

Effects of Drought on Birds, Vegetation, and Surface Flow in a Desert Riparian Woodland

Dominic D. LaRoche^a, Courtney J. Conway^b, Don E. Swann^c, and Chris Kirkpatrick^d

^a Wildlife Biologist, *School of Natural Resources and the Environment*, University of Arizona, Tucson, AZ 85721. USA. dlaroche@email.arizona.edu

^b Assistant Unit Leader, *U.S. Geological Survey, Arizona Cooperative Fish and Wildlife Research Unit*, School of Natural Resources and the Environment, University of Arizona, Tucson, AZ 85721, USA

^c Biologist, *Saguaro National Park*, Tucson, AZ 85730, USA

^d Senior Research Specialist, *School of Natural Resources and the Environment*, University of Arizona, Tucson, AZ 85721. USA

^e Corresponding Author, Email: dlaroche@email.arizona.edu, Phone: 001-520-626-8293, Fax: 001-520-621-8801

ABSTRACT

Most climate projection models predict reduced water availability in southwestern North America within the next 100 years and a shift to a more arid climate. The reductions in available water from a changing environment, coupled with increasing water needs of growing human populations, will pose a substantial threat to desert riparian woodlands in future years. Riparian woodlands in the desert southwest provide habitat for many species of wintering, breeding, and migratory birds. Over 50% of breeding bird species in the southwest U.S. are thought to be dependent upon riparian woodlands even though these areas account for <1% of the landscape. Water, in the form of both ground water and surface water, is critical for maintaining healthy riparian woodlands. We conducted a longitudinal study of a riparian woodland in southeastern Arizona from 2006-2010 to determine how a riparian bird community responds to (and recovers from) drought effects, including decreased surface and ground water, increased plant mortality, and decreased plant cover. We surveyed birds and monitored nests while simultaneously measuring riparian vegetation, surface water, and ground water to track the changes in these variables resulting from a temporary drought. We documented declines in nesting attempts associated with the drought for three species of riparian birds. The presence of surface water was the most important predictor for 9 bird species and overall species richness. Other species responded to drought-induced changes in vegetation. Reductions in available water for desert riparian woodlands pose a substantial risk for many riparian-obligate bird species.

Key Words: Climate Change, Riparian, Birds, Drought, Ground water, Surface Water

1. INTRODUCTION

Most climate models predict substantial changes in global climate over the next 100 years (Karl and Trenberth 2003). Efforts to understand the effects of these predicted changes on plants and animals have focused on building models to predict the effects of temperature increases on species' distributions (Root et al. 2005, Rodenhouse et al. 2008, Sekercioglu et al. 2008). Species' distributions appear to be shifting to both higher latitudes and higher elevations in response to rising temperatures (Chen et al. 2011). However, changes in precipitation may affect species' distributions more so than changes in temperature (McLaughlin et al. 2002). The effects of changes in precipitation over the next century have received far less attention compared to efforts to predict the effects of temperature changes. This is surprising given that many models predict substantial increases in the frequency and severity of drought in several regions of North America (Karl and Trenberth 2003, Seager et al. 2007) and water scarcity is considered by many to be the most pressing environmental problem for the 21st century (Postel 1999).

Riparian woodlands in the desert regions of southwestern U.S. provide habitat for many species of wintering, breeding, and migratory birds. For example, 213 bird species were detected within riparian woodlands in southeastern Arizona during spring and early summer (Conway et al. unpublished data). Over 50% of breeding bird species in the southwestern U.S. are dependent upon water-related habitat, such as riparian woodlands, even though this habitat accounts for <1% of the landscape in the southwestern U.S. (Johnson et al. 1977). In addition, riparian woodlands provide critical stopover habitat for many species of long-distance, neotropical migratory birds (Skagen et al. 1998). Unfortunately, riparian woodlands are under increasing threat from groundwater pumping, water diversions, clearing for agriculture and development, grazing, and recreation (Szaro 1989). In addition to this suite of anthropogenic threats, riparian

woodlands may also be adversely affected by climate change; most climate models predict that the southwestern U.S. will become more arid over the next 100 years (Seager et al. 2007).

Water, in the form of both ground water and surface water, is critical for maintaining healthy riparian woodlands. Avian species richness is often higher in riparian woodlands compared to surrounding vegetative communities and this pattern is commonly attributed to the structural complexity of the vegetation (Anderson and Ohmart 1977, Bull and Skovlin 1982, Knopf and Samson 1994). The high structural complexity of vegetation within riparian woodlands is afforded by the availability of shallow ground water (Stromberg 1996). Surface water also contributes to high species diversity in riparian woodlands, especially for riparian woodlands embedded in desert ecosystems (Brand et al. 2008, Hinojosa-Huerta et al. 2008, Kirkpatrick et al. 2009). Surface water itself (independent of the structural complexity of the vegetation) may increase avian species diversity because riparian woodlands with surface water often support higher densities of invertebrate prey (Jackson and Fisher 1986, Gray 1993).

The quality and quantity of riparian woodlands in the southwestern U.S. has declined in recent decades due to competition for limited water resources from an expanding human population in the region (Stromberg et al. 2004, Webb and Leak 2006). Pumping groundwater for anthropogenic use has caused reductions in both groundwater and surface water and can alter the composition and structure of riparian vegetation (Lite and Stromberg 2005). Global climate change is likely to further reduce the availability of water in the southwestern U.S. by decreasing the amount of winter and spring precipitation (Seager et al. 2007), reducing depth of winter snowpack (Barnett et al. 2004), altering the timing and size of snowmelt (Stewart et al. 2005), increasing temperatures (Bates et al. 2008), and increasing the frequency and severity of drought (Gutowski et al. 2008). These factors will likely exacerbate the competition for limited water

resources and potentially increase the risk to desert riparian woodlands and the plants and animals that depend on them (U.S. Bureau of Reclamation 2005). Even the current level of demand on water resources in the southwest may not be met in future years due to declining water resources (Barnett et al. 2004).

Drought and subsequent reduction of ground and surface water have been shown to affect the composition of bird communities in numerous ecosystems (Smith 1982, Albright et al. 2010). However, no studies have quantified the effect of drought (or groundwater reduction) on riparian bird communities in the southwestern U.S. Managers and regulators need projections regarding how riparian birds will respond to reductions in surface water, ground water, and riparian vegetation given the twin threats presented by increasing human demand for water resources (causing increases in groundwater withdrawal) and global climate change (causing increased incidence of drought). We conducted a longitudinal study of a riparian woodland in southeastern Arizona from 2006-2010, during and after a severe drought, to determine how birds and vegetation responds to (and recovers from) decreased surface water, and ground water. Our objectives were to: 1) determine the response of the bird community to a dramatic decline in both ground and surface water and identify bird species most vulnerable to future droughts, 2) document the rate at which riparian vegetation recovers from a dramatic decline in water availability, and 3) determine the relative importance of water and vegetation to avian species richness in riparian woodlands.

2. METHODS

Rincon Creek is a low-elevation (965 m above sea level) riparian woodland in Saguaro National Park, Pima County, Arizona, USA with mixed-broadleaf riparian vegetation. Dominant

trees include: Arizona sycamore (*Plantanus wrightii*), velvet mesquite (*Prosopis velutina*), velvet ash (*Fraxinus velutina*), Arizona walnut (*Juglans major*), Frémont cottonwood (*Populus fremontii*), and willows (*Salix* spp.). Mesquite and mesquite-hackberry (*Celtis* spp.) woodlands dominate the transitional area between the mixed-broadleaf riparian woodland and the surrounding desert uplands. Climate in the region is arid to semi-arid with approximately 300 mm of precipitation per year. The precipitation annual pattern is bimodal with a brief summer season of localized thunderstorms and a longer winter season of widespread frontal storms.

We used a hand-held Global Positioning System (GPS) receiver to establish survey points along a survey route. Adjacent survey points were 100 m apart along a 1000-m section of the stream channel at Rincon Creek. We chose a 100-m interval between points to capture small-scale differences in conditions (e.g., isolated standing pools of water or dense vegetation) along the stream channel. We conducted point-count surveys at the survey points from 1 April to 25 June in 2006, 2007, 2008, and 2010. We selected this time period based on records of peak breeding activity for the most-common riparian and upland birds found in and near riparian areas in Arizona (Corman and Wise-Gervais 2005). We surveyed birds approximately every 3 weeks (4 surveys at each point per year) and alternated the direction in which we conducted surveys along the survey route from one visit to the next. We conducted all bird surveys in the early morning (between sunrise and 2 hours after sunrise) on days without precipitation and with wind speeds <10 km/hr. At each survey point, observers waited 1 minute and then counted all birds heard and/or seen during an 8-minute survey period.

We monitored nests of all riparian and upland breeding bird species in an area approximately 150 m wide (centered on the stream channel) in 2006, 2007, 2008, and 2010. We focused our search efforts on nests of 4 focal species: 1) Abert's towhee (*Melozone aberti*), 2)

Bell's vireo (*Vireo bellii*), 3) northern cardinal (*Cardinalis cardinalis*), and 4) Lucy's warbler (*Oreothlypis luciae*). We monitored nests every 2-3 days to determine fate (failed or fledged).

After each bird survey, we estimated the amount of surface water within a 50-m radius surrounding each bird survey point. For each standing pool of water, we used a GPS receiver to collect UTM coordinates for the start and end points of the pool and a metric tape to measure its maximum width and length. For each segment of flowing water, we recorded the UTM coordinates for the start and end points of the segment and measured the width of water at 50-m increments (or at the segment mid-point for segments <100 m in length). We then used a geographic information system (GIS) to determine which pools of standing water and what proportion of flowing water segments were within 50 m of each survey point. We calculated the surface area of each pool of standing water using the formula for the surface area of an ellipse (surface area = $\pi \times [0.5 \times \text{max. length}] \times [0.5 \times \text{max. width}]$). We calculated the surface area for each flowing segment of water within 50 m of each survey point by multiplying the length of the segment by the average of the 2 closest stream width measurements that we collected along the segment. Saguaro National Park provided daily water elevations of 3 ground water monitoring wells located 5, 47, and 89 m from the stream channel within our study site from May 2005 through 2010.

We used the point-line-intercept method described by Mills et al. (1991) to estimate vegetation volume each year within a 50-m radius plot surrounding each bird survey point. We used a meter tape to establish six 50-m transects spaced at 60 degree intervals from a random azimuth at each survey point. We sampled vegetation at 5 points on each 50-m transect. We selected the location of each of the 5 vegetation sampling points systematically at irregular

intervals so that we collected samples within uniform areas across the 50-m radius plot. We recorded the volume of both live and dead (or dormant) vegetation.

3. DATA ANALYSIS

We selected the 20 most common bird species detected during our surveys for analysis. We modeled the trend in relative abundance for each bird species and we used Akaike's Information Criteria (AIC) to rank candidate models to evaluate the relative importance of surface water and vegetation variables for predicting relative abundance of each bird species. To reduce the total number of variables in our models, we combined hits of all plant species to derive a total vegetation volume estimate for each survey point. We then divided the total vegetation volume into six categories based on height (low = 0-2.5 m, middle = 2.6-5 m, and high = 5.1-20 m above ground) and vigor (live versus dead or dormant). For each of the 3 height categories, we then calculated the proportion of live vegetation. Ground water and surface water variables were highly correlated ($\rho=0.90$, Spearman's rank correlation) and produced model instability when we included both variables in a model, so we only used surface water in our models. We chose to include surface water because we had detailed data on surface water over the entire extent of the study area. We averaged the surface water measured at each survey point over the four surveys per year to generate a single surface water value at each point for each year of the study. We did this because surface water declined throughout the breeding season while the number of birds detected increased with each subsequent survey (Fig. 1). We did not model the within-year relationship between surface water and birds because we assumed that the increasing number of bird detections was not due to declining surface water but rather the arrival of migrant breeders. We used a non-linear mixed model (Bates and Maechler 2010) in the statistical package R (R Development Core Team 2010) to determine the changes in relative

abundance of each bird species over the 4 years that we conducted surveys. We used a mixed model to account for non-independence among survey points within the survey route and among the 4 annual surveys conducted at each point each year. We modeled abundance of each species as a function of year and we used survey point and survey number (1-4) as nested random factors.

We used variable weights (Anderson 2008) to evaluate the relative importance of each explanatory variable in addition to estimating the model parameters and 95% confidence intervals (95% CI). To generate both parameter estimates and variable weights, we compared models with all possible combinations of our four explanatory variables (average surface water and the proportion of live vegetation within the 3 height categories) for each of the 20 most common bird species and for two parameters that described the entire avian community (total relative abundance, species richness). We used model averaging to produce parameter estimates and standard errors which allowed us to account for model selection uncertainty (Burnham and Anderson 2002). We standardized all variables through conversion to z-scores to ease the interpretation of parameter estimates. We used Restricted Maximum Likelihood estimation (REML) to estimate parameters and standard errors for total relative abundance and species richness. However, REML is not appropriate for model comparison when models contain different fixed effects (Verbeke and Molenberghs 2000, Gurka 2006) so we used Maximum Likelihood (ML) to determine variable importance. We used Poisson regression with parameters estimated by Laplace approximation to more accurately account for the distribution of our count data for individual species (Gotelli and Ellison 2004). A Poisson distribution assumes a variance equal to the mean, but variance was not equal to the mean for 13 of the 20 bird species (Srucca 2004). For these 13 species, we also ran a Negative Binomial regression which includes separate

parameters for the variance and the mean (Skaug et al. 2011). Parameter estimates and errors were similar for both models and did not affect our results so we report results only from the Poisson models.

We used the same non-linear mixed procedure to model trends in vegetation over the course of the study. We divided vegetation into the same three height categories that we used in our bird species models but we kept live and dead vegetation separate in order to model each independently. We modeled each vegetation category as a function of year and included survey point as a random factor.

4. RESULTS

Rincon Creek contained no surface water during the breeding season in 2006 (Fig. 1). Surface water returned to Rincon Creek in 2007 and 2008. Ground water elevation displayed the same trend as surface water from 2006-2010 (Fig. 2). Ground water reached a low point in the winter and early summer of 2006 dropping below the bottom of the monitoring wells. This was the lowest elevation of ground water recorded during the study. Ground water elevation was higher during 2007-2010 compared to 2006. Ground water elevation was lower in the winter of 2010 than during the winters of 2007 – 2009. However, the low ground water elevation in 2010 differed from 2006 in both severity and duration. Ground water elevation recovered in 2010 before the bird breeding season began.

Total live vegetation volume increased each year from 2006-2010 ($t=10.7$, $p<0.001$; Fig. 3). Total live vegetation volume for the low height class increased more than three-fold ($t=12.2$, $p<0.001$), the middle height class more than doubled ($t=4.1$, $p<0.001$), but total live vegetation for the highest height class did not show a significant trend across years ($t = 0.2$, $p=0.872$). Total

dead vegetation decreased each year from 2006-2010 ($t=3.8$, $p<0.001$). Dead vegetation decreased at both the middle ($t=4.9$, $p<0.001$) and high ($t=2.8$, $p=0.009$) height classes, but not at the low height class ($t=1.4$, $p=0.171$).

We did not detect a trend in species richness ($t=1.1$, $p=0.263$) or relative abundance for all species combined ($t=0.1$, $p=0.963$) over the 5-year span of the study. We detected 57 species in 2006, 64 species in 2007, 59 species in 2008, and 66 species in 2010. Birds that were not detected in 2006 during surveys (or incidentally during nest searching and monitoring) but were detected in 2007-2010 included mallard (*Anas platyrhynchos*), belted kingfisher (*Megaceryle alcyon*), yellow-billed cuckoo (*Coccyzus americanus*), common yellowthroat (*Geothlypis trichas*), song sparrow (*Melospiza melodia*), painted bunting (*Passerina ciris*), varied bunting (*Passerina versicolor*), and black phoebe (*Sayornis nigricans*). Of the 20 species we examined, we detected 6 with an increasing trend from 2006 to 2010 and 5 with a decreasing trend (Table 1). Two species had a marginally significant positive trend, brown-crested flycatcher (*Myiarchus tyrannulus*) and house finch (*Carpodacus mexicanus*), and one species had a marginally significant negative trend, ladder-backed woodpecker (*Picoides scalaris*).

Surface water was the most important variable for explaining the relative abundance of 9 species and overall species richness (Table 2). Surface water appeared to have a significant and positive effect on overall species richness as well as the abundance of both lesser goldfinch (*Spinus psaltria*) and vermilion flycatcher (*Pyrocephalus rubinus*). Water also appeared to be an important variable for both brown-crested flycatcher and yellow warbler (*Setophaga petechia*), although the 95% CI for both species overlapped zero. Surface water had a negative effect on just one species: verdin (*Auriparus flaviceps*).

The proportion of live vegetation from the lowest height class ranked as the most important variable for 6 species (Table 2). The parameter estimates for 3 of these species did not overlap zero: Bell's vireo, house finch, and ladder-backed woodpecker. Bell's vireo and house finch were positively affected by the increasing proportion of live vegetation in the lowest height class whereas ladder-backed woodpecker was negatively affected. The proportion of live vegetation from the middle height class was the most important variable for 3 species; house finch (tied with the lowest height class), Lucy's warbler, and mourning dove (*Zenaida macroura*). Of these, only the parameter estimate for house finch did not overlap zero. Finally, the proportion of live vegetation from the highest height class was the most important variable for just one species, rufous-winged sparrow (*Peucaea carpalis*). However, the 95% CI for the parameter estimate overlapped zero. The intercept-only model (null model) was the top-ranked model for total relative abundance and relative abundance of northern cardinal and white-winged dove (*Zenaida asiatica*), suggesting that none of the explanatory variables that we included could explain variation in relative abundance of these species.

We found only one Bell's vireo nest in 2006 (nest failed or was abandoned before it was fully built) compared with 8 in 2008 and 22 in 2010. We also found an increasing number of northern cardinal nests from 2006 through 2010 with only one found in 2006 compared with 4 in 2008 and 10 in 2010. Additionally, we documented a yellow warbler nest in both 2008 and 2010 but none in 2006 or 2007, and both a varied bunting and yellow-billed cuckoo nest for the first time in 2010.

5. DISCUSSION

Rincon Creek suffered a severe drought from September 2005 to July 2006, receiving just 3.3 cm of precipitation over a 10-month period (Saguaro National Park, unpublished data; Online Resource 1). This drought severely lowered the water table and completely eliminated flowing surface water from the creek during the bird breeding season in 2006. Surface water measurements provided by Saguaro National Park from 2003 through 2008 show a pattern of surface water peaking in the spring and declining throughout the breeding season. This pattern was interrupted by drought in 2006 when virtually no surface water was recorded for nearly a full year from July 2005 through early July 2006. Moreover, the years prior to the 2006 drought appear to have less persistent surface water than the years after 2006 (Online Resource 2). This may have contributed to the impact of the 2006 drought on both birds and vegetation. We began monitoring surface water in 2006 and our records agree with those provided by Saguaro National Park for the period in which they overlap (2006, 2007, and 2008). By the time our intensive monitoring began in 2006, riparian vegetation was reduced dramatically from previous levels as evidenced by remaining dead and dormant vegetation. Surface water returned in the fall of 2006 and remained present during the breeding season for the following three years. Riparian vegetation began to recover in the spring of 2007 and the recovery continued through 2010. In 2006, the amount of dead vegetation was nearly double that of live vegetation. It was not until two years later (in 2008) that live vegetation was greater than dead vegetation and live vegetation was nearly three times more abundant than dead vegetation by 2010.

Of the 7 bird species for which we detected a positive trend in abundance from 2006 to 2010, 4 are considered to be riparian obligates and 2 of them (Abert's towhee and Bell's vireo) are in need of conservation action (USGS 2006). Of the 6 species for which we detected a negative trend, only one is considered a riparian obligate (Gila woodpecker). Moreover, 4 of the

6 species for which we detected a negative trend nest in tree cavities and are likely to be associated with dead vegetation which declined from 2006 through 2010: ash-throated flycatcher (*Myiarchus cinerascens*), Bewick's wren (*Thryomanes bewickii*), Gila woodpecker, and ladder-backed woodpecker. The ash-throated flycatcher and verdin typically breed in the surrounding upland and may have moved into the riparian woodland during the drought year due to competitive release or because the riparian corridor was more similar to the surrounding uplands during the drought. Birds which typically breed in the uplands may encroach on riparian woodlands during dry years (Chambers et al. 2011) only to be displaced by riparian-obligate species in subsequent years. Our nest monitoring efforts support the results from our survey data; verdin were more common in the riparian woodland during the drought year (2006). The number of nests initiated by 3 of the 4 focal species increased from 2006 through 2010. We spent considerable time attempting to find nests for our focal species each year but conditions at the site were apparently too poor to support breeding by these species in 2006.

Surface water was an important predictor of bird abundance, even after controlling for the effects of vegetation. Abundance of riparian vegetation is strongly linked to amount of surface or ground water (Stromberg 1996) and teasing apart the relative contribution of each variable is typically very difficult when those two variables are highly correlated. The amount of surface water in Rincon Creek increased substantially from 2006 to 2007, but the riparian vegetation did not recover from the 2006 drought until subsequent years. The difference in these two trends provided us a rare opportunity to discriminate between the effects of surface water and riparian vegetation on bird abundance. For example, our models show that Bell's vireos responded solely to the proportion of live vegetation from 0 - 2 meters and not to the increase in surface water. Conversely, vermilion flycatchers were strongly and positively associated with surface water.

Surface water may be important for some species by relieving water stress (Wingfield et al. 1992) or increasing available arthropod prey. Indeed, several orders of aquatic arthropods were absent in 2006 but present in subsequent years on our study site (Conway and LaRoche, unpublished data).

Breeding bird surveys were conducted along the same stretch of Rincon Creek in 2001, 2002, and 2004 (Powell 2004). Unfortunately, we are unable to make direct comparisons to these data because of differences in sampling methods, but Bell's vireo, vermilion flycatcher, and yellow warbler were relatively abundant in 2001-2004 (Powell 2004) before they became rare or absent from Rincon Creek in 2006 (Online Resource 3). Abundance of many of these species rebounded (and even exceeded previous estimates) within three years following the 2006 drought. The replacement of riparian obligates by more desert-oriented birds in 2006 represents a functional niche shift from a riparian-bird dominated community to a more desert-bird community.

The plants and birds in Rincon Creek recovered substantially within four years after the 2006 drought, indicating that riparian woodlands and riparian birds may be somewhat resilient (over the long-term) to the effects of an occasional drought. Climate change has the potential to shift the drought regime outside of the naturally occurring cycle through a combination of decreased winter precipitation, increased temperatures, and increases in the frequency, size, and duration of drought. Decreased winter and spring precipitation combined with higher temperatures will lead to decreased snowpack which, in turn, will lead to decreased water availability for riparian woodlands (Barnett et al. 2004). Moreover, increased temperatures will cause riparian plants to use more water thereby intensifying the seasonal hydrograph.

The 2006 drought in Rincon Creek was short and localized; nearby riparian woodlands did not experience such dramatic changes in both surface water and vegetation (Kirkpatrick et al. 2009). Furthermore, many of the trees which we classified as dead or dormant in 2006 resprouted from the trunk or roots in 2007 after some dieback. A longer-lasting drought (or a subsequent year of winter drought) may have killed more trees and caused the riparian vegetation to recover much more slowly. Moreover, anthropogenic increases in groundwater withdrawal can potentially cause long-term declines in surface water in some systems and create permanent reductions in the abundance of riparian vegetation and the birds that depend on that vegetation. The transition of the southwestern U.S. to a more arid climate and the increase in groundwater withdrawal to support a growing human population poses a double threat to riparian woodlands. Maintaining an adequate supply of water to riparian woodlands in the southwestern U.S. is vital to maintaining the ecosystem services that these unique systems provide.

Acknowledgements:

Saguaro National Park provided access to the study site, ground water measurements, historical data, and project support (Permit #SAGU-2010-SCI-0006). Brian F. Powell provided bird survey data from previous years. Chuck Perger collected surface and groundwater measurements. Early versions of this manuscript benefitted from comments by Christopher P. Nadeau and Audrey R. Nelson. Any use of trade names is for descriptive purposes only and does not imply endorsement by the U.S. Government. This study was performed under the auspices of University of Arizona IACUC protocol #07-064.

LITERATURE CITED

- Albright, T. P., A. M. Pidgeon, C. D. Rittenhouse, M. K. Clayton, C. H. Flather, P. D. Culbert, B. D. Wardlows, and V. C. Radeloff. 2010. Effects of drought on avian community structure. *Global Change Biology* 16: 2158-2170.
- Anderson, B. W., and R. D. Ohmart. 1977. Vegetation structure and bird use in the lower Colorado River Valley. Pages 23-34 in R.R. Johnson and D. A. Jones, eds. Importance, preservation and management of riparian habitat: a symposium. General Technical Report RM-166. U.S. Forest Service, Fort Collins, CO.
- Anderson, D. R. 2008. Model Based Inference in the Life Sciences. Springer Science + Business Media LLC, New York, NY.
- Bates, B. C., Z. W. Kundzewicz, S. Wu, and J.P. Palutikof (eds.). 2008. Climate Change and Water. Technical paper of the Intergovernmental Panel on Climate Change. IPCC Secretariat, Geneva, Switzerland, 210 pp.
- Bates, D., and M. Maechler. 2010. lme4: Linear mixed-effects models using S4 classes. R package version 0.999375-37. <http://CRAN.R-project.org/package=lme4>
- Barnett, T., R. Malone, W. Pennell, D. Stammer, B. Semtner, and W. Washington. 2004. The Effects of Climate Change on Water Resources in the West: Introduction and Overview. *Climatic Change* 62: 1-11.
- 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: 199-210.
- Bull, E. L., and J. M. Skovlin. 1982. Relations between avifauna and streamside vegetation. *Transactions of the N. A. Wildlife and Natural Resources Conference* 47: 496-506.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach, 2nd ed. Springer Science + Business Media Inc. New York, NY.
- Chambers, M., G. David, C. Ray, B. Leitner, and P. Pyle. 2011. Habitats and conservation of molt-migrant birds in southeastern Arizona. *The Southwestern Naturalist* 56: 204-211.
- Chen, I-C., Hill, J.K., Ohlemüller, R., Roy, D.B., and C.D. Thomas. 2011. Rapid range shifts of species associated with high levels of climate warming. *Science* 333: 1024-1026.
- Corman, T. E., and C. Wise-Gervais. 2005. Arizona breeding bird atlas. University of New Mexico Press, Albuquerque, NM.
- Gotelli, N. J. and A. M. Ellison. 2004. A Primer of Ecological Statistics. Sinauer Associates, Inc., Sunderland, MA.
- Gray, L. J. 1993. Response of insectivorous birds to emerging aquatic insects in riparian habitats of a tallgrass prairie stream. *American Midland Naturalist* 129: 288-300.

- Gurka, M. J. 2006. Selecting the Best Linear Mixed Model Under REML. *The American Statistician* 60: 19-26.
- Gutowski, W.J., G.C. Hegerl, G.J. Holland, T.R. Knutson, L.O. Mearns, R.J. Stouffer, P.J. Webster, M.F. Wehner, and F.W. Zwiers. 2008. Causes of observed changes in extremes and projections of future changes. Pages 81-116 in: *Weather and Climate Extremes in a Changing Climate: Regions of Focus: North America, Hawaii, Caribbean, and U.S. Pacific Islands* [Karl, T.R., G.A. Meehl, C.D. Miller, S.J. Hassol, A.M. Waple, and W.L. Murray (eds.)]. Synthesis and Assessment Product 3.3. U.S. Climate Change Science Program, Washington, DC.
- Hinojosa-Huerta, O., H. Iturribarria-Rojas, E. Zamora-Hernandez, and A. Calvo-Fonseca. 2008. Densities, species richness, and habitat relationships of the avian community of the lower Colorado River, Mexico. *Studies in Avian Biology* 37: 74-82.
- Jackson, J. K., and S. G. Fisher. 1986. Secondary production, emergence, and export of aquatic insects of a Sonoran desert stream. *Ecology* 67: 629-638.
- Johnson, R. R., L. T. Haight, and J. M. Simpson. 1977. Endangered species vs. endangered habitats: A concept. Pages 68-79 in R. R. Johnson and D. A. Jones, eds. *Importance, preservation, and management of riparian habitat: A symposium*. General Technical Report RM-166. U.S. Forest Service, Fort Collins, CO.
- Karl, T.R. and K.E. Trenberth. 2003. Modern global climate change. *Science* 302: 1719-1723.
- Kirkpatrick, C., C. J. Conway, and D. D. LaRoche. 2009. Effects of ground water withdrawal on avian abundance and species richness in riparian areas of National Parks in the Desert Southwest. Wildlife Research Report #2009-07, U.S. Geological Survey, Arizona Cooperative Fish and Wildlife Research Unit, Tucson, AZ.
- Knopf, F. L., and F. B. Samson. 1994. Scale perspectives on avian diversity in western riparian ecosystems. *Conservation Biology* 8: 669-676.
- Lite, S. J., and J.C. Stromberg. 2005. Surface water and ground-water thresholds for maintaining *Populus-Salix* forests, San Pedro River, Arizona. *Biological Conservation* 125: 153-167.
- McLaughlin, J. F., J. J. Hellmann, C. L. Boggs, and P. R. Ehrlich. 2002. Climate change hastens population extinctions. *Proceedings of the National Academy of Sciences* 99: 6070-6074.
- Mills, G. S., J. B. Dunning, Jr., and J. M. Bates. 1991. The relationship between breeding bird density and vegetation volume. *Wilson Bulletin* 103: 486-479.
- Postel, A. 1999. *Pillar of Sand: Can the Irrigation Miracle Last?* W. W. Norton & Company, New York, NY.
- Powell, B. F. 2004. Assessment of the bird community along the middle reach of Rincon Creek, Saguaro National Park. Final report to Saguaro National Park, Arizona, USA.

- Pyle, P., W. A. Leitner, L. Lozano-Angulo, F. Avilez-Teran, H. Swanson, E. Gomez-Limon, and M. K. Chambers. 2009. Temporal, spatial, and annual variation in the occurrence of molt-migrant passerines in the Mexican monsoon region. *The Condor* 111: 583-590.
- R Development Core Team. 2010. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org/>.
- Rodenhouse, N.L., Matthews, S.N., McFarland, K.P., Lambert, J.D., Iverson, L.R., Prasad, A., Sillett, T.S., and R.T. Holmes. 2008. Potential effects of climate change on birds of the Northeast. *Mitigation and Adaptation Strategies for Global Change* 13: 517-540.
- Rogers, L. E., W. T. Hinds, and R. L. Buschbom. 1976. A general weight vs. length relationship for insects. *Annals of the Entomological Society of America* 69: 387-389.
- Root, T. L., D. P. MacMynowski, M. D. Mastrandrea, and S. H. Schneider. 2005. Human modified temperatures induce species changes: Joint attribution. *Proceedings of the National Academy of Sciences* 102: 7465-7469.
- Scrucca, L. 2004. Qcc: an R package for quality control charting and statistical process control. *R News* 4/1, 11-17.
- Seager, R., M. Ting, I. Held, Y. Kushnir, J. Lu, G. Vecchi, H. P. Huang, N. Harnik, A. Leetmaa, N. C. Lau, C. Li, J. Velez, and N. Naik. 2007. Model projections of an imminent transition to a more arid climate in southwest North America. *Science* 316: 1181-1184.
- Sekercioglu, C. H., S. H. Schnieder, J. P. Fay, and S. R. Loarie. 2008. Climate change, elevational range shifts, and bird extinctions. *Conservation Biology* 22: 140-150.
- Skagen, S. K., C. P. Melcher, W. H. Howe, M. H. Olson, D. E., Shindler, and B. R. Herwig. 1998. Comparative use of riparian corridors and oases by migratory birds in southeast Arizona. *Conservation Biology* 12: 896-909.
- Skagen, S. K., J. F. Kelly, C. Van Riper, R. L. Hutto, D. M. Finch, D. J. Krueper, and C. P. Melcher. 2005. Geography of spring landbird migration through riparian habitats in southwestern North America. *The Condor* 107: 212-227.
- Skaug, H., D. Fournier, A. Nielsen, A. Magnusson, and B. Bolker. 2011. glmmADMB: Generalized Linear Mixed Models Using AD Model Builder. R package version 0.5-2/r102. <http://R-Forge.R-project.org/projects/glmmadmb/>
- Smith, K. G. 1982. Drought-Induced Changes in Avian Community Structure Along a Montane Sere. *Ecology* 63: 952-961.
- Stewart, I.T., D.R. Cayan, and M.D. Dettinger. 2005. Changes toward earlier streamflow timing across western North America. *Journal of Climate* 18: 1136-1155.
- Stromberg, J. C., R. Tiller, and B. Richter. 1996. Effects of ground water decline on riparian vegetation of semiarid regions: The San Pedro, AZ. *Ecological Applications* 6: 113-131.

- Stromberg, J.C., Briggs, M., Gourley, C., Scott, M., Shafroth, P., and L. Stevens. 2004. Human alterations of riparian ecosystems. In: Baker Jr., M.B., Ffolliott, P.F., DeBano, L.F., Neary, D.G. (Eds.), *Riparian Areas of the Southwestern United States*, Hydrology, Ecology, and Management. Lewis Publishers, New York, pp. 99–126.
- Szaro, R.C. 1989. Riparian forest and scrubland community types of Arizona and New Mexico. *Desert Plants* 9:70-138.
- USBR (U.S. Department of the Interior, Bureau of Reclamation). 2005. *Water 2025: Preventing Crises and Conflict in the West (Water 2025 Status Report)*. U.S. Department of the Interior, Bureau of Reclamation. 32 pp., <http://www.usbr.gov/water2025/>.
- USGS (U.S. Geological Survey). 2006. Birds as indicators of riparian vegetation condition in the western U.S. – riparian obligate species. <http://www.npwrc.usgs.gov/resource/birds/ripveg/obligate.htm>.
- Verbeke, G., and G. Molenberghs. 2000. *Linear Mixed Models For Longitudinal Data*. Springer-Verlag, New York, NY.
- Webb, R.H., and S. A. Leake. 2005. Ground-water surface-water interactions and long-term change in riverine riparian vegetation in the southwestern United States. *Journal of Hydrology* 320: 302-323.
- Wingfield, J. C., C. M. Vleck, and M. C. Moore. 1992. Seasonal changes of the adrenocortical response to stress in birds of the Sonoran Desert. *The Journal of Experimental Zoology* 264: 419-428.

Table 1. Estimates of linear trend in abundance for all 13 bird species for which we detected some evidence of a trend from 2006-2010 at Rincon Creek, Arizona. Note that negative-trending species are primarily cavity-nesting birds or species commonly associated with dead vegetation.

	Species	Estimate	SE	<i>z</i>	<i>P</i>
Positive Trending Species	Abert's Towhee	0.168	0.071	2.38	0.018
	Brown-crested Flycatcher	0.161	0.092	1.76	0.079
	Black-chinned Hummingbird	0.336	0.139	2.42	0.015
	Bell's Vireo	0.598	0.090	6.61	< 0.001
	House Finch	0.123	0.066	1.88	0.061
	Lesser Goldfinch	0.136	0.042	3.21	0.001
	Yellow Warbler	0.377	0.130	2.90	0.004
Negative Trending Species	Ash-throated Flycatcher	-0.356	0.112	-3.19	0.001
	Bewick's Wren	-0.214	0.071	-3.00	0.003
	Cassin's Kingbird	-0.440	0.154	-2.86	0.004
	Gila Woodpecker	-0.308	0.089	-3.47	0.001
	Ladder-backed Woodpecker	-0.173	0.089	-1.93	0.053
	Verdin	-0.304	0.090	-3.37	0.001

Table 2. Relative importance (weight) of 4 explanatory for explaining variation in total bird abundance, bird species richness, and abundance of 20 bird species in a riparian woodland during and after a 10-month drought in Rincon Creek, Saguaro National Park, Arizona. Confidence intervals for parameter estimates incorporate model selection uncertainty.

<u>Response Variable</u>	Surface Water		Proportion of Live Vegetation from 0-2 m		Proportion of Live Vegetation from 2-5 m		Proportion of Live Vegetation from 5-20 m	
	Weight	95% CI	Weight	95% CI	Weight	95% CI	Weight	95% CI
Total Relative Abundance	0.00	(-0.153,0.265)	0.00	(-0.279,0.147)	0.00	(-0.132,0.102)	0.00	(-0.102,0.163)
Species Richness	0.96	(0.064,0.650)	0.65	(-0.415,0.133)	0.73	(-0.409,0.101)	0.33	(-0.103,0.157)
Abert's Towhee	0.56	(-0.226,0.546)	0.35	(-0.219,0.322)	0.36	(-0.181,0.281)	0.50	(-0.184,0.396)
Ash-throated Flycatcher	0.78	(-1.305,0.239)	0.50	(-0.965,0.461)	0.36	(-0.379,0.601)	0.26	(-0.362,0.325)
Bell's Vireo	0.28	(-0.45,0.533)	1.00	(0.46,1.327)	0.34	(-0.219,0.422)	0.32	(-0.177,0.322)
Bewick's Wren	0.54	(-0.485,0.209)	0.39	(-0.36,0.217)	0.42	(-0.456,0.258)	0.27	(-0.194,0.17)
Brown-crested Flycatcher	0.74	(-0.297,1.161)	0.31	(-0.356,0.42)	0.34	(-0.513,0.357)	0.30	(-0.232,0.317)
Brown-headed Cowbird	0.37	(-0.535,1.805)	0.69	(-0.504,0.578)	0.28	(-0.646,0.475)	0.30	(-0.748,1.11)
Cassin's Kingbird	0.34	(-0.827,0.603)	0.82	(-2.041,0.339)	0.38	(-2.041,0.339)	0.28	(-0.503,0.642)
Gambel's Quail	0.55	(-0.992,0.442)	0.48	(-0.436,0.858)	0.28	(-0.344,0.291)	0.26	(-0.239,0.255)
Gila Woodpecker	0.33	(-0.381,0.266)	0.91	(-1.109,0.005)	0.61	(-1.031,0.395)	0.27	(-0.286,0.266)
House Finch	0.25	(-0.196,0.187)	1.00	(0.281,0.861)	1.00	(-1.217,-0.299)	0.80	(-0.075,0.469)
Ladder-backed Woodpecker	0.36	(-0.311,0.481)	0.95	(-1.252,-0.064)	0.36	(-0.275,0.438)	0.44	(-0.273,0.523)
Lesser Goldfinch	0.96	(0.031,0.295)	0.28	(-0.072,0.069)	0.46	(-0.142,0.074)	0.50	(-0.055,0.119)
Lucy's Warbler	0.29	(-0.069,0.06)	0.27	(-0.056,0.054)	0.70	(-0.044,0.165)	0.30	(-0.045,0.061)
Mourning Dove	0.33	(-0.172,0.24)	0.36	(-0.164,0.259)	0.52	(-0.156,0.354)	0.33	(-0.132,0.195)
Northern Cardinal	0.00	(-0.199,0.24)	0.00	(-0.334,0.207)	0.00	(-0.245,0.186)	0.00	(-0.274,0.189)
Rufous-winged Sparrow	0.37	(-0.659,0.411)	0.27	(-0.354,0.391)	0.60	(-1.37,0.54)	0.76	(-0.218,1.052)
Vermillion Flycatcher	1.00	(0.496,1.884)	0.39	(-0.651,0.379)	0.99	(-1.931,-0.309)	0.25	(-0.273,0.28)
Verdin	0.99	(-0.96,-0.208)	0.26	(-0.246,0.244)	0.34	(-0.237,0.371)	0.26	(-0.229,0.202)
White-winged Dove	0.00	(-0.207,0.267)	0.00	(-0.194,0.225)	0.00	(-0.2,0.274)	0.00	(-0.175,0.185)
Yellow Warbler	0.85	(-0.313,2.913)	0.32	(-0.834,0.981)	0.38	(-0.66,1.084)	0.29	(-0.494,0.388)

Online Resource 1. Seasonal precipitation in the Rincon Mountains, Arizona from February 2001 to January 2011. Seasons are divided into summer (June-September), Fall/Winter (October through January), and Winter/Spring (February through May). Winter/Spring precipitation was lowest in 2001, 2002, and 2006.

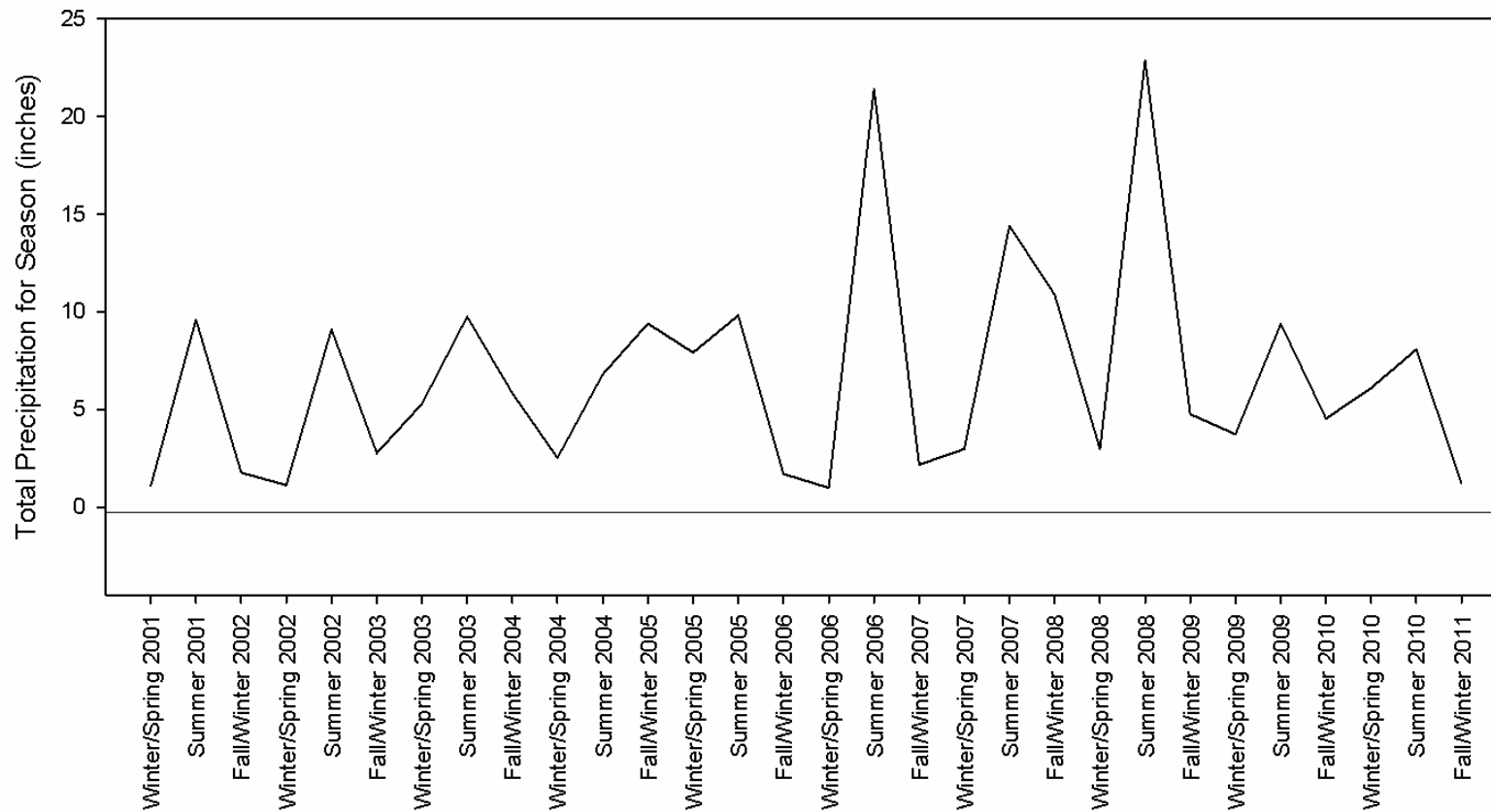
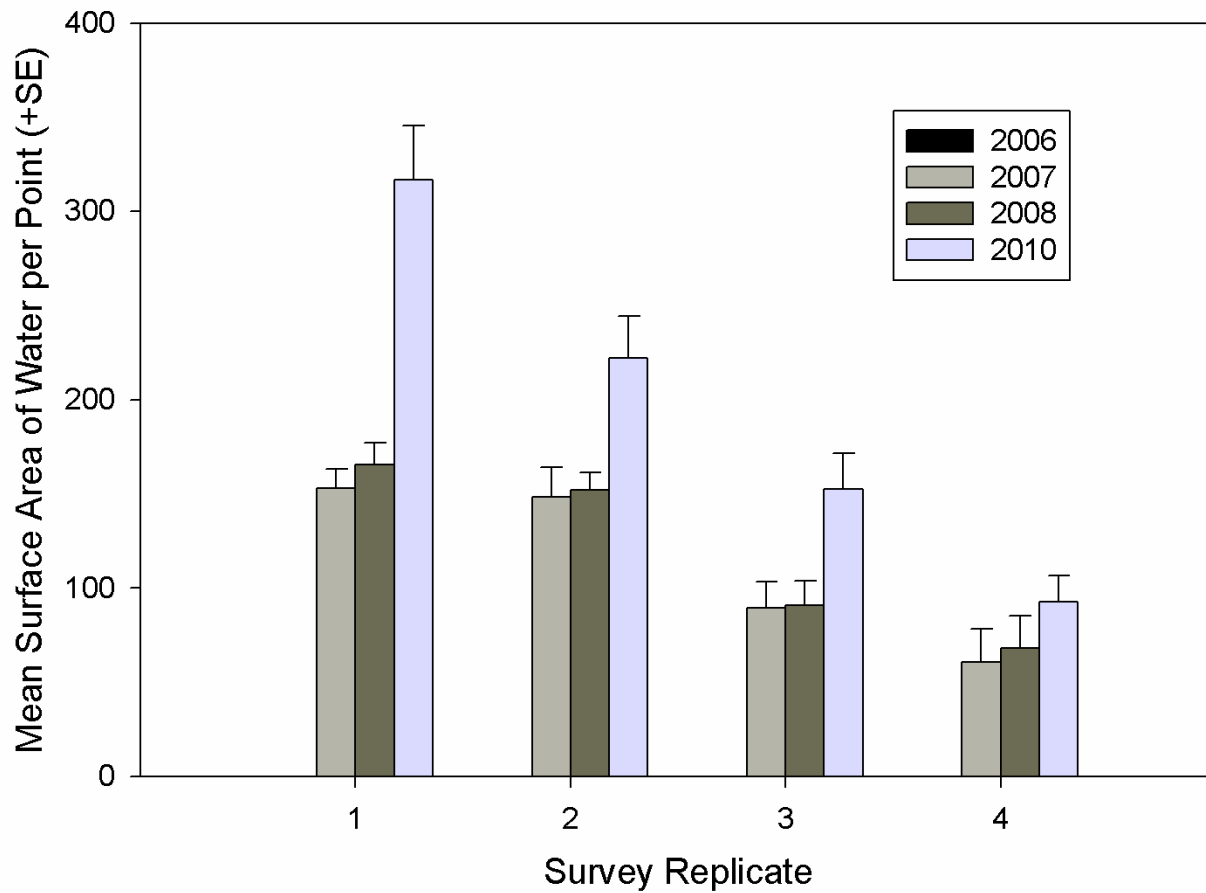


Figure 1. Mean area of surface water (m^2) within 50 m of 10 bird survey points averaged across four replicate bird surveys (April 1 – June 23) at Rincon Creek, Saguaro National Park, Arizona in 2006, 2007, 2008, and 2010. Note that no water was present in Rincon Creek in 2006.



Online Resource 2. Total length of a 900-meter portion of Rincon Creek (Saguaro National Park, Arizona) with surface water present from June 2003 through January 2011. Gaps in the line are due to missing data. Note the sustained period without water during Winter/Spring of 2006 and the increase in surface water persistence after 2006. Courtesy of Saguaro National Park, Arizona.

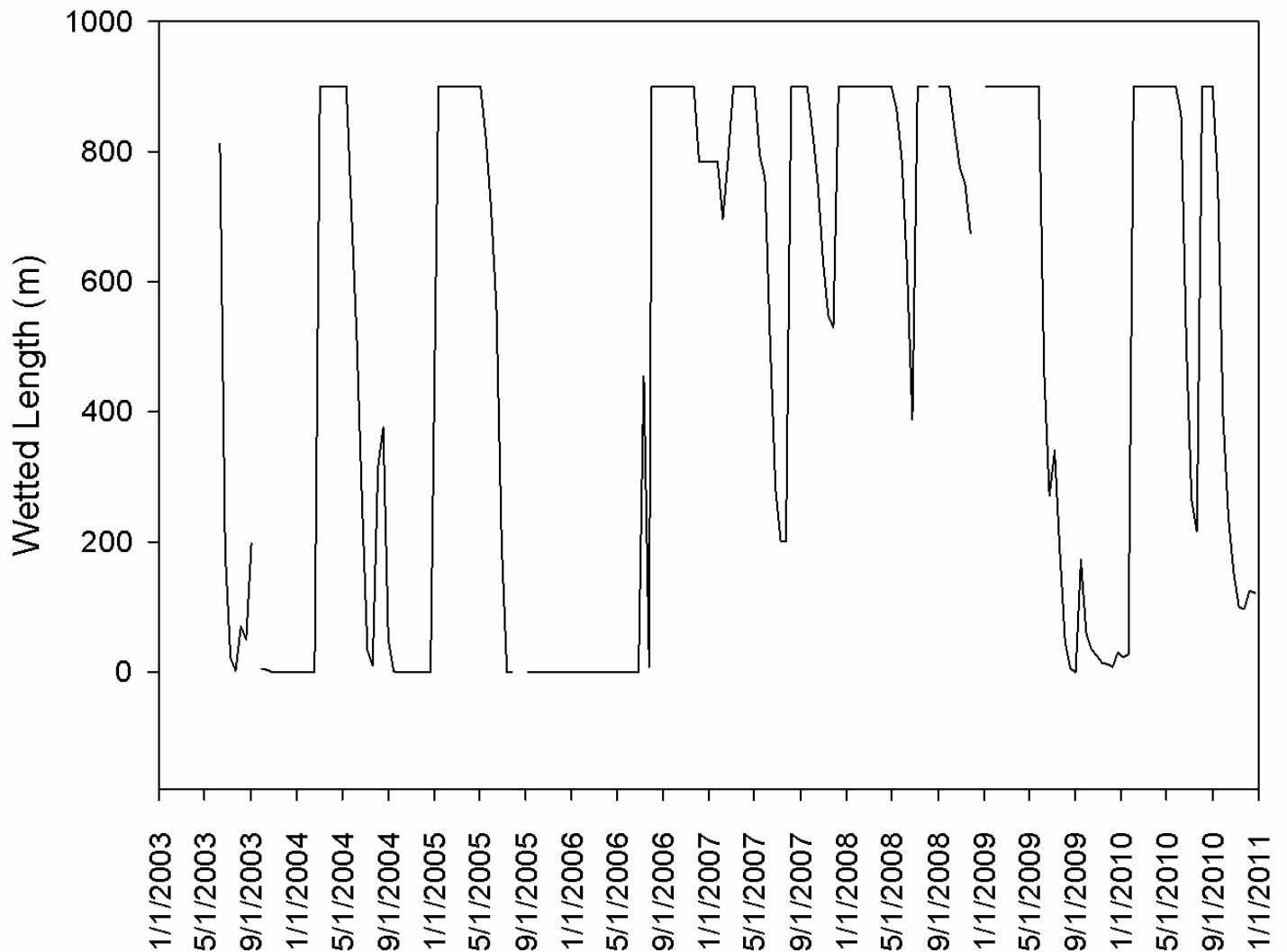


Figure 2. Average water elevation from three ground water monitoring wells within our study site at Rincon Creek, Saguaro National Park, Arizona. The horizontal line represents the average elevation of the stream channel near the three wells (3155 ft.). Winter/Spring drought in 2006 is noticeable by reduction in the elevation of ground water. Courtesy of Saguaro National Park, Arizona.

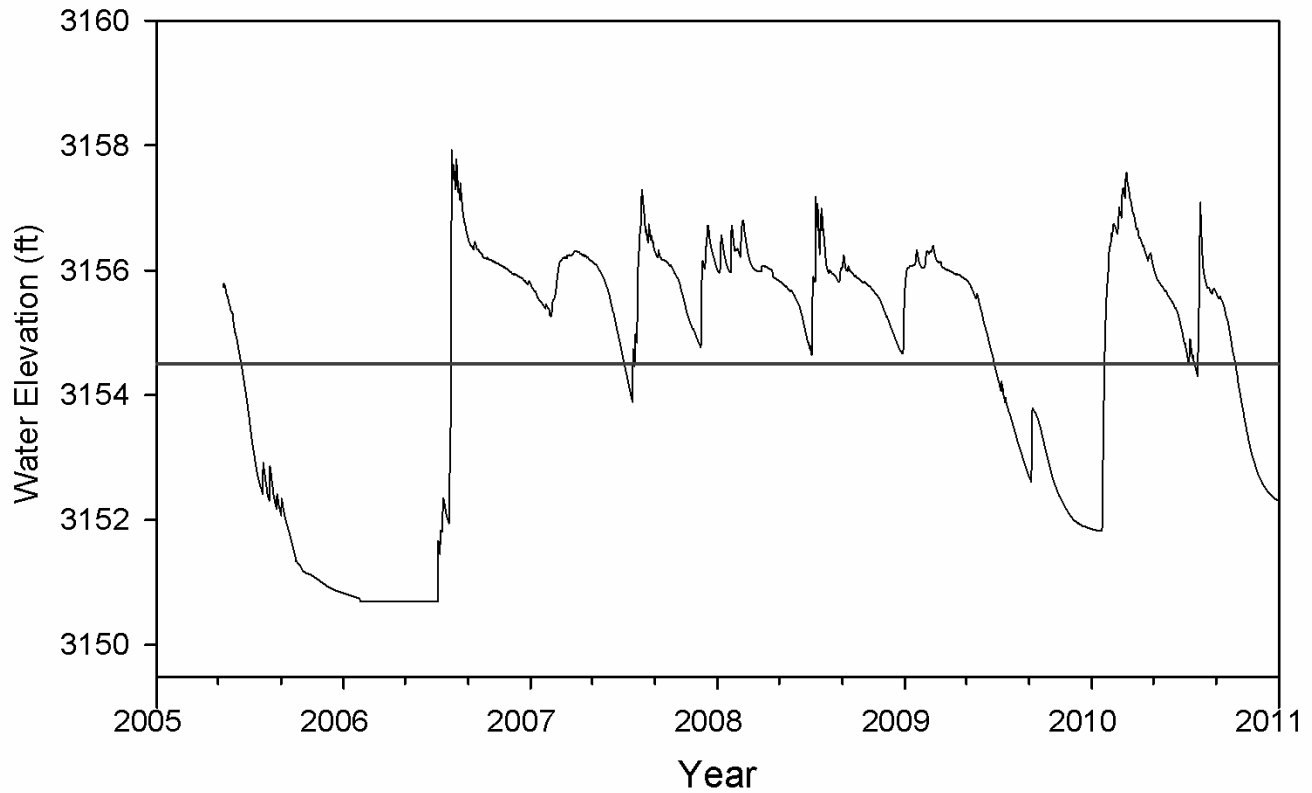
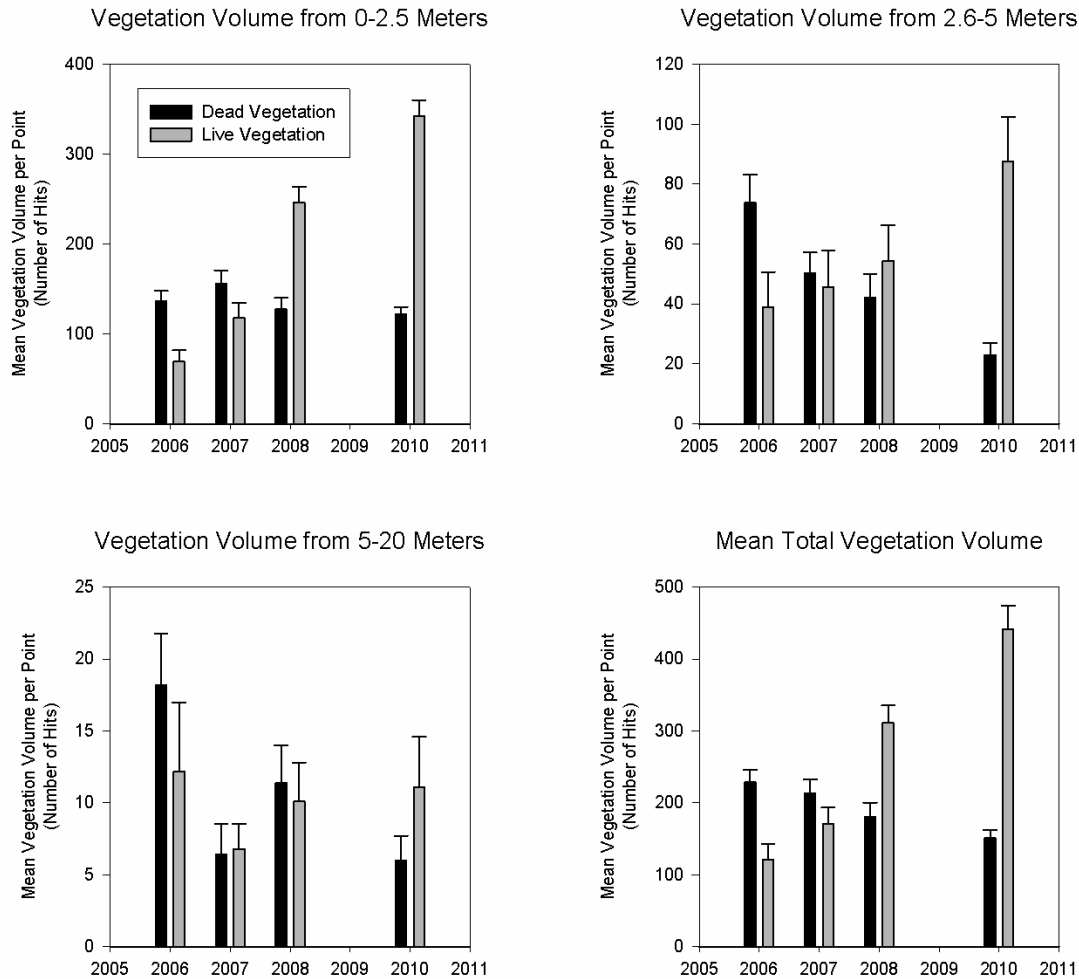


Figure 3. Mean live and dead vegetation volume from 2006-2010 at Rincon Creek, Saguaro National Park, Arizona. We used number of hits of vegetation on point-line-intercept surveys to approximate vegetation volume (see methods). Error bars represent 1 SE. Note the low proportion of live vegetation during Summer 2006 and the shift toward more live vegetation over the subsequent 4 years.



Online Resource 3. Data prior to 2006 is from Powell (2004). Data from 2006 through 2010 were collected in the current study. Both sets of survey points cover approximately the same stretch of Rincon Creek but Powell collected data at fewer points (5). We limited bird observations from both studies to those within 50 m of each point and excluded birds flying overhead during surveys. Similar reductions in Winter/Spring precipitation occurred in 2001, 2002, and 2006 (Online Resource 1). Error bars represent $\pm$ SE.

