure 2). Within the low-, moderate-, and high-use sites, beaver-gnawed (but standing) trees represented 5.5 %, 3.5%, and 5.2% of the summed basal area of cottonwood trees, and 4.2%, 7.9%, and 3% of willow trees, respectively (Figure 2).

Beaver dams were typically located at or near wash-inlets or other areas where obvious sediment deposits or exposed bedrock would obstruct channel morphology to such an extent that water might be pooled upriver from the inlet (Johnson and van Riper in press). The water impounded by beaver dams raised the water level in the river from 0.1 m to >1m (in correlation with the size of dams), and in some cases also affected the water table in the surrounding riparian floodplain (USGS unpublished groundwater data). However in many cases the impounded backwater was restricted to areas which were naturally pooled already or the backwater was within an incised channel (i.e., ≥ 1 m below the lower floodplain). Thus, the beaver-impounded water rarely breached the channel bank or created classic stream braiding along the lowest channel shelf and other areas of the lower floodplain. An exception to the above pattern was a unique area (between Hereford Road and Hunter Wash) which had reduced canopy cover due to two fires within the prior ten years (one in 1999, another in 2003, M. Fredlake, personal communication), and a generally less-incised channel. Here, braiding, multiple smaller channels, and a higher water table appeared to be associated with beaver presence. Perhaps due to the reduced woody canopy cover in this reach beaver apparently consumed mostly cattail and bulrush, and other non-woody emergent riparian vegetation, in addition to willow and cottonwood where available. Dams in this area were largely constructed of mud, rocks, and a higher percentage of non-woody vegetation than seen in other reaches (Johnson and van Riper in press).

Non-random Spatial Association between Beaver and Birds

The majority of the eight species groupings I considered had higher richness and/or abundance (P <0.001, from two-tailed t tests for difference in means, degrees of freedom = 239) at sites where beaver presence had been documented as compared to where they had not (Table 5, Figures 3 and 4). The greatest difference in the number of species was riparian specialists, with a 26.9% mean difference (= 2.3 species/survey), and the least significant difference was the number of conservation concern species with 7.4% more species (P= 0.035) found at sites where beaver have been documented (Table 5). Total breeding bird community species richness was greater at sites where beaver had been documented, with a mean difference of 12.8% (= 2.4 species). The only non-significant difference in mean number of species detected at beaver presence versus absence sites was for the number of riparian generalist species, with only a 0.2 % difference (*P* = 0.947, Table 5). As well, relative abundance was higher at sites with beaver for the two groups for which this metric was analyzed, with 25.2% more insectivorous birds (= 1.66 more birds) and total breeding bird relative abundance 27.1% higher (= 2.7 more birds) on average per visit.

Of the 76 breeding species that I considered, a total of 31 had sufficient detections to test for non-random spatial association (two-tailed *t* tests, 239 degrees of freedom) with beaver (Table 6). Of these 31 species, relative abundance was significantly greater ($P \leq 0.05$) for 11, including three species of conservation concern: Yellow-billed Cuckoo, Northern Flicker, and Yellow Warbler. Two species had significantly fewer ($P \leq 0.05$) individuals detected per visit at sites where beaver were documented, Ash-throated Flycatcher and Northern Beardless-Tyrannulet, the latter being a species of conservation concern. Additionally, there were 7 species that were more common at sites where beaver had been documented, though the differences were non-significant at the $P \leq 0.05$ level; this group included Mallard, Ladder-backed Woodpecker, and Gila Woodpecker (Table 6).

Bird-Habitat Associations

I modeled bird-habitat associations for 13 species (Table 7), 12 of which showed least a 50% difference in relative abundance at beaver presence compared to absence sites and for which this difference was significant ($P \leq 0.05$) (Table 6). Although Yellow

Warbler relative abundance was only 32% greater at sites where beaver had been documented, I included this species in habitat models because this difference was highly significant (P <0.001), it was the most common bird detected, and is a species of regional conservation concern. Additionally, I built environmental covariate models (Table 7) for the seven species groups that showed a non-random association with beaver presence (Table 5).

Relative abundance of bird populations and species groups was consistently explained by a small set of the 18 environmental variables that I considered. Surface water was an important explanatory factor in more than half of models (Table 7). For individual species, both the presence of surface water in May or the persistence of perennial surface water throughout the summer were included in 46% and 62% of the models, respectively, and for species groups the presence of water in May was especially important (included in 86% of models) and perennial surface water was included in two models (29%). Perennial water was the only factor in the models that explained relative abundance of Brown-headed Cowbirds. Cottonwood and willow (cover and/or abundance) were included in 62% and 31%, respectively, of the individual species relative abundance models, whereas for species groups cottonwood and willow were included in 43% and 86% of models, respectively. Relative abundance of 23% of species and no species group richness or relative abundance included mesquite cover or basal area, and relative abundance of two (15%) species and two (29%) species groups included tamarisk cover or basal area.

Despite the consistent importance of several factors in explaining relative abundance of birds, the proportion of variation explained by vegetation and water factors varied somewhat depending on the response variable. Percent variation in abundance that was explained by habitat models (R^2) ranged from as low as 7-8% for species with fewer detections such as Black Phoebe, Brown-headed Cowbird, and Yellow-billed Cuckoo to as high as 35-42% for more common species such as Song Sparrow, Yellow Warbler, Common Yellowthroat, and Lesser Goldfinch (Table 8). Among seven species groups, percent of variation in richness explained by the environmental covariates (Table 7) was low for total number of conservation concern species ($R^2 = 0.13$) and highest for the number of riparian specialist species ($R^2 = 0.44$)(Table 8). Percent variation explained by the two species groups' relative abundance models was relatively high ($R^2 = 0.44$), both for all breeding species and all insectivorous birds.

Effects of Beaver versus Vegetation/Habitat

After accounting for variation in relative abundance and species richness attributable to environmental factors (Table 7), models that included beaver presence, intensity, and number of years with dams within 50 m ranked higher for 46 % of species, and 71% of species groups (Table 8 and 9) than the habitat/covariate-only models. Conversely, models containing beaver-related factorsdid not explain more variation in relative abundance better than the habitat-only models for 54% of the 13 species, or more species richness for 28% of the 7 species groups (Table 8 and 9).

Models with beaver-related variables did not perform better for either of the two bird species for which mean relative abundance was negatively associated with beaver activity (Ash-throated Flycatcher and Northern Beardless-Tyrannulet, Table 6), and though R^2 values were marginally higher when beaver terms were included in the models, the habitat-only models were weighted with higher probabilities (w_i = 0.39 and 0.53 probability) of containing the best model, after delta AIC rankings (Table 8). For the 11 species that were positively associated with beaver activity from *t*-tests (Table 6), the multiple linear regression models that included beaver factors were ranked higher than those with only water or vegetation factors for 55% of species. For the remaining 45% of these 11 species, model weights indicated a <0.005 to 0.34 probability that beaver factors might explain relative abundance (Table 8). For the four species of conservation concern included in the model-fitting due to their non-random association with beaver, beaver-models for only one (Yellow Warbler, habitat + number of years dams present within 50 m) indicated this as the highest probability model (w_i = 0.57), whereas for the other three species (Yellow-billed Cuckoo, Northern Flicker, and Northern Beardless Tyrannulet) the habitat-only model was the best performing and model weights indicated a 0.22 to 0.28 probability that beaver factors explained relative abundance (Table 8). For the six species for which beaver related-variables improved model performance, four of these (Common Yellowthroat, Lesser Goldfinch, White-breasted Nuthatch, and Cassin’s Kingbird) had habitat models further than 2.0 ΔAIC from the top-model, and two species (Yellow Warbler and Song Sparrow) still retained the habitat-only model within 2.0 ΔAIC.

There was little evidence that beaver-related variables explained relative abundance for 2 of the 7 species groups positively associated with beaver activity, including for the number of 14 riparian conservation concern species, or the relative abundance of insectivorous birds (Table 8). For 5 of the 7 species groups which were positively associated with beaver activity, model performance improved when I constructed models containing beaver-related variables over the environmental covariate-only model. These groups included the overall richness and relative abundance for all breeding bird species, and species richness of all 42 riparian-associated species, riparian specialists, and insectivorous birds (Table 8). For the five groups for which beaver related-variables improved model performance, four of these had environmental covariate-only models that were displaced by the beaver models to greater than 2.0 ΔAIC within the top-model, with only one group (insectivorous bird species richness) still retaining the covariate-only model within 2.0 ΔAIC (Table 8).

Multi-model inference according to lowest AIC score and Akaike weights (w_i) indicated that models including beaver-related variables better explained bird abundance or richness (6 of 13 species, and 5 of 7 species groups), though the estimates of the effects of beaver and their relative magnitude of influence were usually smaller relative to other covariates (Table 9). For example, after accounting for habitat variables, there was some evidence ($P = 0.06$) that Yellow Warbler abundance might decline with the greater number of years a site had beaver dams present within 50 m (Table 9). However, since both the response and explanatory variables are in the log(10) scale, the effect (a

1% increase in the number of years with a dam would lead to a 0.097 % decrease in mean relative abundance) turns out to be small, even though statistically significant and contributing to model performance (Table 9). Similarly, a 1% increase in the number of years a site had dams within 50 m was associated with 0.07 % increase Song Sparrow abundance. For species groups, the models containing beaver-related variables contained estimates that were both on the same order of magnitude as other factors and the beaver-related variables were significant, or at least nearly so, at the $P < 0.05$ level. For example, a 1% increase in the number of years a site had dams was associated with a 2.5 % increase in the number of breeding species.

DISCUSSION

I found evidence that relative bird abundance and species richness along the upper San Pedro River were better explained by models that included beaver presence or intensity of use as compared to models that incorporated only environmental habitat factors. Whereas other researchers—all from outside the southwestern U.S.—reported more dramatic differences in bird communities in areas with and without beaver influence (e.g., Bulluck and Rowe 2006, Cooke and Zack 2008), and sometimes soon after a reintroduction occurred (e.g., Medin and Clary 2001), on the upper San Pedro the effect sizes of beaver-related variables were relatively small (though highly significant) compared to the other environmental factors. Considering previous avian research in the study area (Brand et al. 2008, 2010a, 2011, Krueper et al.2003) and in the region (Carothers et al. 1974, Anderson and Ohmart 1984), the finding that riparian vegetation and surface water strongly influence avian communities on the upper San Pedro is not surprising. However, the strong association between beaver activity and bird abundance and richness that we found on the upper San Pedro indicates that beaver reintroduction in southwestern riparian systems may have an important additive influence on avian populations —especially given the relatively short length of time beavers had been in system.

In the majority of species or species groups where model performance was enhanced by fitting rich models containing beaver-related variables, the significance and effect size of the beaver variables was relatively small as compared to the environmental factors related to woody vegetation and surface water. As well, the statistically significant relationship observed between beaver activity and bird metrics (from *t*-tests) and the associated effect sizes were reduced after accounting for the habitat/environment covariates (from multiple linear regressions). However, though the beaver-related parameter estimates associated with bird species groups and relative abundance of individual bird species may seem biologically negligible, one needs to remember these estimates pertain to average abundance and species richness at the scale of a 50 m sampling stations across a 68.5-km river reach. When extrapolated across the study area even a seemingly negligible difference across 50-m plots may in fact scale up to be biologically important across the entire study area. For example, a 73.6% difference in Song Sparrow abundance at sites with beaver as compared to sites without beaver equates to only 0.33 more birds per station-visit (Table 6); however this is a biologically significant number of individuals when considering all the individual birds at the stations where both beavers and Song Sparrows were detected (78 stations = 78 *0.33 = 25.74 more birds) or when extrapolated to the proportion of the study area these sampling stations represent (78/240 = 32.5% of the study reach, 22.26 km is 32.5% of 68.5 km, 22.26 km would host 445.2 plots of 50-m, so [445.2 * 0.33] = 146.9 birds per visit across the study area). For birds of conservation concern which are rare on the landscape, e.g., Yellow-billed Cuckoo, even small differences in the total number of individual birds may be crucially important for population maintenance (Table 6).

Jones et al. (2010) described predictive equations related to four straight forward cause-and-effect criteria for interpreting ecosystem engineering. These included: 1) the engineer causes structural change, 2) structural change leads to abiotic change, 3), structural and abiotic change leads to biotic change, and 4), structural, abiotic, and/or biotic change can feedback to the engineer (Jones et al. 2010). While I did not formally incorporate their approach in my study, the upper San Pedro would be extremely well-suited for inclusion as a replicate sampling site in a comparative study which included other sites with different levels of the parameters described by Jones et al. (2010; i.e., time since engineering species establishment, magnitude of potential engineer effects given abiotic conditions and other species present, etc.).

In my study system, the abiotic effect of beavers on the bird community that I anticipated was either a reduction in canopy cover due to tree-felling and/or that beavers could increase surface water retention. I did not find evidence that beavers had substantially reduced canopy cover since being reintroduced, as sites with beaver had similar tree stem density as sites without beaver. The potential for increased surface water retention due to beaver dam construction was compromised because the dams on the San Pedro typically failed every summer during monsoon flooding, and because active dams raised water levels within a highly entrenched channel that was often a natural backwater area already (Mark Fredlake, personal communication), and thus there was little widening of the water courses or a braiding effect on floodplain. Thus, the initial (abiotic) pathways of an ecosystem engineering interaction were not pronounced or obvious within the time between when the reintroduction began and when I conducted my study.

Nonetheless, USGS groundwater wells adjacent to beaver ponds showed a measurable increase groundwater levels (C. van Riper, personal communication). Any increase in the soil-water interface during the dry season may facilitate increased riparian vegetation production thus provide more vegetation and other habitat components for the breeding riparian bird community. As well, it is likely that an increase in water retention will benefit water-obligate bird species. I included all water obligates detected within 50 m and the cottonwood-willow obligates into the “riparian specialist” group (due to low numbers of water-obligate birds detected), which as an entire group were indeed strongly associated with beaver activity.

While I found that beaver activity was associated with sites that contained higher number of species and relative abundance of many species and species groups, I could not rule out the possibility that beaver may have just selected habitat which already contained these features. The fairly short length of time between the reintroduction and my study, and the apparent lack of signature, pronounced ecosystem-engineering effects of beavers, supports this hypothesis. Future studies of the ecosystem engineering effects of beavers in relation to birds or other taxa need to account for the possibility that beaver habitat selection may confound the finding of an effect of beavers in relation to birds. This is especially the case in the desert Southwest, where riparian vegetation provides abiotic resources (amelioration of extreme temperatures and aridity, nest substrate, predator-free-space, etc.) as well as facilitating trophic opportunities (e.g., herbivory, insect habitat and foraging, etc.). In fact, willow (Salicaceae) has recently been cited for its ecosystem engineer-like ability to alter river hydrology and how this feeds back to the (willow) population as well as the surrounding riparian vegetation (Moggridge and Gurnell 2009). No work to date has explicitly evaluated the relative or interactive ecosystem engineering effects of beaver *and* willow (or cottonwood) in relation to birds, but this is fertile ground for future research.

Beavers are potentially beneficial for some riparian attributes and the ecosystem engineering concept is can provide valuable insights in the study of beaver, birds, and riparian restoration. However, land managers, scientists, and the public should have realistic expectations informed by the site-specific context of a potential reintroduction, and ideally make comparisons with other, similar sites before moving forward with a reintroduction project. Since the relative effect of any organism on its environment will likely be different in a given situation, it may be important to investigate potential engineering effects along environmental gradients in order to predict when the strongest “engineering” effects (i.e., feedbacks to the engineer and other species in the area) are likely to occur (Wright et al. 2006, Jones and Gutiérrez 2007, Hastings et al. 2007). The reach of the San Pedro I surveyed contains an environmental gradient in terms of water and riparian vegetation cover—both important explanatory factors for beaver and birds, and is situated in a more arid region than previous investigations of the relationship between birds metrics and beaver activity. In the Southwest region beaver could potentially provide resources (namely water) and/or disturbance processes (opening canopy gaps through herbivory) that might not otherwise occur, or at least in greater proportion than would occur without the “engineer” species.

Though we found evidence that beaver activity was strongly associated with bird abundance and richness, the magnitude of the ecosystem engineering effect may have been reduced by the unique environmental context occurring on the San Pedro. First, each year all beaver dams failed during heavy monsoon-season flooding (M. Fredlake, personal communication, Johnson and van Riper in press). Second, since water is limited to certain reaches where groundwater from the local aquifer supplies the surface water in the river, and beavers were limited to these reaches, beaver are only able to settle in certain sites where water is already present. Third, geomorphic processes exert a dominant influence in the system, including large flood disturbances that create patches of early successional habitat, and also tributary washes dumping sediment loads within the main channel and creating a back-water behind them (an abiotic process mimicking the consequences of dam-building), where beavers often chose to settle. Within these back-water areas, channel morphology remained incised and thus there was little opportunity for immediate increases in channel width, even after beaver built dams and raised the water level. Fourth, beavers were newly re-introduced (5-6 years before the study) to the system and thus there was little time for the engineering effects to accrue, or for bird populations to respond to these changes. Lastly, the upper San Pedro bird community is already highly diverse, and yet within this diverse community there is actually a limited pool of the bird species groups which have (in other studies) shown the most marked responses to beaver activity (e.g., Medin and Clary 1990, Cook and Zack 2009). For example, during the breeding season there is only one waterfowl species, three woodpeckers, one shorebird, and two herons regularly present on the San Pedro (Krueper 1999).

Spatial or temporal scales can be important considerations in the study of ecosystem engineers, for example, beaver activity can influence stream morphology at the watershed scale, especially when many beavers are present (Wright et al. 2006). Similarly, the effect of a single beaver's activity can extend for many decades beyond its lifetime, e.g., if impounded areas become full of sediment and undergo succession from a wetland, to meadow, and finally to forest (Wright et al. 2002, 2003, Wright 2009, Hastings et al. 2007, Jones et al. 2010). For two years I studied a 70 km reach of a watershed, and at 240 sampling stations within that reach, but did not investigate multiple temporal or spatial scales (e.g., station as compared to a 1 km , 2 km, or 10 km reach). To gain further insight it would likely be beneficial to consider other watersheds, or finer-scale reaches within a watershed (e.g., 1-2 km), and naturally occurring beavers at the same time as re-introduced beavers, and ideally within a before/after- control/impact study design. A collaboration is underway with other researchers who conducted studies prior to beaver reintroduction on the San Pedro (Krueper et al. 2003, Brand et al. 2010a) to re-survey sites with and without beaver influence (Johnson and van Riper in press). We anticipate this study and future work in the upper San Pedro will help determine the extent to which the bird community *changed* after beaver reintroduction, in addition to my current study which measured the *association* after the reintroduction occurred.

CONCLUSION

Most organisms modify their environment to various degrees, and interact with other organisms in that environment. To the extent that an ecosystem engineering process and its consequences affect community dynamics, ecologists can consider whether this environmental modification constitutes an interaction, either through indirect, direct, or cascading effects. I found that, though bird abundance and species richness were certainly associated with beaver activity, the ecosystem engineering-type interaction was not as pronounced compared to what has been found in other regions. More study is needed to ascertain whether this was due to the relatively short time beavers had been in the system, unique environmental conditions, or both. The environmental context of the San Pedro which could limit the ecosystem engineering effect of beavers included disturbance effects greater than those of the beaver (monsoon floods) and a deeply entrenched channel which (together) may have resulted in an ephemeral or marginal influence of beaver dams. Other conditions important to consider at this site include the presence of cottonwood and willow, reaches without surface water (limiting the beaver settlement opportunities), and a bird community which was already known for being highly-diverse and abundant (Brand et al. 2010b). These factors likely contributed to a situation in which the potential ecosystem engineering effects of beaver may not be as profound as those seen in other studies.

Riparian bird communities, especially in the southwestern U.S., are noted for their generally high bird abundance and diversity as well as other important ecosystem services, and consequently land managers, scientists, and the public support efforts to predict how human-influenced impacts such as groundwater withdrawal or climate change will affect this ecosystem type (e.g., Steiner et al. 2000, Brand et al. 2011, Steinitz et al. 2005). Considerable effort and over 400 million dollars has been allocated toward riparian restoration projects in the Southwest since 1990, and providing habitat for birds and other wildlife is one of the major intentions—as well as criteria for success—for these projects (Follstad-Shah et al. 2007). Restoration ecologists, land managers and the public need to set realistic goals for ecosystem restoration (Hobbs 2007), and part of this process, especially in the Southwest, should involve an evaluation of when and where beaver reintroduction may assist in well-defined restoration objectives.

For example, I found that beaver reintroduction did not appear to be having detrimental effects to any species of conservation concern, and in fact there was evidence that breeding bird community is more abundant and more diverse where beavers were present. Future research is needed to determine when, and under what conditions, beaver may be helpful to the full complement of riparian restoration goals as defined by Fredlake (1997) and under what conditions they may be detrimental to conservation objectives (e.g., recovery or maintenance of Yellow-billed Cuckoo populations). My findings indicate that there appears to be no cause for alarm when beavers are found actively utilizing riparian vegetation (e.g., see also Longcore et al. 2007), at least in areas where beaver are native. My study, as well as most of the prior avian research in the region, also suggests that beaver reintroduction and conservation of riparian bird communities in the southwestern U.S. can co-exist, especially if monitoring of cottonwood and willow occurs in conjunction with the effort.

Though more time and investigation is needed to determine the full extent of beaver influence on the upper San Pedro, it is clear that the spatial association of beaver activity and a highly abundant and diverse bird community represent an important opportunity to evaluate the ecosystem engineering effects of beaver in a unique environmental context. While we did not investigate other attributes of ecosystem restoration that beaver may contribute to, we conclude that beaver are more likely to benefit rather than harm San Pedro's bird community—as long as an adaptive management program continues along with monitoring in areas with beaver activity, dense willow or other riparian vegetation, and bird species of conservation concern. Rigorous assessment of beaver reintroduction projects need to incorporate before-after/control-impact studies (Johnson and van Riper in press) and thorough evaluation of unique, site-level ecological context and history, so that the potential for beavers to act as riparian restoration agents via their ecosystem engineering behaviors and its consequences can be evaluated and repeated where appropriate.

REFERENCES

Albert, S., and T. Trimble. 2000. Beavers are partners in riparian restoration on the Zuni Indian Reservation. Ecological Restoration 18(2): 87-92.

Apple, L.L. 1985. Riparian habitat restoration and beavers. Riparian Ecosystems and Their Management: Reconciling Conflicting Uses, North American Riparian Conference, April 16-18, 1985, University of Arizona, Tucson, Arizona, USA.

American Ornithologist's Union. 2011. Checklist of North American Birds, 7th-edition, with changes incorporated through.52nd supplement. Available at: www.aou.org.

Anderson, B.W., and R.D. Ohmart. 1984. Vegetation structure and bird use in the lower Colorado River Valley. Pages 23-34 *In* R.R. Johnson and D.A. Jones (technical coordinators), Importance, Preservation and Management of Riparian Habitat: A symposium. General Technical Report RM-43. U.S. Forest Service, Fort Collins, Colorado.

Arner, D.H. 1963. Production of duck food in beaver ponds. Journal of Wildlife Management 27: 76-81.

Aznar, j. and A. Desrochers. 2008. Building for the future: abandoned beaver ponds promote bird diversity. Ecoscience 15(2): 250-257.

Badano, E.I., and L.A. Cavieres. 2006. Ecosystem engineering across ecosystems: do engineer species sharing common features have generalized or idiosyncratic effects on species diversity? Journal of Biogeography 33(2): 304–313.

Baker, B. W., and E. P. Hill. 2003. Beaver (Castor canadensis). Pages 288-310 *In* G. A. Feldhamer, B. C. Thompson, and J. A. Chapman, editors. Wild Mammals of North America: Biology, Management, and Conservation. Second Edition. The Johns Hopkins University Press, Baltimore, Maryland, USA.

Berke, S.K. 2010. Functional groups of ecosystem engineers: a proposed classification with comments on current issues. Integrative and Comparative Biology 50(2):147–157.

Boogert, N.J., D.M. Paterson, and K.N. Laland. 2006. The implications of niche construction and ecosystem engineering for conservation biology. BioScience 56(7): 570–578.

Boyle, S., and S. Owens. 2007. North American Beaver (Castor canadensis): a technical conservation assessment. USDA Forest Service, Rocky Mountain Region. Available at: http://www.fs.fed.us/r2/projects/scp/assessments/northamericanbeaver.pdf [Accessed November 11, 2011].

Brand, L.A, G.C White, and B.R Noon. 2008. Factors influencing species richness and community composition of breeding birds in a desert riparian corridor. The Condor: 110(2): 199–210.

Brand, L.A, J.C. Stromberg, and B.R. Noon. 2010a. Avian Density and Nest Survival on the San Pedro River: Importance of Vegetation Type and Hydrologic Regime. Journal of Wildlife Management 74:739-754.

Brand, L.A., D.J. Cerasale, T.D. Rich, and D.J. Krueper. 2010b. Breeding and migratory birds: patterns and processes. Page 153-174 *In* Ecology and Conservation of the San Pedro River. Edited by J.C. Stromberg and B. Tellman. University of Arizona Press, Tucson, AZ.

Brand, L.A., J.C. Stromberg, D.C. Goodrich, M.D. Dixon, K. Lansey, D. Kang, D.S. Brookshire, and D.J. Cerasale. 2011. Projecting avian response to linked changes in groundwater and riparian floodplain vegetation along a dryland river: a scenario analysis. Ecohydrology 4(1): 130-142.

Brown, M. K., and G.R. Parsons. 1979. Waterfall production on beaver flowages in a part of northern New York. New York Fish and Game Journal 26(2): 142-153.

Buckland, S.T., D.R. Anderson, K.P. Burnham, J.L. Laake, D.L. Borchers, and L. Thomas. 2001. Introduction to Distance Sampling: Estimating abundance of biological organisms. Oxford University Press, Oxford U.K.

Bulluck, J.F., and M.P. Rowe. 2006. The use of southern Appalachian wetlands by breeding birds, with a focus on neotropical migratory species. The Wilson Journal of Ornithology 118: 399-410.

Byers, J.E., K. Cuddington, C.G. Jones, T.S. Talley, A. Hastings, J.G. Lambrinos, J. A. Crooks, and W. G. Wilson. 2006. Using ecosystem engineers to restore ecological systems. Trends in Ecology and Evolution 21(9): 493-500.

Carothers, S.W., R.R. Johnson, R.R., and S.W. Aitchison. 1974. Population structure and social organization of Southwestern riparian birds. American Zoology 14:97-108.

Carr, W.H. 1940. Beaver and Birds. Bird Lore 42(2): 141-146.

Chandler, R.B., D.I. King, and S. Destefano. 2009. Scrub–Shrub Bird Habitat Associations at Multiple Spatial Scales in Beaver Meadows in Massachusetts. The Auk 126:186-197.

Cooke, H.A., and S. Zack. 2008. Influence of beaver dam density on riparian areas and riparian birds in shrub steppe of Wyoming. Western North American Naturalist 68(3): 365–373.

Crain, C.M., and M.D. Bertness. 2006. Ecosystem engineering across environmental gradients: implications for conservation and management. Bioscience 56(3): 211–218.

Cuddington, K., J.E. Byers, W.G. Wilson, and A. Hastings (editors). 2007. Ecosystem engineers: plants to protists. Volume 4 in the Theoretical Ecology Series. Academic Press/Elsevier.

Cuddington, K., W.G. Wilson, and A. Hastings. 2009. Ecosystem Engineers: Feedback and Population Dynamics. The American Naturalist 173 (April): 488-498. doi:10.1086/597216.

Davis, T. 2004. A thirst for growth. High Country News 36(16): 7-12.

Dunster, J.A., and K.J. Dunster. 1996. Dictionary of Natural Resource Management. UBC Press, University of British Columbia, Vancouver, BC.

Edwards, N.T., and D.L. Otis. 1999. Avian communities and habitat relationships in South Carolina piedmont beaver ponds. American Midland Naturalist 141: 158-171.

Emlen, J.T. 1971. Population densities of birds derived from transect counts. The Auk 88(2): 323–342.

Finch, D.M., J. Agyagos, T. McCarthey, R.M. Marshall, S.H. Stoleson, and M.J. Whitfield. 2000. Chapter 10: Management Recommendations, *In* Status, Ecology, and Conservation of the Southwestern Willow Flycatcher (Finch, D.M., and S.H. Stoleson, eds.). Gen. Tech. Rep. RMRS-GTR-60. Ogden, UT: U.S. Dept. of Agriculture, Forest Service, Rocky Mountain Research Station.

Follstad-Shah, J.J., C.N. Dahm, S.P. Gloss, S. P., and E.S. Bernhardt. 2007. River and riparian restoration in the Southwest: results of the National River Restoration Science Synthesis Project. Restoration Ecology 15(3): 550-562.

Fouty, S.C. 2002. Cattle and Streams: Piecing together a story of change. Pages 184-187 *In* Welfare Ranching: The subsidized destruction of the American West. Edited by G. Wuerthner and Mollie Matteson. Island Press.

Fredlake, M. 1997. Re-establishment of North American Beaver (Castor Canadensis) into the San Pedro Riparian National Conservation Reserve Area.

Environmental Assessment EA AZ-060-97-004. Bureau of Land Management, Tucson, AZ.

Griffiths, C.J., C.G. Jones, D.M. Hansen, M. Puttoo, R.V. Tatayah, C.B. Muller, and S.Harris. 2010. The Use of Extant Non-Indigenous Tortoises as a Restoration Tool to Replace Extinct Ecosystem Engineers. Restoration Ecology 18(1): 1-7.

Grover, A.M., and G.A. Baldassarre. 1995. Bird species richness within beaver ponds in south-central New York. Wetlands 15(2): 108-118.

Gurnell, A.M. 1998. The hydrogeomorphological effects of beaver dam-building activity. Progress in Physical Geography 22:167–89.

Hartke, K.M., and G.R. Hepp. 2004. Habitat use preferences of breeding female wood ducks. Journal of Wildlife Management 68(1): 84-93.

Hobbs, R.J. 2007. Setting effective and realistic restoration goals: key directions for research. Restoration Ecology 15(2): 354–357.

Hupp, C.R., and W.R. Osterkamp. 1996. Riparian vegetation and fluvial geomorphic processes. Geomorphology 14(4): 277–295.

Johnson, G.E., and C. van Riper III. In press. An investigation of important factors associated with riparian bird community structure along the upper San Pedro River in southeastern Arizona and northern Sonora. USGS Open File Report, based on an unpublished 2008 report to Sonoran Joint Venture/U.S. Fish and Wildlife Service, 738 North Fifth Ave., Suite 215 Tucson, Arizona, 85705.

Johnson, G.E., and C. van Riper III. In preparation. Southwestern Willow Flycatcher nest records and recovery potential at southernmost confirmed breeding distribution.

Johnson, M.J., R.T. Magill and C. van Riper III. 2010. Yellow-billed Cuckoo distribution and habitat associations in Arizona, 1998-1999. Pp. 197-212, *In* The Colorado Plateau IV: Integrating research and resources in management for effective conservation (van Riper, C. III, B.F. Wakeling, and T.D. Sisk, Eds). University of Arizona Press, Tucson, AZ. 335 pp.

Jones, C.G., J.H. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers. Oikos 69:373-386.

Jones, C.G., J.H. Lawton, and M. Shachak. 1997. Positive and negative effects of organisms as physical ecosystem engineers. Ecology 78(7):1946-1957.

Jones, C.G., and J.L. Gutiérrez. 2007. On the purpose, meaning, and usage of the physical ecosystem engineering concept. Pages 3-20 *In* Cuddington, K., J.E. Byers, W.G. Wilson, A. Hastings (editors), Ecosystem engineers: plants to protists. Theoretical Ecology Series IV. Academic Press/Elsevier.

Jones, C.G., J.L. Gutiérrez, J.E. Byers, J.A. Crooks, J.G. Lambrinos, and T.S. Talley. 2010. A framework for understanding physical ecosystem engineering by organisms. Oikos 119 (12): 1862-1869.

Krueper, D. J. 1999. Annotated checklist to the birds of the Upper San Pedro River Valley, Arizona. U.S. Bureau of Land Management, Department of Interior, 12661 East Broadway, Tucson, Arizona 85748-7208T.

Krueper, D., J. Bart, and T.D. Rich. 2003. Response of Vegetation and breeding birds to the removal of cattle on the San Pedro River, Arizona (U.S.A.). Conservation Biology 17(2): 607-615.

Laland, K.N., and N.J. Boogert. 2010. Niche construction, co-evolution and biodiversity. Ecological Economics 69 (4): 731–736.

Leenhouts, J.M., J.C. Stromberg, and R.L. Scott. 2005. Hydrolic requirements of and consumptive ground-water use by riparian vegetation along the San Pedro River, Arizona. U.S. Geological Survey Scientific Investigations Report 2005-5163. 154 p.

Longcore, T., C. Rich, and D. Mueller-Schwarze. 2007. Management by assertion: Beavers and songbirds at Lake Skinner (Riverside County, California). Environmental Management 39(4): 460-471.

Mac Nish, R., K.J. Baird, and T. Madock III. 2010. Groundwater Hydrology of the San Pedro River Basin. Pages 285-299, *In* Ecology and Conservation of the San Pedro River. Edited by J.C. Stromberg and B. Tellman. University of Arizona Press, Tucson, AZ.

Marques, T.A., L. Thomas, S.G. Fancy, and S.T. Buckland. 2007 Improving estimates of bird density using multiple covariate distance sampling. The Auk 127: 1229–1243.

McFarland, T.M, C. van Riper III, and G.E. Johnson. 2012. The usefulness of riparian NDVI models in assessing avian abundance and richness. Journal of Arid Environments 77: 45-53.

McKinstry, M.C., P. Caffrey, and S.H. Anderson. 2001. The importance of beaver to wetland habitats and waterfowl in Wyoming. Journal of the American Water Resources Association 37(6): 1571–1577.

Medin, D.E., and W.P. Clary. 1990. Bird population in and adjacent to a beaver pond ecosystem in Idaho. U.S. Forest Service Research Paper INT-432.

Merendino, M.T., G.B. McCullough, and N.R. North. 1995. Wetland availability and use by breeding waterfowl in southern Ontario. Journal of Wildlife Management 59(3): 527-532.

Moggridge, H.L., and A.M. Gurnell. 2009. Controls on the sexual and asexual regeneration of Salicaceae along a highly dynamic, braided river system. Aquatic Sciences 71(3): 305-317.

Moore, J.W. 2006. Animal ecosystem engineers in streams. BioScience 56(3): 237–246.

Muller-Schwarze, D. 1992. Beaver waterworks. Natural History, May 1992: 52-53.

Naiman, R.J., C.A. Johnston, and J.C. Kelly. 1988. Alterations of North American streams by beaver. Bioscience 38: 753-762.

Nijhuis, M. 2011. River keepers: long maligned as pests, beavers are proving indispensable. Audubon September-October 2011: 20.

Nummi, P. 1989. Simulated effects of the beaver on vegetation, invertebrates and ducks. Annales-Zoologici Fennici 26: 43-52.

Nummi, P. 1992. The importance of beaver ponds to waterfowl broods: an experiement. Annales-Zoologici-Fennici 29(1): 47-55.

Nummi, P., and A. Hahtola. 2008. The beaver as an ecosystem engineer facilitates teal breeding. Ecography 31 (4): 519–524.

Nummi, P., and H. Poyosa. 1997. Population and Community level responses in Anas species to patch disturbance caused by an ecosystem engineer—the beaver. Ecography 20(6): 580-584.

Olson, R., and W.A. Hubert. 1994. Beaver: Water resources and riparian habitat manager. University of Wyoming, Laramie, Wyoming, U.S.A. 48 p.

Prettyman, B. 2009. Utah wildlife: Leave it to Beavers. The Salt Lake Tribune, October 16, 2009. Accessed November 11, 2011 at: http://archive.sltrib.com/article.php?id=13545172&itype=NGPSID&keyword=beaver&sdate=2009-10-15&edate=2009-10-20&qtype=

Ralph, C. J., G.R. Geupel, P. Pyle, P.Martin, and D.F. Desante. 1993. Handbook of field methods for monitoring landbirds. General Technical Report PSW-GTR-144-www. Pacific Southwest Research Station, Albany, CA

Ramsey, F.L., and D.W. Schafer. 2002. The Statistical Sleuth: A Course in Methods and Data Analysis. Second Edition. Duxbury (Thomsom Learning, Wadsworth Group), Pacific Grove, CA.

Reese, K.P., and J.D. Hair. 1976. Avian species diversity in relation to beaver pond habitats in the Piedmont region of South Carolina. Proceedings of the Annual Conference of Southeastern Association of Fish and Wildlife Agencies 30: 437-447.

Renouf, R.N. 1972. Waterfowl utilization of beaver ponds in New Brunswick. Journal of Wildlife Management 36(3): 740-744.

Reynolds, R.T., J.M. Scott, and R.A.Nussbaum. 1980. A variable circular-plot method for estimating bird numbers. The Condor 82: 309-313.

Rojo, H.R., J. Bredehoeft, R. Lacewell, J. Price, J. Stromberg, and G.A. Thomas. 1999. Sustaining and enhancing migratory bird habitat on the upper San Pedro River. Commission for Environmental Cooperation, Montreal, Canada.

Rosell F., and H. Parker. 1996. The beaver's (Castor sp.) role in forest ecology: a key species returns. Fauna (Oslo) 49(4): 192-211.

Rosell, F., O. Bozser, P. Collen, and H. Parker. 2005. Ecological impact of beavers Castor fiber and Castor canadensis and their ability to modify ecosystems. Mammal Review 35 (3-4): 248–276.

Schwarz, G. 1978. Estimating the dimension of a model. Annals of Statistics 6**:**461-464.

Skagen, S.K., C.P. Melcher, W.H. Howe, F.L. Knopf. 1998. Comparative use of riparian corridors and oases by migrating birds in southeast Arizona. Conservation Biology 12(4): 896-909.

Sogge, M. K., and R.M. Marshall. 2000. A survey of current breeding habitats, pages 13-24 *In* Status, Ecology, and Conservation of the Southwestern Willow Flycatcher (D.M. Finch and S.H. Stoleson, eds), Gen. Tech. Rep. RMRS-GTR-60. U.S. Dept. of Agriculture, Forest Service, Rocky Mountain Research Station, Ogden Utah.

Speake, D.W. 1956. Waterfowl use of creeks, beaver swamps, and small impoundments in Lee County, Alabama. Proceedings of the Southeast Association of Game and Fish Commissioners Meeting 2: 178-185.

Steiner, F., J. Blair, L. McSherry, S. Guhathakurta, J. Marruffo, and M. Holm. 2000. A watershed at a watershed: the potential for environmentally sensitive area protection in the upper San Pedro Drainage Basin (Mexico and USA). Landscape and Urban Planning 49: 129-148.

Steinitz, C., R. Anderson, H. Arias, S. Bassett, M. Flaxman, T. Goode, T. Maddock III, D. Mouat, R. Peiser, and A. Shearer. 2005. Alternative Futures for Landscapes in the Upper San Pedro River Basin of Arizona and Sonora. USDA Forest Service General Technical Report PSW-GTR-191.

Stromberg, J. 1998. Dynamics of Fremont cottonwood (*Populus fremontii*) and saltcedar (*Tamarix chinensis*) populations alongthe San Pedro River, Arizona. Journal of Arid Environments 40:133– 155.

Stromberg, J. C. 2001. Restoration of riparian vegetation in the south-western United States: importance of flow regimes and fluvial dynamism. Journal of Arid Environments 49: 17-34.

Stromberg, J.C., and R. Tiller. 1996. Effects of Groundwater Decline on Riparian Vegetation of Semiarid Regions: The San Pedro, Arizona. Ecological Applications 6(1): 113-131.

Stromberg, J.C., and B. Tellman. 2010. Ecology and Conservation of the San Pedro River. University of Arizona Press. Tucson, Arizona.

Thomas, L., S.T. Buckland, E.A. Rexstad, J.L. Laake, S. Strindberg, S.L. Hedley, J.R.B. Bishop, T.A. Marques, and K.P. Burnham. 2010. Distance software: design and analysis of distance sampling surveys for estimating population size. Journal of Applied Ecology 47: 5-14.

Thomsen, M.S., T. Wernberg, A. Altieri, F. Tuya, D. Gulbransen, K.J. McGlathery, M. Holmer and B.R. Silliman. 2010. Habitat cascades: the conceptual context and global relevance of facilitation cascades via habitat formation and modification. Integrative and Comparative Biology 50(2): 158–175.

U.S. Fish and Wildlife Service. 2008. Birds of Conservation Concern 2008. United States Department of Interior, Fish and Wildlife Service, Division of Migratory Bird Management, Arlington, Virginia. 85 pp. [Online version available at <http://www.fws.gov/migratorybirds/>]

Webb, R. H., S.A. Leake, and R.M. Turner. 2007. The Ribbon of Green: Change in Riparian Vegetation in the Southwestern United States. University of Arizona Press, Tucson, Arizona, U.S.A.480 p.

Wilkinson, T. 2003. The benefits of beavers. National Parks, January-February 2003.

Wright, J.P., C.G. Jones, and A.S. Flecker. 2002. An ecosystem engineer, the beaver, increases species richness at the landscape scale. Oecologia 132: 96-101.

Wright, J.P., A.S. Flecker, and C.G. Jones. 2003. Local vs. landscape controls on plant species richness in beaver meadows. Ecology 84(12): 3162–3173.

Wright, J.P., and C.G. Jones. 2006. The concept of organisms as ecosystem engineers ten years on: progress, limitations, and challenges. BioScience 56(3): 203–209.

Wright, J.P., C.G. Jones, B. Boeken, and M. Shachak. 2006. Predictability of ecosystem engineering effects on species richness across environmental variability and spatial scales. Journal of Ecology 94(July): 815-824.

Wright, J.P. 2009. Linking populations to landscapes: richness scenarios resulting from changes in the dynamics of an ecosystem engineer. Ecology 90(12): 3418–3429.

TABLES

Table 1. Environmental variables used in stepwise variable selection and final habitat/covariate models. Variables followed by "Lg" were transformed using Log10 (X +1).

Abbreviation	Description
Wash <200	Indicator (=1) if a wash inlet within 200 m, (brings in sediment, beavers may settle).
H2O May	Indicator (=1) if there is water at the point in late May.
H2O PER	Indicator (=1) if water persists throughout summer (perennial).
Rip Veg Width Lg	Total width of riparian area vegetation, measured perpendicular to river (includes river channel).
BACH Av%Cov Lg	Average percent cover of *Bacharis* (seep willow) within 3 lowest height layers.
MESQ Av%Cov Lg	Average percent cover of Mesquite within 5 lowest height layers.
TAMI Av%Cov Lg	Average percent cover of Tamarisk within 4 lowest height layers.
SALI Av%Cov Lg	Average percent cover of Willow *Salix goodingi* within 6 lowest height layers.
POFR Av%Cov Lg	Average percent cover of Cottonwood *Populus freemontii* within 9 height layers measured.
SumPOFR %Cov 20-30m Lg	The summed percent cover of Cottonwood from both of the upper canopy strata (20-25m, 25-30m).
ALL TAMI LT Lg	Summed basal area of live Tamarisk stems, in $m^2/2826\ m^2$ (tree basal area per 30m radius plot), all size classes summed.
ALL MESQ Lg	Summed basal area of live Mesquite stems, in $m^2/2826\ m^2$ (tree basal area per 30m radius plot), all size classes summed.
SALI <12cmDBH Lg	Summed basal area of small Willow stems (<12 cm DBH size class), per $m^2/2826\ m^2$ (tree basal area, per 30m radius plot).
POFR 12-25cmDBH Lg	Summed basal area of medium Cottonwood stems (12-25 cm DBH size class), per $m^2/2826\ m^2$ (tree basal area, per 30m radius plot).
SALI 12-25cmDBH Lg	Summed basal area of medium Willow stems (12-25 cm DBH size class), per $m^2/2826\ m^2$ (tree basal area, per 30m radius plot).

Abbreviation	Description
POFR >25cmDBH Lg	Summed basal area of large Willow trees (>25 cm DBH size class), per m^2/2826 m^2 (tree basal area, per 30m radius plot).
SALI >25cmDBH Lg	Summed basal area of large Cottonwood trees (>25 cm DBH size class), per m^2/2826 m^2 (tree basal area, per 30m radius plot).
Veg Diversity Lg	Index of vegetation structure, from 1-8, summed values from allocating a "1" to each height strata level with vegetation in it.
Beaver Presence	Presence inferred by dams and/or sign within 100 m of the station (in any year), and included gnawed trees, stumps, bank dens, and other signs of occupation (= 1, indicator variable).
Num Yr BD <51 Lg	Number of years a beaver dam was within 50 meters of point (continuous variable)
Beaver Level 1	Low use: beaver occupancy in one or more years (2000-2006) within 100 meters of the avian survey station, no dams documented (n = 34)
Beaver Level 2	Moderate use: stations where a dam was documented within 100 m upstream or 150 m downstream during one or two years, and no more than one year with a dam within 50 m (n = 33).
Beaver Level 3	High use: stations where dams were located within 50 m for two or more years, and/or where dams were located within 100 m for 3 or more years (n = 19).

Table 2. Number of survey stations where beaver dams were documented and total number of dams documented each year from 2000-2006 within the San Pedro National Riparian Conservation Area. Survey stations were established in 2005; dams were documented using GPS and/or GIS prior to spring 2005 by BLM personnel and by bird surveyors in 2005 and 2006, and were complete censuses.

	2000	2001	2002	2003	2004	2005	2006
All Dams on upper River[1]	5	6	17	20	25	25	32
Stations with Dam ≤ 50m	2	5	8	8	11	8	22
Stations with Dam 51-100m	2	1	5	11	9	5	7
Stations w/ Dam 101-150m[2]	0	0	2	1	3	2	3
Total stations with Dams	4	6	15	20	23	15	32

[1] Includes total count of dams, i.e., when more than one dam was located within 100 m of a station, or when dams were more than 150 m downriver or 100 m upriver from any station.

[2] Includes only dams 100-150 m downriver from stations.

Table 3. Beaver activity from 2000-2006 at 240 stations in the San Pedro Riparian National Conservation Area, used to quantify beaver presence/absence and beaver intensity.

Beaver Influence	Number of Stations
Beaver occupancy within 100 m ≥ 1year, but no dams	**34**
Beaver dams impounding water within 100m:	
Dam present 1 year	26
Dam present 2 years	8
Dam present 3 years	8
Dam present 4 years	5
Dam present 5 years	2
Dam present 6 years	2
Dam present 7 years	1
Total stations with Dams	**52**
Total stations with some beaver influence	**86**
No beaver activity documented (within 100 meters)	154
Total number of stations	**240**

Table 4. Common and scientific names of 76 breeding bird species detected within 50 meters of 240 survey stations on the San Pedro Riparian National Conservation Area, 2005-2006. Includes total detections, number and percent of stations where detected. Riparian and species groupings used for species richness, riparian and insectivorous species group analyses include the following grouping codes: Riparian (R) and if so whether a cottonwood, willow, and/or water specialist (CW) or riparian generalist (Gen) in my study system according to Kruper (1999) and/or Brand et al. (2010a), if a conservation concern species as designated by the U.S. Fish and Wildlife Service (2008; "C") and/or Hunter et al. (1987, "c"), and if primarily insectivorous (I). Common and scientific nomenclature follow the American Ornithologists Union (2011).

Common Name	Scientific Name	Total Detections	No. Sta. Detected	Freq (%)	Riparian/ Spp. Group
Yellow Warbler	*Setophaga petechial*	1,721	224	93	R(CW),C, I
Yellow-breasted Chat	*Icteria virens*	1,170	227	95	R(Gen),c, I
Lesser Goldfinch	*Spinus psaltria*	991	191	80	R(CW)
Bewick's Wren	*Thryomanes bewickii*	724	217	90	R(Gen), I
Song Sparrow	*Melospiza melodia*	702	177	74	R(CW), I
House Finch	*Carpodacus mexicanus*	616	192	80	
White-winged Dove	*Zenaida asiatica*	612	199	83	
Brown-headed Cowbird	*Molothrus ater*	564	192	80	R(Gen), I
Abert's Towhee	*Melozone aberti*	562	196	82	R(Gen)
Vermilion Flycatcher	*Pyrocephalus rubinus*	518	183	76	R(CW),c, I
Cassin's Kingbird	*Tyrannus vociferans*	510	163	68	R(CW), I
Gila Woodpecker	*Melanerpes uropygialis*	494	188	78	R(CW),C, I
Common Yellowthroat	*Geothlypis trichas*	472	172	72	R(CW), I
Summer Tanager	*Piranga rubra*	424	178	74	R(CW),c, I
Bell's Vireo	*Vireo bellii*	357	149	62	R(Gen),C, I
Mourning Dove	*Zenaida macroura*	242	123	51	
White-breasted Nuthatch	*Sitta carolinensis*	233	130	54	R(CW), I
Western Wood-Pewee	*Contopus sordidulus*	227	116	48	R(CW), I

Common Name	Scientific Name	Total Detections	No. Sta. Detected	Freq (%)	Riparian/ Spp. Group
Brown-crested Flycatcher	*Myiarchus tyrannulus*	174	99	41	R(CW),c, I
Lucy's Warbler	*Oreothlypis luciae*	169	112	47	R(Gen),C, I
Blue Grosbeak	*Passerina caerulea*	166	104	43	R(Gen), I
Ash-throated Flycatcher	*Myiarchus cinerascens*	136	87	36	I
Ladder-backed Woodpecker	*Picoides scalaris*	129	94	39	R(Gen), I
Northern Flicker	*Colaptes auratus*	104	66	28	R(CW),c, I
Black-chinned Hummingbird	*Archilochus alexandri*	99	76	32	R(Gen)
Phainopepla	*Phainopepla nitens*	99	42	18	C
Mallard	*Anas platyrhynchos*	90	45	19	R(CW)
Northern Beardless-Tyrannulet	*Camptostoma imberbe*	89	62	26	R(Gen),C, I
Common Ground-Dove	*Columbina passerina*	84	61	25	
Northern Mockingbird	*Mimus polyglottos*	76	55	23	I
Bullock's Oriole	*Icterus bullockii*	74	57	24	R(CW), I
Western Kingbird	*Tyrannus verticalis*	70	37	15	I
Gambel's Quail	*Callipepla gambelii*	66	44	18	
Northern Rough-winged Swallow	*Stelgidopteryx serripennis*	65	32	13	R(CW), I
Black Phoebe	*Sayornis nigricans*	64	44	18	R(CW), I
Cliff Swallow	*Petrochelidon pyrrhonota*	62	14	6	R(CW), I
Gray Hawk	*Buteo nitidus*	62	39	16	R(CW)
Yellow-billed Cuckoo	*Coccyzus americanus*	61	45	19	R(CW),C, I
Bushtit	*Psaltriparus minimus*	58	23	10	I
Northern Cardinal	*Cardinalis cardinalis*	55	42	18	R(Gen), I
Great Blue Heron	*Ardea herodias*	50	35	15	R(CW)
Red-winged Blackbird	*Agelaius phoeniceus*	44	15	6	R(CW), I
Botteri's Sparrow	*Peucaea botterii*	26	17	7	C, I

Common Name	Scientific Name	Total Detections	No. Sta. Detected	Freq (%)	Riparian/ Spp. Group
Black-throated Sparrow	*Amphispiza bilineata*	24	12	5	I
Verdin	*Auriparus flaviceps*	22	14	6	I
Great Horned Owl	*Bubo virginianus*	21	14	6	R(CW)
Turkey Vulture	*Cathartes aura*	17	8	3	
Chihuahuan Raven	*Corvus cryptoleucus*	15	9	4	
Killdeer	*Charadrius vociferus*	15	5	2	R(CW), I
Cooper's Hawk	*Accipiter cooperii*	13	9	4	R(CW),c
Common Raven	*Corvus corax*	12	7	3	
House Sparrow	*Passer domesticus*	12	2	1	
Tropical Kingbird	*Tyrannus melancholicus*	11	5	2	R(CW), I
Varied Bunting	*Passerina versicolor*	11	9	4	C, I
Black-headed Grosbeak	*Pheucticus melanocephalus*	10	10	4	R(Gen), I
Bridled Titmouse	*Baeolophus wollweberi*	10	4	2	R(CW), I
Canyon Towhee	*Melozone fusca*	9	6	3	C
Crissal Thrasher	*Toxostoma crissale*	9	6	3	I
Red-tailed Hawk	*Buteo jamaicensis*	8	7	3	
American Kestrel	*Falco sparverius*	7	7	3	I
Cassin's Sparrow	*Peucaea cassinii*	7	7	3	,C, I
Hooded Oriole	*Icterus cucullatus*	7	6	3	R(Gen),c, I
Lesser Nighthawk	*Chordeiles acutipennis*	6	4	2	I
Common Nighthawk	*Chordeiles minor*	5	5	2	I
Greater Roadrunner	*Geococcyx californianus*	4	4	2	
Curve-billed Thrasher	*Toxostoma curvirostre*	3	3	1	I
European Starling	*Sturnus vulgaris*	3	1	0	I
Pyrrhuloxia	*Cardinalis sinuatus*	3	2	1	

Common Name	Scientific Name	Total Detections	No. Sta. Detected	Freq (%)	Riparian/ Spp. Group
Say's Phoebe	*Sayornis saya*	3	3	1	I
Willow Flycatcher	*Empidonax traillii*	3	2	1	R(CW),c, I
Cactus Wren	*Campylorhynchus brunneicapillus*	2	2	1	I
Green Heron	*Butorides virescens*	2	2	1	R(CW)
Scaled Quail	*Callipepla squamata*	2	2	1	
Eastern Meadowlark	*Sturnella magna*	1	1	0	I
Western Screech-Owl	*Megascops kennicottii*	1	1	0	R(Gen)
White-tailed Kite	*Elanus leucurus*	1	1	0	

Table 5. Species richness and relative abundance of species groups at sites without beaver and where beavers present (two sided *t* test for difference in means, DF = 239)

	Beaver absent (*n*= 154)			Beaver present (*n* = 86)			Difference (%)	Significance	
Species Group	Freq. (%)	Mean	SE	Freq. (%)	Mean	SE		*t*	*P*
No. of Breeding Bird Species (Of 76 spp.)	100	18.90	0.29	100	21.31	0.38	12.8	5.44	<0.001
Relative Abund. of Breeding Bird Species	100	9.99	0.23	100	12.70	0.31	27.1	7.04	<0.001
No. of Riparian Species (of 42)	100	14.76	0.25	100	17.08	0.33	15.7	5.67	<0.001
No. of Riparian Specialists Species (of 14)	100	8.56	0.21	100	10.87	0.28	26.9	6.61	<0.001
No. of Riparian Generalist Species (of 28)	100	6.19	0.13	100	6.21	0.17	0.2	0.07	0.947
No. of Riparian Conservation C. Spp. (of 14)	100	6.29	0.13	100	6.76	0.17	7.4	2.12	0.035
No. of Insectivorous Spp. (of 52)	100	12.42	0.22	100	14.20	0.29	14.3	4.90	<0.001
Relative Abundance of Insectivorous Group	100	6.59	0.18	100	8.25	0.24	25.2	5.60	<0.001

Table 6. Mean relative abundance for most commonly detected bird species (*n* = 31) at sites without beaver and where beavers present (two sided *t* test for difference in means, DF = 239); * denotes species of conservation concern from U.S. Fish and Wildlife Service (2008), and/or Hunter et al. (1987).

	Beaver absent (n= 154)			Beaver present (n = 86)			Difference (%)	Significance	
Species	Freq. (%)	Mean	SE	Freq. (%)	Mean	SE		t	P
Yellow-billed Cuckoo*	12	0.03	0.010	30	0.08	0.013	167.4	3.14	0.002
Common Yellowthroat	63	0.28	0.029	87	0.57	0.039	105.2	5.95	<0.001
Black Phoebe	15	0.04	0.010	24	0.07	0.014	90.4	2.06	0.041
Lesser Goldfinch	73	0.63	0.059	92	1.13	0.078	79.4	5.11	<0.001
Northern Flicker*	21	0.07	0.014	38	0.12	0.018	78.0	2.27	0.024
Song Sparrow	64	0.45	0.042	91	0.78	0.056	73.6	4.75	<0.001
White-breasted Nuthatch	50	0.15	0.019	62	0.25	0.025	65.2	3.24	0.001
Mallard	14	0.06	0.017	27	0.10	0.023	59.4	1.27	0.205
Western Wood-Pewee	39	0.15	0.020	65	0.24	0.027	55.8	2.58	0.011
Brown-headed Cowbird	77	0.39	0.034	85	0.59	0.046	50.2	3.41	0.001
Cassin's Kingbird	64	0.35	0.035	76	0.52	0.047	48.6	2.91	0.004
Ladder-backed Woodpecker	34	0.09	0.012	49	0.13	0.017	45.1	1.94	0.054
Blue Grosbeak	40	0.12	0.015	49	0.17	0.020	44.2	2.01	0.045
Mourning Dove	45	0.17	0.021	62	0.24	0.028	43.4	2.11	0.036
House Finch	74	0.44	0.041	91	0.61	0.054	40.6	2.61	0.010
White-winged Dove	81	0.44	0.032	87	0.60	0.043	37.9	3.07	0.002
Yellow Warbler*	90	1.24	0.062	99	1.64	0.083	32.1	3.81	0.000
Gila Woodpecker*	75	0.37	0.032	85	0.46	0.042	25.8	1.80	0.073
Common Ground-Dove	25	0.07	0.011	26	0.08	0.015	13.9	0.49	0.626
Lucy's Warbler*	45	0.13	0.016	49	0.14	0.021	5.5	0.28	0.780
Summer Tanager*	74	0.34	0.026	74	0.35	0.034	3.2	0.25	0.799

Species	Beaver absent (n= 154) Freq. (%)	Mean	SE	Beaver present (n = 86) Freq. (%)	Mean	SE	Difference (%)	Significance t	P
Yellow-breasted Chat*	95	0.93	0.046	93	0.94	0.061	1.6	0.20	0.844
Abert's Towhee	81	0.45	0.029	83	0.45	0.039	-0.7	-0.06	0.951
Brown-crested Flycatcher*	39	0.14	0.018	45	0.14	0.023	-0.9	-0.04	0.966
Gray Hawk*	15	0.05	0.010	19	0.05	0.014	-4.7	-0.14	0.892
Bell's Vireo*	65	0.29	0.025	57	0.27	0.034	-6.7	-0.47	0.642
Vermilion Flycatcher	75	0.43	0.029	78	0.39	0.039	- 8.8	-0.79	0.433
Bullock's Oriole	25	0.06	0.010	21	0.06	0.013	-10.8	-0.40	0.686
Bewick's Wren	90	0.61	0.034	91	0.53	0.046	-13.4	-1.42	0.158
Ash-throated Flycatcher	44	0.14	0.015	23	0.06	0.020	-55.3	-3.03	0.003
Northern Beardless-Tyrannulet*	31	0.09	0.011	17	0.04	0.014	-60.0	-3.02	0.003

Table 7. Habitat and Environmental Covariate models for species and species groups from multiple linear regression (n = 240) using stepwise variable selection (minimum BIC to enter) selected model terms. Significant *P*-values (≤ 0.05) indicated by *.

Parameter	Estimate	SE	*t*	*P*
Yellow-billed Cuckoo				
Intercept	0.002	0.005	0.420	0.6745
H2O PER	0.016	0.006	2.790	0.0057*
SumPOFR %Cov 20-30m Lg	0.017	0.006	2.610	0.0097*
Common Yellowthroat				
Intercept	-0.094	0.073	-1.280	0.2034
H2O May	0.048	0.019	2.530	0.0121*
BACH Av%Cov Lg	0.102	0.021	4.800	<.0001*
MESQ Av%Cov Log	-0.061	0.017	-3.490	0.0006*
TAMI Av%Cov Lg	-0.047	0.019	-2.500	0.0132*
POFR Av%Cov Lg	-0.121	0.028	-4.380	<.0001*
POFR 12-25cmDBH Lg	-0.163	0.060	-2.700	0.0075*
Veg Diversity Lg	0.306	0.098	3.110	0.0021*
Black Phoebe				
Intercept	0.000	0.008	-0.060	0.9494
H2O PER	0.020	0.006	3.420	0.0007*
POFR Av%Cov Lg	0.040	0.012	3.190	0.0016*
POFR >25cmDBH Lg	-0.047	0.016	-2.970	0.0033*
Lesser Goldfinch				
Intercept	0.087	0.020	4.310	<.0001*
H2O May	0.086	0.028	3.100	0.0022*
H2O PER	0.106	0.023	4.680	<.0001*
SALI <12cmDBH Lg	1.573	0.494	3.180	0.0016*
POFR 12-25cmDBH Lg	0.437	0.085	5.110	<.0001*
SumPOFR %Cov 20-30m Lg	-0.073	0.023	-3.160	0.0018*
Northern Flicker				
Intercept	0.046	0.008	5.760	<.0001*
H2O PER	0.026	0.008	3.440	0.0007*
MESQ Av%Cov Lg	-0.036	0.010	-3.470	0.0006*
POFR >25cmDBH Lg	-0.034	0.014	-2.350	0.0197*

Parameter	Estimate	SE	*t*	*P*
Song Sparrow				
Intercept	0.014	0.015	0.950	0.3417
H2O May	0.148	0.019	7.610	<.0001*
H2O PER	0.047	0.017	2.840	0.0049*
SALI <12cmDBH Lg	1.555	0.374	4.160	<.0001*
White-breasted Nuthatch				
Intercept	0.027	0.009	3.000	0.0030*
POFR >25cmDBH Lg	0.055	0.023	2.360	0.0192*
SumPOFR %Cov 20-30m Lg	0.034	0.013	2.540	0.0117*
Western Wood-Pewee				
Intercept	-0.003	0.011	-0.320	0.7528
H2O May	0.054	0.013	4.320	<.0001*
POFR >25cmDBH Lg	0.069	0.021	3.330	0.0010*
Brown-headed Cowbird				
Intercept	0.117	0.010	11.950	<.0001*
H2O PER	0.068	0.015	4.630	<.0001*
Cassin's Kingbird				
Intercept	0.091	0.011	8.320	<.0001*
H2O PER	0.058	0.016	3.600	0.0004*
SALI <12cmDBH Lg	0.976	0.401	2.430	0.0157*
Yellow Warbler				
Intercept	0.080	0.023	3.470	0.0006*
Wash <200	0.057	0.021	2.710	0.0073*
H2O May	0.148	0.020	7.290	<.0001*
POFR Av%Cov Lg	0.180	0.026	6.820	<.0001*
SALI >25cmDBH Lg	0.242	0.092	2.620	0.0094*
Ash-throated Flycatcher				
Intercept	0.072	0.009	8.310	<.0001*
Wash <200	-0.026	0.010	-2.580	0.0105*
H2O May	-0.039	0.009	-4.150	<.0001*
ALL TAMI LT Lg	0.419	0.174	2.410	0.0168*
Northern Beardless-Tyrannulet				
Intercept	0.037	0.004	8.780	<.0001*
H2O PER	-0.029	0.006	-4.740	<.0001*
ALL MESQ Lg	0.155	0.045	3.480	0.0006*

Parameter	Estimate	SE	*t*	*P*
Species Richness 76 Breeding Bird Species (BBS)				
Intercept	22.075	2.076	10.630	<.0001*
H2O May	2.679	0.590	4.540	<.0001*
Rip Veg Width Lg	-2.977	0.972	-3.060	0.0025*
SALI Av%Cov Lg	2.279	0.834	2.730	0.0068*
Relative Abundance of 76 BBS				
Intercept	3.168	1.575	2.0100	0.0455*
H2O May	2.675	0.456	5.8700	<.0001*
H2O PER	1.045	0.361	2.8900	0.0042*
SALI <12cmDBH Lg	36.390	8.085	4.5000	<.0001*
Veg Diversity Lg	5.465	1.951	2.8000	0.0055*
Species Richness of 42 Riparian BBS				
Intercept	11.811	0.630	18.760	<.0001*
H2O May	2.027	0.547	3.700	0.0003*
TAMI Av%Cov Lg	-1.512	0.537	-2.820	0.0053*
SALI Av%Cov Lg	2.008	0.664	3.030	0.0028*
POFR Av%Cov Lg	1.876	0.559	3.360	0.0009*
Species Richness of Riparian Specialists				
Intercept	0.893	1.403	0.640	0.5254
H2O May	2.771	0.403	6.870	<.0001*
H2O PER	1.115	0.315	3.540	0.0005*
Veg Diversity Lg	6.774	1.739	3.900	0.0001*
Species Richness of 14 conservation concern species				
Intercept	1.629	0.976	1.670	0.0966
SALI >25cmDBH Lg	3.143	1.134	2.770	0.0060*
Veg Diversity Lg	5.346	1.134	4.720	<.0001*
Species Richness of Insectivorous Riparian Birds				
Intercept	10.350	0.576	17.960	<.0001*
H2O May	1.446	0.501	2.890	0.0042*
TAMI Av%Cov Lg	-1.457	0.491	-2.970	0.0033*
SALI Av%Cov Lg	1.494	0.608	2.460	0.0147*
POFR Av%Cov Lg	1.447	0.512	2.830	0.0051*
Relative Abundance of Insectivorous Riparian Birds				
Intercept	1.013	1.201	0.840	0.3996
H2O May	2.065	0.339	6.090	<.0001*
BACH Av%Cov Lg	1.403	0.426	3.290	0.0012*
POFR 12-25cmDBH Lg	-2.926	1.053	-2.780	0.0059*
SALI 12-25cmDBH Lg	6.220	1.960	3.170	0.0017*
Veg Diversity Lg	4.261	1.525	2.790	0.0056*

Table 8. Comparison of models incorporating beaver-related variables to habitat- and environmental covariate-only models for species and species groups, respectively. Habitat and Environmental Covariate models for species and species groups, from multiple linear regression (*n* = 240) using stepwise variable selection (minimum BIC to enter) selected model terms.

Species	Model	R^2	K	LL	AICc	BIC	ΔAIC	W_i
Yellow-billed Cuckoo								
	Habitat	0.083	3	10122.93	-829.52	-815.77	0.00	0.4261
	Habitat + Beaver presence	0.088	4	13541.18	-828.69	-811.55	0.83	0.2819
	Habitat + No. years with dam	0.083	4	13522.09	-827.52	-810.38	1.99	0.1572
	Habitat * Beaver presence	0.093	6	20414.80	-825.81	-801.93	3.71	0.0666
	Habitat + Beaver intensity	0.088	6	20383.28	-824.53	-800.65	4.99	0.0352
	Habitat * No. years with dam	0.086	6	20372.06	-824.08	-800.20	5.44	0.0281
	Habitat * Beaver intensity	0.097	9	30825.23	-820.58	-786.73	8.94	0.0049
Common Yellowthroat								
	Habitat * Beaver presence	0.400	10	19799.39	-472.30	-435.17	0.00	0.4046
	Habitat + Beaver presence	0.391	9	17686.49	-470.82	-436.98	1.48	0.1933
	Habitat + No. years with dam	0.390	9	17668.01	-470.33	-436.48	1.97	0.1512
	Habitat	0.384	8	15634.42	-470.25	-439.71	2.04	0.1456
	Habitat + Beaver intensity	0.399	11	21750.17	-469.61	-429.21	2.69	0.1053
Black Phoebe								
	Habitat	0.074	4	13283.43	-812.92	-795.77	0.00	0.4767
	Habitat + No. years with dam	0.078	5	16654.03	-811.88	-791.36	1.03	0.2842
	Habitat + Beaver presence	0.076	5	16639.10	-811.16	-790.63	1.76	0.1975
	Habitat + Beaver intensity	0.080	7	23405.33	-808.04	-780.82	4.88	0.0416
Lesser Goldfinch								
	Habitat + Beaver presence	0.353	7	7309.42	-252.35	-225.13	0.00	0.6760
	Habitat + Beaver intensity	0.359	9	9400.81	-250.25	-216.41	2.10	0.2370
	Habitat	0.334	6	6118.41	-247.50	-223.62	4.85	0.0598
	Habitat + No. years with dam	0.336	7	7123.20	-245.92	-218.70	6.43	0.0272

Species	Model	R^2	K	LL	AICc	BIC	ΔAIC	W_i
Northern Flicker								
	Habitat	0.118	4	11451.70	-700.82	-683.67	0.00	0.5347
	Habitat + Beaver presence	0.119	5	14340.68	-699.11	-678.59	1.71	0.2272
	Habitat + No. years with dam	0.118	5	14334.03	-698.78	-678.26	2.04	0.1932
	Habitat + Beaver intensity	0.123	7	20156.18	-695.87	-668.65	4.95	0.0450
Song Sparrow								
	Habitat + No. years with dam	0.424	5	7734.22	-377.04	-356.52	0.00	0.4922
	Habitat	0.417	4	6148.79	-376.29	-359.15	0.75	0.3383
	Habitat + Beaver presence	0.417	5	7675.94	-374.20	-353.68	2.84	0.1189
	Habitat + Beaver intensity	0.423	7	10789.54	-372.50	-345.27	4.55	0.0507
White-breasted Nuthatch								
	Habitat + Beaver presence	0.134	4	9265.38	-567.02	-549.88	0.00	0.5456
	Habitat + Beaver intensity	0.144	6	13982.59	-565.62	-541.73	1.41	0.2700
	Habitat	0.116	3	6884.05	-564.11	-550.36	2.91	0.1272
	Habitat + No. years with dam	0.117	4	9191.67	-562.51	-545.36	4.51	0.0572
Western Wood-Pewee								
	Habitat	0.172	3	6783.03	-555.83	-542.08	0.00	0.4971
	Habitat + Beaver presence	0.175	4	9062.17	-554.59	-537.44	1.25	0.2666
	Habitat + No. years with dam	0.172	4	9049.93	-553.84	-536.69	2.00	0.1833
	Habitat + Beaver intensity	0.178	6	13630.09	-551.36	-527.48	4.48	0.0530
Brown-headed Cowbird								
	Habitat	0.083	2	2940.18	-362.93	-352.59	0.00	0.3884
	Habitat + Beaver presence	0.088	3	4421.74	-362.34	-348.58	0.59	0.2889
	Habitat + Beaver intensity	0.101	5	7413.46	-361.41	-340.88	1.52	0.1814
	Habitat + No. years with dam	0.083	3	4404.28	-360.91	-347.15	2.02	0.1413

Species	Model	R^2	K	LL	AICc	BIC	ΔAIC	W_i
Cassin's Kingbird								
	Habitat + Beaver intensity	0.134	6	8457.73	-342.13	-318.25	0.00	0.6016
	Habitat	0.101	3	4144.77	-339.64	-325.89	2.49	0.1736
	Habitat + No. years with dam	0.108	4	5544.08	-339.29	-322.14	2.84	0.1453
	Habitat + Beaver presence	0.103	4	5524.34	-338.08	-320.93	4.05	0.0795
Yellow Warbler								
	Habitat + No. years with dam	0.420	6	7810.14	-315.93	-292.05	0.00	0.5665
	Habitat	0.411	5	6450.42	-314.46	-293.94	1.47	0.2712
	Habitat + Beaver presence	0.412	6	7729.67	-312.68	-288.80	3.26	0.1113
	Habitat + Beaver intensity	0.418	8	10343.60	-311.12	-280.57	4.82	0.0510
Ash-throated Flycatcher								
	Habitat	0.122	4	10847.07	-663.82	-646.67	0.00	0.3943
	Habitat + No. years with dam	0.129	5	13611.57	-663.56	-643.04	0.25	0.3472
	Habitat + Beaver presence	0.126	5	13594.09	-662.71	-642.19	1.11	0.2268
	Habitat + Beaver intensity	0.127	7	19081.82	-658.78	-631.56	5.04	0.0317
Northern Beardless-Tyrannulet								
	Habitat	0.126	3	9572.06	-784.38	-770.63	0.00	0.5395
	Habitat + Beaver presence	0.128	4	12789.83	-782.71	-765.57	1.67	0.2345
	Habitat + No. years with dam	0.126	4	12784.03	-782.36	-765.21	2.02	0.1964
	Habitat + Beaver intensity	0.128	6	19247.15	-778.57	-754.69	5.80	0.0296
Species Groups								
Species Richness 76 Breeding Bird Species								
	Habitat + Beaver intensity	0.296	7	-36014.83	1243.37	1270.59	0.00	0.7948
	Habitat + Beaver presence	0.274	5	-25572.86	1246.68	1267.20	3.31	0.1520
	Habitat + No. years with dam	0.265	5	-25631.20	1249.52	1270.04	6.15	0.0367
	Habitat	0.254	4	-20443.72	1251.11	1268.26	7.74	0.0165

Species	Model	R^2	K	LL	AICc	BIC	ΔAIC	W_i
Relative Abundance of 76 Breeding Bird Species								
	Habitat + Beaver presence	0.457	6	-27095.11	1096.04	1119.92	0.00	0.6868
	Habitat + Beaver intensity	0.460	8	-36532.86	1098.84	1129.38	2.80	0.1689
	Habitat	0.443	5	-22561.15	1099.86	1120.38	3.82	0.1016
	Habitat + No. years with dam	0.444	6	-27232.54	1101.59	1125.48	5.56	0.0426
Species Richness of 42 Riparian Breeding Bird Species								
	Habitat + Beaver intensity	0.393	8	-37986.41	1142.56	1173.10	0.00	0.5584
	Habitat + Beaver presence	0.379	6	-28279.08	1143.93	1167.81	1.37	0.2818
	Habitat + No. years with dam	0.373	6	-28329.78	1145.98	1169.86	3.42	0.1010
	Habitat	0.365	5	-23529.50	1147.06	1167.59	4.50	0.0588
Species Richness of Riparian Specialists								
	Habitat + Beaver intensity	0.467	7	-30194.09	1042.42	1069.64	0.00	0.3540
	Habitat + Beaver presence	0.457	5	-21384.78	1042.51	1063.03	0.09	0.3380
	Habitat	0.450	4	-17052.20	1043.56	1060.71	1.14	0.1998
	Habitat + No. years with dam	0.452	5	-21431.51	1044.79	1065.31	2.37	0.1082
Species Richness of 14 Conservation Concern Spp.								
	Habitat	0.134	3	-10851.80	889.24	903.00	0.00	0.5283
	Habitat + No. years with dam	0.135	4	-14558.93	890.98	908.12	1.73	0.2223
	Habitat + Beaver presence	0.134	4	-14562.27	891.18	908.33	1.94	0.2007
	Habitat + Beaver intensity	0.139	6	-22100.92	894.01	917.89	4.77	0.0487
Species Richness of Insectivorous Riparian Birds								
	Habitat + Beaver intensity	0.319	8	-36691.52	1103.61	1134.16	0.00	0.3587
	Habitat + Beaver presence	0.306	6	-27286.92	1103.79	1127.68	0.18	0.3275
	Habitat	0.298	5	-22658.75	1104.61	1125.14	1.00	0.2174
	Habitat + No. years with dam	0.299	6	-27347.42	1106.24	1130.12	2.63	0.0964

Species	Model	R^2	K	LL	AICc	BIC	ΔAIC	W_i
Relative Abundance of Insectivorous Riparian Birds								
	Habitat	0.433	6	-23896.12	966.63	990.51	0.00	0.3866
	Habitat + Beaver presence	0.436	7	-28025.13	967.53	994.76	0.90	0.2461
	Habitat + Beaver intensity	0.446	9	-36351.82	967.70	1001.55	1.07	0.2267
	Habitat + No. years with dam	0.433	7	-28057.59	968.65	995.88	2.02	0.1406

Table 9. Result of multiple linear regression (n = 240) models after adding beaver-related factors to habitat/covariate models (Table 7), for species and species groups. Significant *P*-values (≤ 0.05) indicated by *.

Parameter	Estimate	SE	*t*	*P*
Yellow-billed Cuckoo				
Habitat + Beaver Presence				
Intercept	0.001	0.005	0.310	0.7554
H2O PER	0.012	0.007	1.860	0.0644
SumPOFR %Cov 20-30m Lg	0.016	0.007	2.430	0.0160*
Beaver Presence	0.008	0.007	1.110	0.2660
Habitat + No. years with dam				
Intercept	0.002	0.005	0.420	0.6744
H2O PER	0.016	0.006	2.570	0.0108*
SumPOFR %Cov 20-30m Lg	0.017	0.006	2.570	0.0107*
Num Yr BD <51 Lg	0.005	0.018	0.300	0.7627
Common Yellowthroat				
Habitat * Beaver presence				
Intercept	-0.051	0.075	-0.680	0.4983
BACH Av%Cov Lg	0.100	0.021	4.720	<.0001*
MESQ Av%Cov Lg	-0.056	0.018	-3.210	0.0015*
TAMI Av%Cov Lg	-0.036	0.019	-1.860	0.0640
POFR Av%Cov Lg	-0.122	0.028	-4.410	<.0001*
POFR 12-25cmDBH Lg	-0.155	0.060	-2.570	0.0108*
Veg Diversity Lg	0.296	0.098	3.020	0.0028*
H2O May	-0.012	0.035	-0.330	0.7397
Beaver Presence	0.059	0.024	2.480	0.0137*
(H2O May)*(Beaver Presence)	-0.171	0.091	-1.880	0.0609
Habitat + Beaver Presence				
Intercept	-0.088	0.073	-1.200	0.2316
H2O May	0.043	0.019	2.260	0.0245*
BACH Av%Cov Lg	0.100	0.021	4.660	<.0001*
MESQ Av%Cov Lg	-0.055	0.018	-3.120	0.0020*
TAMI Av%Cov Lg	-0.040	0.019	-2.090	0.0378*
POFR Av%Cov Lg	-0.117	0.028	-4.230	<.0001*
POFR 12-25cmDBH Lg	-0.153	0.061	-2.530	0.0121*
Veg Diversity Lg	0.287	0.099	2.910	0.0040*
Beaver Presence	0.022	0.014	1.630	0.1045
Habitat + No. years with dam				
Intercept	-0.087	0.073	-1.190	0.2358
H2O May	0.048	0.019	2.520	0.0123*
BACH Av%Cov Lg	0.098	0.022	4.550	<.0001*

Parameter	Estimate	SE	*t*	*P*
MESQ Av%Cov Lg	-0.058	0.017	-3.310	0.0011*
TAMI Av%Cov Lg	-0.043	0.019	-2.280	0.0234*
POFR Av%Cov Lg	-0.118	0.028	-4.290	<.0001*
POFR 12-25cmDBH Lg	-0.158	0.060	-2.620	0.0094*
Veg Diversity Lg	0.292	0.098	2.970	0.0032*
Num Yr BD <51 Lg	0.055	0.037	1.480	0.1413
Black Phoebe				
Habitat + No. years with dam				
Intercept	-0.001	0.008	-0.080	0.9398
H2O PER	0.018	0.006	2.870	0.0044*
POFR Av%Cov Lg	0.039	0.012	3.140	0.0019*
POFR >25cmDBH Lg	-0.046	0.016	-2.910	0.0040*
Num Yr BD <51 Lg	0.019	0.019	1.030	0.3064
Habitat + Beaver presence				
Intercept	-0.001	0.008	-0.130	0.8967
H2O PER	0.018	0.007	2.570	0.0108*
POFR Av%Cov Lg	0.040	0.012	3.170	0.0017*
POFR >25cmDBH Lg	-0.047	0.016	-2.950	0.0035*
Beaver Presence	0.004	0.007	0.580	0.5628
Lesser Goldfinch				
Habitat + Presence				
Intercept	0.087	0.020	4.360	<.0001*
H2O May	0.077	0.028	2.790	0.0057*
H2O PER	0.080	0.024	3.310	0.0011*
SALI <12cmDBH Lg	1.516	0.488	3.110	0.0021*
POFR 12-25cmDBH Lg	0.448	0.085	5.300	<.0001*
SumPOFR %Cov 20-30m Lg	-0.079	0.023	-3.440	0.0007*
Beaver Presence	0.060	0.023	2.620	0.0093*
Habitat + Beaver intensity				
Intercept	0.085	0.020	4.260	<.0001*
H2O May	0.073	0.028	2.620	0.0094*
H2O PER	0.087	0.025	3.510	0.0005*
SALI <12cmDBH Lg	1.583	0.491	3.230	0.0014*
POFR 12-25cmDBH Lg	0.459	0.085	5.410	<.0001*
SumPOFR %Cov 20-30m Lg	-0.077	0.023	-3.310	0.0011*
Beaver Level 1	0.082	0.029	2.870	0.0045*
Beaver Level 2	0.030	0.031	0.950	0.3406
Beaver Level 3	0.059	0.037	1.600	0.1108

Parameter	Estimate	SE	*t*	*P*
Northern Flicker				
Habitat + Beaver presence				
Intercept	0.045	0.008	5.570	<.0001*
H2O PER	0.023	0.009	2.580	0.0104*
MESQ Av%Cov Lg	-0.036	0.010	-3.440	0.0007*
POFR >25cmDBH Lg	-0.033	0.014	-2.330	0.0207*
Beaver Presence	0.006	0.009	0.620	0.5359
Song Sparrow				
No. years with dam				
Intercept	0.014	0.015	0.970	0.3329
H2O May	0.146	0.019	7.580	<.0001*
H2O PER	0.040	0.017	2.320	0.0209*
SALI <12cmDBH Lg	1.514	0.374	4.050	<.0001*
Num Yr BD <51 Lg	0.077	0.046	1.680	0.0949
White-breasted Nuthatch				
Habitat + Beaver presence				
Intercept	0.022	0.009	2.360	0.0193*
POFR >25cmDBH Lg	0.060	0.023	2.560	0.0110*
SumPOFR %Cov 20-30m Lg	0.026	0.014	1.840	0.0671
Beaver Presence	0.023	0.010	2.230	0.0268*
Habitat + Beaver intensity				
Intercept	0.022	0.009	2.400	0.0172*
POFR >25cmDBH Lg	0.058	0.023	2.470	0.0142*
SumPOFR %Cov 20-30m Lg	0.026	0.014	1.900	0.0590
Beaver Level 1	0.036	0.014	2.540	0.0118*
Beaver Level 2	0.022	0.015	1.540	0.1261
Beaver Level 3	0.001	0.018	0.050	0.9634
Western Wood-Pewee				
Habitat + Beaver presence				
Intercept	-0.004	0.011	-0.350	0.7252
H2O May	0.049	0.014	3.650	0.0003*
POFR >25cmDBH Lg	0.070	0.021	3.380	0.0008*
Beaver Presence	0.010	0.011	0.910	0.3641
Habitat + No. Years w/ Dam				
Intercept	-0.003	0.011	-0.310	0.7566
H2O May	0.055	0.013	4.290	<.0001*
POFR >25cmDBH Lg	0.068	0.021	3.320	0.0011*
Num Yr BD <51 Lg	-0.009	0.031	-0.300	0.7648

Parameter	Estimate	SE	*t*	*P*
Brown-headed Cowbird				
Beaver presence				
Intercept	0.115	0.010	11.410	<.0001*
H2O PER	0.056	0.017	3.220	0.0015*
Beaver Presence	0.022	0.018	1.210	0.2277
Beaver intensity				
Intercept	0.113	0.010	11.280	<.0001*
H2O PER	0.061	0.018	3.440	0.0007*
Beaver Level 1	0.038	0.022	1.710	0.0880
Beaver Level 2	-0.009	0.025	-0.350	0.7293
Beaver Level 3	0.033	0.030	1.100	0.2711
Cassin's Kingbird				
Beaver intensity				
Intercept	0.086	0.011	7.830	<.0001*
H2O PER	0.060	0.019	3.200	0.0016*
SALI <12cmDBH Lg	0.998	0.398	2.510	0.0128*
Beaver Level 1	0.053	0.023	2.260	0.0245*
Beaver Level 2	-0.016	0.026	-0.600	0.5485
Beaver Level 3	-0.031	0.031	-1.020	0.3089
Yellow Warbler				
Habitat + No. Years w/ Dam				
Intercept	0.078	0.023	3.400	0.0008*
Wash <200	0.065	0.021	3.040	0.0027*
H2O May	0.155	0.020	7.550	<.0001*
POFR Av%Cov Lg	0.178	0.026	6.800	<.0001*
SALI >25cmDBH Lg	0.272	0.093	2.910	0.0040*
Num Yr BD <51 Lg	-0.098	0.052	-1.880	0.0614
Ash-throated Flycatcher				
Habitat + No. Years w/ Dam				
Intercept	0.072	0.009	8.260	<.0001*
Wash <200	-0.024	0.010	-2.270	0.0243*
H2O May	-0.036	0.010	-3.790	0.0002*
ALL TAMI LT Lg	0.407	0.174	2.340	0.0201*
Num Yr BD <51 Lg	-0.034	0.025	-1.350	0.1787
Habitat + Beaver presence				
Intercept	0.072	0.009	8.300	<.0001*
Wash <200	-0.024	0.010	-2.350	0.0198*
H2O May	-0.035	0.010	-3.450	0.0007*
ALL TAMI LT Lg	0.405	0.175	2.320	0.0211*
Beaver Presence	-0.009	0.009	-0.990	0.3234

Parameter	Estimate	SE	*t*	*P*
Northern Beardless-Tyrannulet				
Habitat + Beaver presence				
Intercept	0.037	0.004	8.700	<.0001*
H2O PER	-0.026	0.007	-3.610	0.0004*
ALL MESQ Lg	0.155	0.045	3.470	0.0006*
Beaver Presence	-0.005	0.008	-0.640	0.5206
Species Groups				
Species Richness 76 Breeding Bird Species (BBS)				
Intensity				
Intercept	22.075	2.076	10.630	<.0001*
H2O May	2.679	0.590	4.540	<.0001*
Rip Veg Width Lg	-2.977	0.972	-3.060	0.0025*
SALI Av%Cov Lg	2.279	0.834	2.730	0.0068*
Beaver Level 1	1.849	0.604	3.060	0.0025
Beaver Level 2	0.012	0.064	0.020	0.9855
Beaver Level 3	2.061	0.777	2.650	0.0086
Beaver presence				
Intercept	22.423	2.057	10.900	<.0001*
H2O May	2.248	0.607	3.700	0.0003*
Rip Veg Width Lg	-3.114	0.963	-3.230	0.0014*
SALI Av%Cov Lg	1.996	0.832	2.400	0.0173*
Beaver Presence	1.204	0.473	2.550	0.0115*
No. years with dam				
Intercept	22.338	2.069	10.800	<.0001*
H2O May	2.538	0.592	4.290	<.0001*
Rip Veg Width Lg	-3.082	0.968	-3.180	0.0017*
SALI Av%Cov Lg	2.124	0.834	2.550	0.0115*
Num Yr BD <51 Lg	2.522	1.321	1.910	0.0574
Relative Abundance of 76 BBS				
Beaver presence				
Intercept	3.3385	1.5608	2.14	0.0335*
H2O May	2.5347	0.455	5.57	<.0001*
H2O PER	0.6368	0.3954	1.61	0.108
SALI <12cmDBH Lg	35.849	8.0052	4.48	<.0001*
Veg Diversity Lg	5.232	1.9332	2.71	0.0073*
Beaver Presence	0.9223	0.3808	2.42	0.0162*
Intensity				
Intercept	3.2037	1.5676	2.04	0.0421*
H2O May	2.4921	0.4573	5.45	<.0001*
H2O PER	0.702	0.403	1.74	0.0828

Parameter	Estimate	SE	*t*	*P*
SALI <12cmDBH Lg	36.726	8.0481	4.56	<.0001*
Veg Diversity Lg	5.3918	1.9411	2.78	0.0059*
Beaver Level 1	1.1451	0.4729	2.42	0.0162*
Beaver Level 2	0.4944	0.5214	0.95	0.344
Beaver Level 3	1.099	0.6189	1.78	0.0771
Species Richness of 42 Riparian BBS				
Intensity				
Intercept	11.472	0.629	18.250	<.0001*
H2O May	1.814	0.547	3.320	0.0011*
TAMI Av%Cov Lg	-1.159	0.542	-2.140	0.0335*
SALI Av%Cov Lg	1.957	0.658	2.980	0.0032*
POFR Av%Cov Lg	2.030	0.553	3.670	0.0003*
Beaver Level 1	1.336	0.514	2.600	0.0099*
Beaver Level 2	0.076	0.522	0.150	0.8840
Beaver Level 3	1.541	0.656	2.350	0.0197*
Beaver presence				
Intercept	11.600	0.631	18.390	<.0001*
H2O May	1.804	0.551	3.270	0.0012*
TAMI Av%Cov Lg	-1.253	0.544	-2.300	0.0222*
SALI Av%Cov Lg	1.859	0.661	2.810	0.0053*
POFR Av%Cov Lg	1.992	0.557	3.580	0.0004*
Beaver Presence	0.890	0.391	2.280	0.0237*
Species Richness of Riparian Specialists				
Intensity				
Intercept	0.804	1.396	0.580	0.5653
H2O May	2.621	0.404	6.480	<.0001*
H2O PER	0.957	0.354	2.700	0.0074*
Veg Diversity Lg	6.865	1.730	3.970	<.0001*
Beaver Level 1	0.947	0.421	2.250	0.0256*
Beaver Level 2	-0.048	0.463	-0.100	0.9169
Beaver Level 3	0.864	0.552	1.570	0.1186
Beaver presence				
Intercept	1.002	1.399	0.720	0.4744
H2O May	2.677	0.405	6.610	<.0001*
H2O PER	0.846	0.349	2.420	0.0162*
Veg Diversity Lg	6.622	1.733	3.820	0.0002*
Beaver Presence	0.602	0.341	1.760	0.0791

Parameter	Estimate	SE	*t*	*P*
Species Richness of 14 Conservation Concern Spp.				
No. years with dam				
Intercept	1.694	0.984	1.720	0.0864
SALI >25cmDBH Lg	3.022	1.154	2.620	0.0094*
Veg Diversity Lg	5.254	1.146	4.580	<.0001*
Num Yr BD <51 Lg	0.372	0.630	0.590	0.5552
Beaver presence				
Intercept	1.684	0.989	1.700	0.0898
SALI >25cmDBH Lg	3.048	1.163	2.620	0.0093*
Veg Diversity Lg	5.255	1.161	4.530	<.0001*
Beaver Presence	0.084	0.217	0.380	0.7010
Species Richness of Insectivorous Riparian Birds				
Intensity				
Intercept	10.115	0.580	17.450	<.0001*
H2O May	1.300	0.504	2.580	0.0106*
TAMI Av%Cov Lg	-1.219	0.500	-2.440	0.0154*
SALI Av%Cov Lg	1.481	0.607	2.440	0.0154*
POFR Av%Cov Lg	1.541	0.510	3.020	0.0028*
Beaver Level 1	1.142	0.474	2.410	0.0166*
Beaver Level 2	-0.046	0.481	-0.100	0.9240
Beaver Level 3	0.801	0.605	1.320	0.1866
Beaver presence				
Intercept	10.205	0.580	17.590	<.0001*
H2O May	1.293	0.507	2.550	0.0114*
TAMI Av%Cov Lg	-1.280	0.501	-2.560	0.0112*
SALI Av%Cov Lg	1.392	0.608	2.290	0.0230*
POFR Av%Cov Lg	1.527	0.512	2.980	0.0032*
Beaver Presence	0.611	0.360	1.700	0.0907

Parameter	Estimate	SE	*t*	*P*
Relative Abundance of Insectivorous Riparian Birds				
Beaver presence				
Intercept	1.092	1.203	0.910	0.3649
H2O May	1.969	0.350	5.630	<.0001*
BACH Av%Cov Lg	1.385	0.427	3.250	0.0013*
POFR 12-25cmDBH Lg	-2.746	1.065	-2.580	0.0106*
SALI 12-25cmDBH Lg	5.756	2.004	2.870	0.0045*
Veg Diversity Lg	4.160	1.527	2.720	0.0069*
Beaver Presence	0.297	0.271	1.100	0.2736
Intensity				
Intercept	0.955	1.199	0.800	0.4265
H2O May	1.903	0.350	5.440	<.0001*
BACH Av%Cov Lg	1.476	0.430	3.430	0.0007*
POFR 12-25cmDBH Lg	-2.683	1.062	-2.530	0.0122*
SALI 12-25cmDBH Lg	6.549	2.047	3.200	0.0016*
Veg Diversity Lg	4.266	1.522	2.800	0.0055*
Beaver Level 1	0.743	0.353	2.100	0.0365*
Beaver Level 2	-0.136	0.377	-0.360	0.7188
Beaver Level 3	0.111	0.453	0.240	0.8070

FIGURES

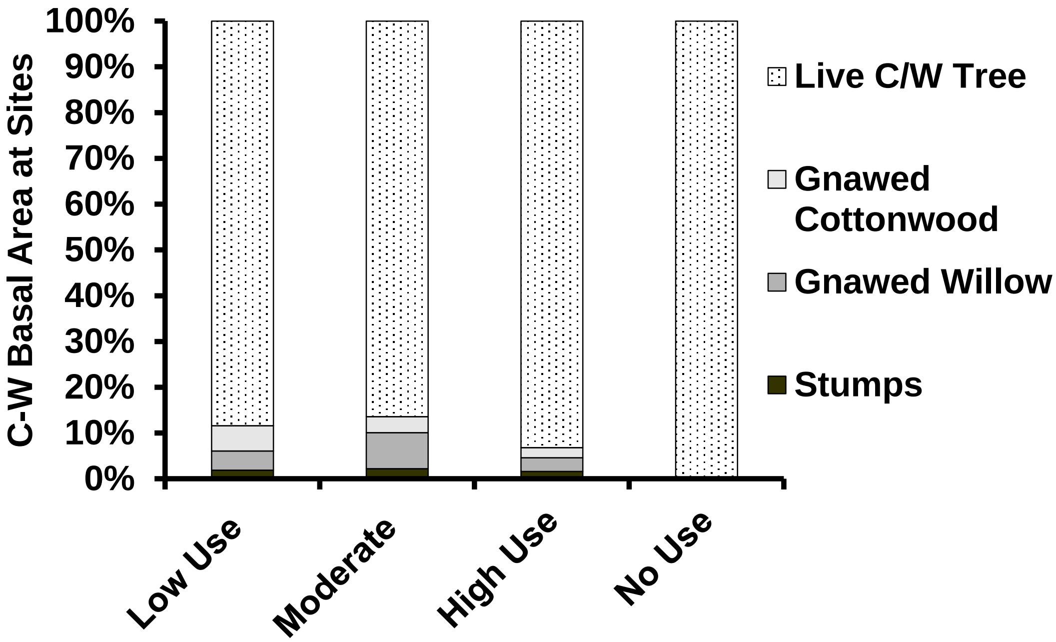

Figure 2. Percentage of total basal area of all beaver-gnawed (but standing) cottonwood and willow trees, and combined basal area of cottonwood-willow stumps and live trees (unaffected by beaver) across all sites within each of the low-, moderate-, and high-use beaver intensity classes, and sites with no beaver use.

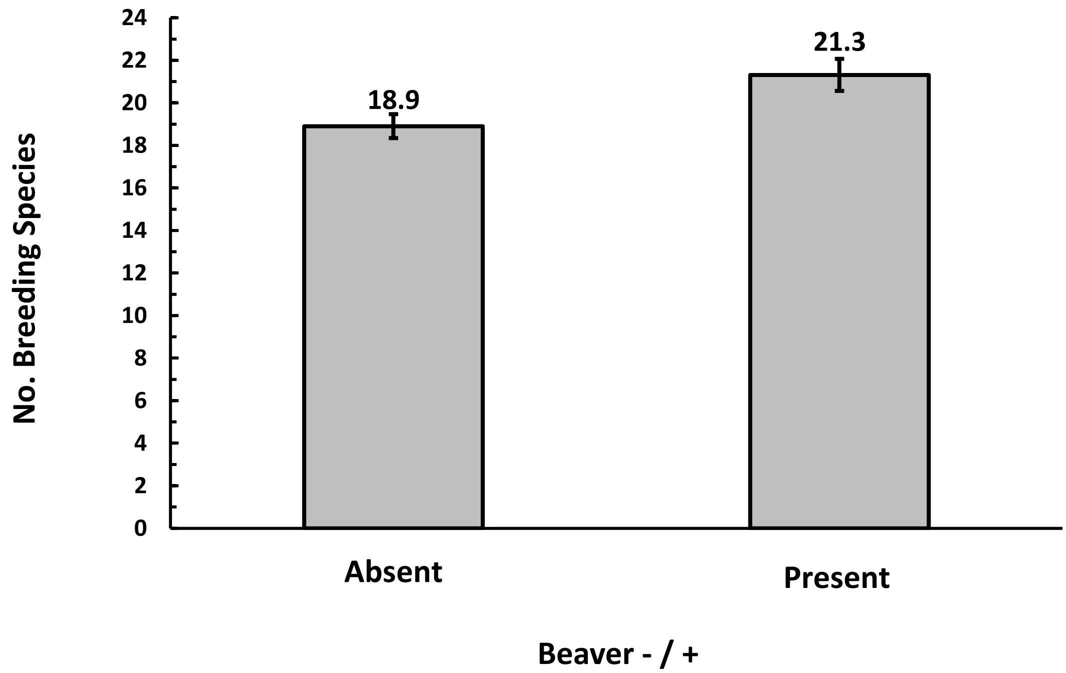

Figure 3. Breeding bird species richness (mean number of 76 species detected within 50 meters of stations) at sites where beavers absent (*n* = 154) and present (*n* = 86); includes 95% confidence intervals from *t* test (Table 5).

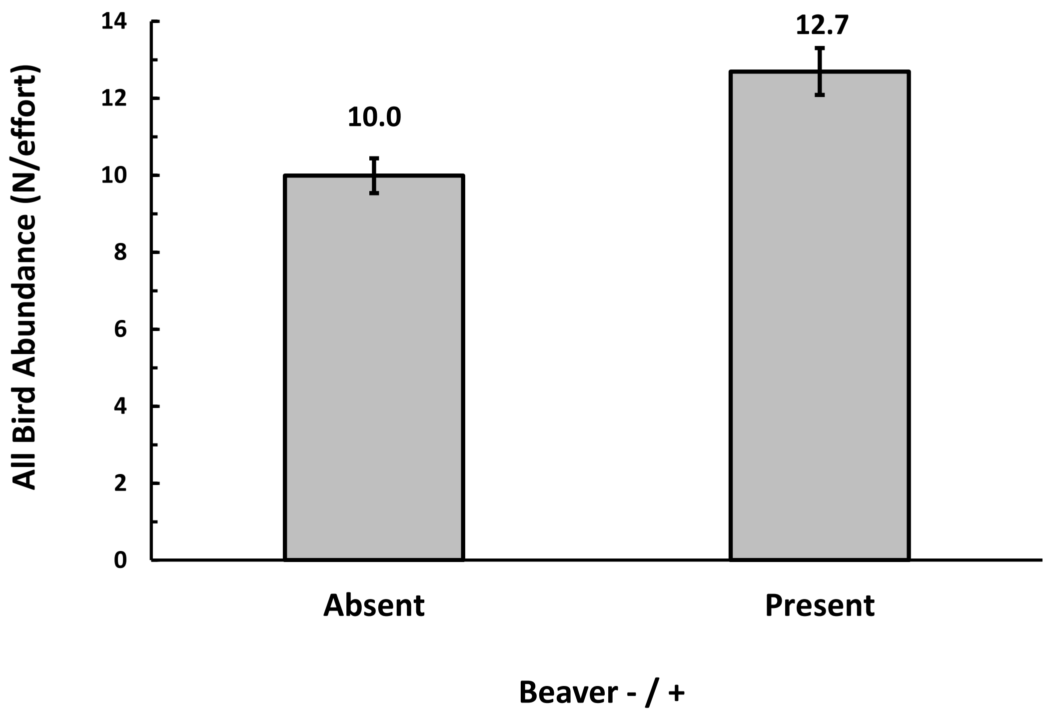

Figure 4. Relative abundance of all breeding birds (average number of individuals detected per survey visit within 50 m) at sites where beavers absent (*n* = 154) and present (*n* = 86); includes 95% confidence intervals from *t* test (Table 5).

APPENDIX

Table 20. Name and location of the 240 point count stations used to survey breeding birds in 2005-2006 on the San Pedro Riparian National Conservation Area, listed from northern-most to southernmost station. Included are the unique station number identifier, station identifier used during field work (an abbreviation of local landmarks and station number within the reach), and geographic coordinates (UTM, NAD 1983 datum).

Unique Station ID	Reach-station ID (Field Name)	Easting	Northing
1	AF1	574901	3525266
2	AF2	575028	3524992
3	AF3	574785	3524935
4	AF3.5	574515	3524859
5	AF4	574439	3524571
6	AF5	574615	3524397
7	AF6	574797	3524203
8	AF7	574627	3524028
9	AF7.5	574712	3523791
10	AF8	574845	3523549
11	AF9	574682	3523324
12	AF10	574420	3523215
13	AF11	574252	3522987
14	AF12	574143	3522718
15	AF13	574200	3522452
16	AF14	574356	3522217
17	AF15	574230	3521984
18	AF16	574151	3521718
19	AF17	574156	3521469
20	AF18	574136	3521192
21	AF19	574122	3520942
22	SDD7	574118	3520681
23	SDD6	574155	3520425
24	SDD5	574264	3520157
25	SDD4	574452	3519970
26	SDD3	574566	3519741
27	SDD2	574725	3519550
28	SDD1	574887	3519362
29	CWW13	574910	3519121
30	CWW12	574714	3518965
32	CWW10	574401	3518602
33	CWW9	574269	3518379
34	CWW8	574078	3518169
35	CWW7	573997	3517911

Unique Station ID	Reach-station ID (Field Name)	Easting	Northing
36	CWW6	574057	3517653
37	CWW5	573972	3517389
38	CWW4	573648	3517281
39	CWW3.5	573500	3517056
40	CWW2	573847	3516907
41	CWW1	574124	3516815
42	CON16	574184	3516549
43	CON15	574124	3516323
44	CON14	574288	3516098
45	CON13	574529	3516035
46	CON12	574803	3515915
47	CON11	575041	3515798
48	CON10	575199	3515617
49	CON9	575108	3515394
50	CON8	574891	3515248
51	CON7	575109	3515099
52	CON6	575310	3514923
53	CON5	575584	3514876
54	CON4	575620	3514579
55	CON3	575502	3514345
56	CON2	575429	3514100
57	CON1	575464	3513848
58	FBN15	575450	3513571
59	FBN14	575531	3513326
60	FBN13	575686	3513093
61	FBN12	575818	3512857
62	FBN11	576005	3512672
63	FBN10	576124	3512457
64	FBN9	576197	3512191
65	FBN8	576184	3511902
66	FBN7	576245	3511662
67	FBN6	576325	3511393
68	FBN5	576351	3511128
69	FBN4	576253	3510871
70	FBN3	576160	3510603
71	FBN2	576160	3510352
72	FBN1	576373	3510194
73	FBS1	576390	3509781
74	FBS2	576471	3509555
75	FBS3	576567	3509305
76	FBS4	576786	3509104
77	BRWE12	576833	3508725
78	BRWE11	577034	3508499
79	BRWE10	577294	3508372
80	BRWE9	577454	3508108
81	BRWE8	577532	3507875
82	BRWE7	577597	3507615

Unique Station ID	Reach-station ID (Field Name)	Easting	Northing
83	BRWE6	577606	3507376
84	BRWE5	577485	3507144
85	BRWE4	577498	3506872
86	BRWE3	577465	3506607
87	BRWE2	577264	3506432
89	BRS3	576723	3506516
90	BRS4	576474	3506505
91	BRS5	576226	3506427
92	BRS6	576206	3506186
93	BRS7	576384	3505993
94	BRS8	576574	3505814
95	BRS9	576760	3505649
96	BRS10	576982	3505505
97	BRS11	577058	3505279
98	BRS12	577278	3505126
99	BRS2	577346	3504874
100	BRS1	577556	3504777
101	GNAR1	577486	3504504
102	GNAR2	577727	3504398
103	GNAR3	577947	3504225
104	GNAR4	578041	3503974
105	GNAR5	577879	3503743
106	GNAR6	577725	3503521
107	GNAR7	577574	3503290
108	GNAR8	577588	3503031
109	GNAR9	577504	3502787
110	GNAR10	577570	3502517
111	GNAR11	577839	3502440
112	GNAR12	578029	3502283
113	NAR1	578111	3502022
114	NAR2	578066	3501761
115	NAR3	577930	3501529
116	NAR4	577851	3501263
117	NAR5	577883	3501015
118	NAR6	578059	3500823
119	NAR7	578152	3500593
120	NAR8	578214	3500334
121	NAR9	577969	3500176
122	NAR10	577849	3499920
123	NAR11	578016	3499696
124	NAR12	578179	3499506
125	GHEW10	578467	3499057
126	GHEW9	578706	3498949
127	GHEW8	578885	3498701
128	GHEW7	579086	3498514
129	GHEW6	579234	3498276
130	GHEW5	579030	3498115

Unique Station ID	Reach-station ID (Field Name)	Easting	Northing
131	GHEW4	578923	3497841
132	GHEW3	579118	3497623
133	GHEW2	579444	3497557
134	GHEW1	579512	3497308
135	GRHA5	579651	3497103
136	GRHA4	579908	3497110
137	GRHA3	580144	3497196
138	GRHA2	580300	3496972
139	GRHA1	580378	3496729
140	LBN18	580866	3495255
141	LBN17	580975	3494966
142	LBN16	581095	3494719
143	LBN15	581060	3494416
144	LBN14	581005	3494154
145	LBN13	581188	3493975
146	LBN12	581400	3493808
147	LBN11	581563	3493598
148	LBN10	581615	3493296
149	LBN9	581468	3493090
150	LBN8	581375	3492868
151	LBN7	581301	3492646
152	LBN6	581351	3492435
153	LBN5	581400	3492159
154	LBN4	581485	3491940
155	LBN3	581558	3491745
156	LBN2	581628	3491504
157	LBN1	581616	3491265
158	LBS1	581937	3490730
159	LBS2	582100	3490579
160	LBS3	582194	3490372
161	LBS4	582354	3490194
162	LBS5	582453	3489917
163	LBS6	582424	3489692
164	LBS7	582322	3489458
165	LBS8	582344	3489235
166	LBS9	582481	3489045
167	LBS10	582643	3488804
168	LBS11	582705	3488630
169	LBS12	582810	3488358
170	LBS13	582792	3488145
171	LBS14	582776	3487930
172	COT1	582723	3487684
173	COT2	582707	3487444
174	COT3	582659	3487192
175	COT4	582755	3486965
176	COT5	582918	3486757
177	COT6	582858	3486505

Unique Station ID	Reach-station ID (Field Name)	Easting	Northing
178	COT7	582756	3486323
179	COT8	582658	3486074
180	COT9	582696	3485827
181	COT10	582938	3485807
182	COT11	583040	3485564
183	COT12	582890	3485363
184	COT13	582874	3485090
185	COT14	583089	3484917
186	HNWA1	583061	3484658
187	HNWA2	583126	3484415
188	HNWA3	583342	3484319
189	HNWA4	583567	3484124
190	HNWA5	583544	3483860
191	HNWA6	583603	3483641
192	HNWA7	583723	3483474
193	HNWA8	583722	3483253
194	HNWA9	583829	3483006
195	HNWA10	584097	3482901
196	HNWA11	583987	3482632
197	HNWA12	584174	3482402
198	HBN21	584338	3482229
199	HBN20	584588	3482259
200	HBN19	584777	3482112
201	HBN18	584626	3481876
202	HBN17	584878	3481868
203	HBN16	585000	3481646
204	HBN15	584961	3481376
205	HBN14	584689	3481339
206	HBN13	584594	3481102
207	HBN12	584859	3481033
208	HBN11	585050	3480836
209	HBN10	584930	3480641
210	HBN9	584711	3480497
211	HBN8	584575	3480260
212	HBN7	584590	3480040
213	HBN6	584733	3479805
214	HBN5	584928	3479601
215	HBN4	584755	3479391
216	HBN3	584701	3479123
217	HBN2	584711	3478872
218	HBN1	584768	3478665
219	HBS1	584825	3478417
220	HBS2	584843	3478161
221	HBS6	585325	3477388
222	HBS7	585332	3477124
223	HBS8	585206	3476894
224	HBS9	585109	3476659

Unique Station ID	Reach-station ID (Field Name)	Easting	Northing
225	HBS10	585031	3476416
226	HBS11	584991	3476175
227	HBS12	585067	3475932
228	HBS13	585112	3475645
229	HBS14	585269	3475437
230	PAL1	584489	3471806
231	PAL2	584554	3471553
232	PAL3	584330	3471407
233	PAL4	584135	3471274
234	PAL5	584006	3471046
235	PAL6	583821	3470897
236	PAL7	583844	3470661
237	PAL8	583653	3470486
238	PAL9	583441	3470367
239	PAL10	583441	3470125
240	PAL11	583278	3469912
241	PAL12	583296	3469647
242	PAL13	583083	3469509