Reframing the Grazing Debate: Evaluating Ecological Sustainability and Bioregional Food Production

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Abstract. The semi-arid grasslands of the Colorado Plateau are productive, diverse, and extensive ecosystems. The majority of these ecosystems have been altered by human land use, primarily through the grazing of domestic livestock, yielding a plethora of environmental and social consequences that are tightly interconnected. From an agroecological perspective, untangling these issues requires both an understanding of the role of livestock grazing in bioregional food production and the effect of that grazing on ecological sustainability. To address the former, we discuss the importance of cattle ranching as a bioregional food source, including estimates of meat production and water use in Arizona. To address the latter, we present data from a long-term project addressing changes in native plant community composition, under a range of alternative livestock management strategies. Our study site near Flagstaff, AZ includes four different management treatments: (1) conventional low-intensity, long-duration grazing rotations; (2) high-intensity, short-duration rotations; (3) very high-impact, very short-duration grazing (to simulate herd impact); and, (4) livestock exclosure. Preliminary results suggest belowground properties are responding more quickly to grazing treatments than aboveground properties. Particular

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response variables, such as cyanobacteria and diatoms, show a marked short-term response to very high-impact, short-duration grazing, but long-term implications are as yet unknown.

Key words: ecological sustainability, bioregional food production, livestock grazing, biological diversity, participatory research.

INTRODUCTION

Two years ago, we addressed the 4th Biennial Conference of Research on the Colorado Plateau on the issue of the ecological sustainability of cattle grazing on arid rangelands (Sisk et al. 1999). At that time, our focus was on the role of science in helping to resolve the contentious and often bitter social battle over grazing policy and practices, and the opportunities presented by public participation in the scientific process (Sclove 1998). We demonstrated that the current level of understanding of grazing impacts in the Southwest often lacked a rigorous scientific foundation, and we suggested an approach for designing research efforts to address scientific issues underlying environmental conflict. The centerpiece of our efforts has been an experiment designed to test a set of hypotheses derived from differing claims voiced by ranchers, resource managers, and environmentalists about the ecological impacts of livestock grazing on the Colorado Plateau. Here we provide an update, expanding on the scientific and policy themes that are so closely interwoven in the grazing debate.

Currently, consensus on the issue of livestock grazing in the Southwest does not appear to be on the near horizon of the socio-political landscape. This impression is particularly apparent in the mainstream media that tend to emphasize the contentiousness of environmental issues (e.g., Rotstein 1999). However, deeper investigation into the ecological literature provides some evidence of a broad agreement on livestock impacts. For example, Belsky et al. (1999) summarized roughly 100 papers from the scientific literature that measured the effects of cattle grazing on riparian zones in the western U.S. Their review found considerable evidence that cattle grazing often has negative effects on stream channel morphology, soils, vegetation, and wildlife. This review and others (e.g., Platts 1991, Kauffman and Krueger 1984, Armour et al. 1994), make a compelling case that livestock grazing should be carefully controlled, if not altogether eliminated, along riparian zones.

Riparian ecosystems, however, represent only a fraction of grazed lands in the Southwest, and information from this sensitive habitat-type does not necessarily pertain to other ecosystems. Upland grasslands, which constitute the majority of grazed lands, differ substantially from riparian ecosystems in structure, function, and evolutionary history, and the impacts of livestock grazing on these two ecosystems may be very different. Although we know of no rigorous scientific comparison of Southwestern riparian and upland responses to similar grazing systems, the literature suggests that the response of upland systems are more varied. Rambo and

Faeth (1999), studied semi-arid grasslands that had been excluded from grazing for over eight years, and showed that ungrazed grasslands had fewer plant species than adjacent, grazed plots. Insect species richness, however, showed no significant difference. In studies of ground-foraging birds, Bock et al. (1984) found that grazed areas and adjacent exclosures had similar abundances in years of average rainfall, but exclosures supported nearly 3 times as many birds as the grazed areas following two consecutive drought years (Bock and Bock 1999). This complexity of organismal responses to grazing, as well as an overall paucity of rigorous scientific information, has motivated our efforts to address relevant ecological questions through manipulative experiments conducted in concert with ranch management teams. We provide a brief retrospective on our involvement with two such groups that include environmental advocates and policy makers, and explain how this experience has provided a broader context for considering trade-offs associated with livestock grazing in the Southwest.

Ground Zero for Grazing Policy

For several decades, the center of conflict regarding grazing policy has focused on whether grazing degrades "the land." Fifty years of research provides clear, but equivocal evidence: it does in some places and at some times, and at other times and places it does not. In fact, there is also compelling evidence that livestock grazing can speed the recovery of certain degraded sites (van Wieren 1991), and that grazing may increase productivity in some ecosystems (McNaughton et al. 1997, Milchunas et al. 1989). Clearly, further efforts to characterize grazing as "good" or "bad" are overly simplistic and, we believe, problematic. Instead, two broad questions emerge: (1) how and where can grazing be practiced in an ecologically sustainable manner; and (2) how do we, the public, wish to manage our public grasslands in the Southwest? The answers to the former question will come from greater collaborative interaction among ranchers, research scientists, environmental groups, and the public who plan and apply on-the-ground management. We are optimistic that the collaborative groups, being founded with increasing frequency across the West, will be at the forefront of collaborative decision-making. The latter question however, is less tractable. Extreme, polarizing views are propagated daily through the media as demonstrated by the well-circulated jingle "cattle-free by '93" (now "2003") and the directly opposing political views espoused through the ranching industry. In fact, the contest has become so mythologized and self-referential that it is easy to lose sight of the real questions, such as whether regional agriculture is important to the four-corners states, what lands can be grazed sustainably and profitably, and what alternative land management should replace grazing in areas where it is unsustainable or not desired by the public.

Bioregional Perspective of Food Production

The scientific debate over livestock grazing has focused primarily on single species' responses (such as endangered species) and overall forage production. Ecosystems grazed by livestock have justifiably been compared to ungrazed areas to ascertain human impacts on natural systems. Interestingly, few comparisons are made between the biological diversity and ecosystem function of grazed ecosystems and other agroecosystems. In other words, if we assume that humans are going to impact natural ecosystems to produce food and fiber through agriculture, it seems appropriate to consider the relative ecological impacts of different agricultural practices in the arid Southwest.

Inherent to conventional agroecosystems dedicated to annual crop production is the nearly total replacement of native plant and animal communities. They generally consist of non-native plants (both crops and weeds), and fauna (especially birds, mammals, and arthropods) that can exist in communities that experience disturbance at high frequencies and intensities through actions such as plowing soils, which often increase erosion rates and contribute to a decline in soil organic matter (Davidson and Ackerman 1993). Rarely do modern agricultural systems generate sufficient nutrients internally to balance nutrients exported in crops, thus most farms depend on large inputs of synthetic fertilizers (Doerge et al. 1991). The crop uptake of these fertilizers however is fairly inefficient, often not higher than 50%, with residue nutrients often making their way into waterways, or the atmosphere (Matson et al. 1998). Inputs of pesticides including insecticides, herbicides and fungicides are also commonplace in conventional agroecosystems. While the pesticides applied today are less persistent in the environment than those used in previous decades, they are nonetheless highly toxic and relatively indiscriminate in the species that they affect. Finally, modern agroecosystems require substantial fossil fuel subsidies in the production process. The energy used to cultivate, harvest, synthesize and apply fertilizers, and irrigate, primarily comes from fossil fuels. The energy return on each fossil-fuel calorie invested in agriculture tends to be quite low (Pimentel and Pimentel 1996).

When compared with agro-ecosystems dedicated to annual agriculture, plant species diversity in grazed, upland agroecosystems in the Southwest appear relatively intact (Hughes 1996, Rambo and Faeth 1999). The specific ecological impacts of cattle grazing are often difficult to estimate, given the lack of non-grazed ecosystems that can be used as controls. However, this is not to say that livestock grazing is innocuous, because there is strong evidence that grazing can alter community composition of particular ecosystems through mechanisms such as selective biomass removal, alteration of soil properties, fire suppression, and transport of exotic species (Fleischner 1994). Indirect consequences of livestock grazing, such as the introduction of grasses for forage, especially Lehmann lovegrass (*Eragrostis lehmanniana*) and buffelgrass (*Pennisetum ciliare*), have had profound impacts on community dynamics in the Southwest (Bock and Bock 1998, Burquez and Martinez-Yrizar 1997). Where exotics have not been intentionally introduced, however, grazed ecosystems are generally dominated by native, perennial species (Rambo and Faeth 1999).

Estimating total costs of any agriculture is challenging given the gulf that exists between actual and perceived costs of natural resources. But without accurate cost estimates, the grazing debate remains awash with ambiguous statements. In 1990, crop agriculture in Arizona used approximately 5.2 million acre feet of water (Eden and Wallace 1992). Livestock in Arizona consume approximately 15 gallons animal-unit $^{-1}$ day $^{-1}$, which translates into an estimated annual water consumption by all range-fed Arizona livestock of only 8,384 acre-feet of water (1 acre-foot water = 1233.482 m^3; Table 1). When ranchers manage their livestock using horses, livestock grazing on Western rangelands may represent the only food production system in the United States that is based largely on solar energy rather than fossil fuel inputs. In other words, the work performed and inputs used to grow crops or raise animals in most agroecosystems involves a very significant reliance on commercial energy (Pimentel and Pimentel 1996). Producing livestock on western rangelands, however, relies heavily on native rates of net primary productivity, while using wind, gravity and/or solar panels to provide water.

Tradeoffs

Livestock grazing may have lower ecosystem impacts than annual agriculture, but it is also much less productive. A critical question, therefore, is whether the production of food from rangelands balances the tradeoffs in native ecosystem diversity and productivity that may occur with livestock grazing. To begin to address this question, it is important to develop a sense of arid rangeland food productivity. Following, we estimate levels of meat produced by cattle grazing on Arizona rangelands, excluding feedlot productivity. While these estimates are crude, we believe they provide a reasonable, approximate understanding of potential protein production.

Table 1. Estimated annual meat production and livestock water consumption according to ecosystem type in Arizona.

Ecosystem	Acres AUM$^{-1,}$ [1]	Area (ha)	% cover	Ha animal unit^{-1} year^{-1}	edible beef prod.[3,4] kg year^{-1}	protein[5] kg year^{-1}	water consumed[6] m^3 year^{-1}
Chaparral	12.5	1,303,452	4	61	1,871,842	411,805	442,808
Grassland	4.1	5,793,686	24	20	25,376,344	5,582,795	6,003,092
Pinon-Juniper	12.5	5,164,781	18	61	7,416,964	1,631,732	1,754,576
Ponderosa	19.8	885,079	3	96	807,634	177,679	191,056
Desert	20.0	9,143,387	31	97	8,257,226	1,816,611	1,953,374
Total		**22,290,385**	**80**		**43,730,113**	**9,620,625**	**10,344,905**

[1] AUM = animal unit month = the area (in acres) required to feed one steer or cow/calf unit for 1 month. AUMs based on actual stocking rates for different Arizona ecosystems reported in USFW (1999)

[2] D. Brown (pers. comm.)

[3] In an animal's first year on the range, it will gain ~190 kg, and if it is left for a second year, it will gain ~330 kg in a good (wet) year and as low as 165 in a dry year. On average, therefore, an animal gains approximately 219 kg yr^{-1} (A. Kessler and D. Moroney, pers. comm.)

[4] Edible meat constitutes ~40% of the total animal weight

[5] Beef is ~22% protein (Ensminger et al. 1983) and the average yearly protein requirement for a person is ~23.7 kg

[6] One cow or steer requires 15 gallons of water per day (Naeser and St. John 1998)

Stocking rates of livestock on lands in Arizona range between 4 and 20 acres AUM^{-1} (an animal unit month is either one steer or cow-calf pair) for desert, chaparral and woodland ecosystems (USFW 1999). This range in stocking rates reflects the variation in herbaceous, aboveground net primary productivity of the different ecosystems. By making conservative assumptions about stocking rates, we estimate that the current grazing of 80% of Arizona's land surface (Mayes and Archer 1982) results in sufficient protein production to supply one million people with 40% of their annual requirements (assuming 65g protein capita^{-1} day^{-1}). Alternatively, if livestock numbers were decreased by 50% across all ecosystem types, then the 40% of Arizona land that would remain grazed could supply one million people with approximately one-fifth of their annual protein requirements. This latter level of food production is large enough that we believe the value of bioregional food production needs to be considered in the debate regarding livestock grazing in the arid Southwest. Elimination of livestock grazing in the Southwest would substantially impede any regional movement toward greater reliance on bioregional food production, and would shift agricultural activity, as well as the concomitant environmental impacts, to other regions. The potential socio-economic implications of such a proposal are beyond the scope of this paper, but undoubtedly warrant further consideration.

Reshaping the Debate

Native Habitats as the Endpoint

Although plant surveys have been a mainstay of the vast majority of grazing studies, the emphasis has often been placed on total forage, without regard for the particular species that make up the community (e.g., Holechek et al. 1999). Increasing public recognition of the value of native habitats and native species has made this an issue of contention in the current grazing debate. Dramatic declines in native habitats, such as the degradation or loss of 80% of Western riparian ecosystems (U.S. Department of Interior 1994), underscore the rapidity of change wrought by humans. Moreover, the list of nonnative plant species in Arizona has doubled in the past 50 years to roughly 330 and continues to grow (Burgess et al. 1991). Complicating this issue is the fact that the establishment of many nonnative plants in grasslands was aided in the early 1900s by government-subsidized seeding programs that intentionally (and unintentionally) included nonnative plants (Bahre 1995, Cox and Ruyle 1998). This trend in the loss of native habitats and native species is the product of multiple land-use actions, many of which are historically associated with, but not inherently necessary to livestock production (e.g., road building, erosion of streambanks, extensive fencing, chaining of trees, etc.).

Many examples of landscapes severely degraded by overgrazing exist and the mismanagement of rangeland has fueled a widespread anti-grazing sentiment. Many environmental groups have advocated the complete removal of cattle from large tracts of land, and this approach has been implemented on many National Park Service lands (Anderson 1993). The responses of arid and semi-arid grasslands to exclusion from cattle grazing have been mixed, with changing richness of native species ranging from dramatic increases (Brady et al. 1989) to slight decreases (Rambo and Faeth 1999). When interpreting vegetation responses to livestock removal, however, it is important to recognize that virtually all lands that are accessible to cattle or sheep in the Southwest have been grazed intensively at one time or another. Lands currently excluded from grazing do not necessarily represent the state of semi-arid grassland ecosystems prior to the introduction of domestic livestock (Milton et al. 1994), an ecological state that remains poorly understood and whose restoration is beyond current technical capacity. Instead, lands where grazing has been eliminated represent the likely endpoint of cattle removal from similar ecosystems that are currently being grazed. Thus, constructive approaches to resolving the present grazing debate will include the assessment of expected outcomes of different levels and styles of rangeland management (including livestock removal), rather than a restricted and largely theoretical choice between current conditions and those that predominated prior to the arrival of domestic grazers.

A Role for Research

Clearly, a broad range of land management options currently exists, and many are being implemented and evaluated across the Southwest. Science provides a framework for measuring and interpreting the environmental implications of each option. To assess some key elements of the ecological sustainability of grazing in semi-arid grasslands, we asked the following question: Do belowground and aboveground variables affecting grassland composition and function, respond in a predictable manner to increasing grazing intensity? For belowground properties, we measured soil compaction and specific members of the microbiotic community, whereas we measured plant cover and macro-arthropods as aboveground properties.

METHODS

Meaningful application of science to grazing issues will require comparisons of the effects of actual management practices, as well as experimental treatments designed to elucidate the relationships between grazing and ecosystem sustainability. In 1997 we initiated a study of grazing impacts in a semi-arid grassland in Arizona. Our experimental design, replicated in time and space, consists of four treatments in three blocks on the landscape (a total 12 study plots; see Sisk et al. 1999). The four treatments are as follows: (1) conventional low-density, long-duration grazing rotations (CON); (2) high-density, short-duration rotations inspired by Savory (1988) Holistic Resource Management (HRM); (3) very high-impact, short-duration grazing to simulate herd impact (VHI); and (4) livestock exclosure (EXC). Stocking rates and rotations for the first two treatments are determined by ranchers and land management agencies on adjoining pastures, while the latter two treatments are implemented on fenced 1-ha experimental plots created and managed by researchers. The timing of the graze event for each of the three cattle treatments falls within the months of May-October, but specific dates vary between years due to fluctuating environmental conditions and ranching logistics. Of the four treatments, only the VHI treatment does not represent a current grazing policy, but it does simulate herd behavior, and serves as a critical upper-end treatment to study the potential spectrum of responses. In all CON and HRM plots, we have carefully matched elevation, exposure, soil type, and vegetation type so that spatially and temporally extensive treatment effects can be complemented with the exclosure and VHI treatments implemented on 1-ha plots. For the purpose of this paper, we present data from one study site on the southern edge of the Colorado Plateau.

Site Description

Located at 2160m elevation in north-central Arizona, our primary field site is Reed Lake, characterized by Upper Great Basin grassland (Brown 1994) surrounded by Ponderosa Pine forest. Dominant perennial grasses are *Agropyron smithii* (western wheat grass) and *Elymus elymoides* (squirrel-tail grass). Soil type is fairly homogeneous among study plots and across our study site of approximately 25 ha, with a standard error of less than 10% for each soil particle size class. The top 8 cm of soil is, on average, comprised of 42% sand, 12% silt, and 44% clay (Fig. 1). Annual precipitation averages between 300 mm and 460 mm with the majority generally falling as monsoonal rains between June and September (Brown 1994).

Response Variables

Soil Compaction

As the intensity of cattle grazing increases, the amount of trampling increases. We measured soil compaction in the top 5 cm of the soil surface with a pocket soil penetrometer (Ben Meadows Company, Atlanta, GA 30341). In October of 1999,

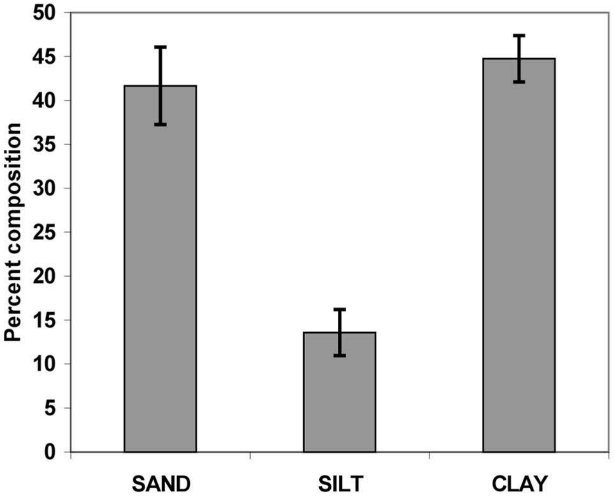

Figure 1. Soil composition for 12, 1-ha plots at the Reed Lake study site. Consistency in proportional representation of particle size classes suggests that results from the grazing experiment are not confounded by differences in soil type.

each plot was measured in three locations that were haphazardly selected (except for one of three plots in the conventional treatment that was missed due to a rainstorm). Within each of these locations the average of three readings was used as a final soil compaction measurement. This sampling event followed the conclusion of grazing for 1999, and was chosen to represent the cumulative compaction for that year. Data were analyzed with ANOVA.

Soil Microbiotic Community

Alterations of soil quality can have effects on cyanobacteria populations and, consequently, on their role as nitrogen fixers (Evans and Belnap 1999). In 1999, we employed a slide-incubation technique to assess cyanobacteria and diatoms (Rossi and Riccardo 1927, Rossi et al. 1935). Prior to the 1999 grazing season, five microscope slides were placed in each corner of EXC and VHI plots, which minimized potential disruption due to researchers in the plot. Slides remained in the ground for 26 days to incubate microbes and were subsequently transported to the laboratory. Cyanobacteria filaments and diatoms were then counted at 20X magnification with a phase contrast microscope. Data were analyzed with a nested ANOVA.

Plant Cover

Beginning in 1997, before the EXC and VHI treatments were initiated, we conducted annual ground cover (both basal and foliar cover) surveys using the modified-Whittaker plot design (Stohlgren et al. 1995). A modified-Whittaker plot was placed within each of the 12 plots and permanently marked, so that the researchers can return annually to conduct surveys. Data were analyzed for 1997-99 with a repeated measures ANOVA.

Arthropods

In 1998 we conducted sweep-net surveys of plots in the EXC and VHI treatments before and after the VHI grazing event. Total abundance of these vegetation-dwelling arthropods was calculated for each plot. Data were analyzed with a repeated measures ANOVA.

RESULTS

Soil Compaction

In comparison with the EXC and CON treatments, the HRM and VHI treatments showed greater soil compaction (df=3, F=15.308, P=0.006; Fig. 2). These increases are likely to have effects on other soil properties, including bulk density and infiltration rates, but the extent of these effects will depend on the persistence of these differences, which can only be determined through longer-term study.

Soil Microbiotic Community

Our VHI treatment had roughly 50% less colonization by cyanobacteria and diatoms, in comparison with the EXC plots (df=1, F=8.98, P=0.0047; Fig. 3). Because these organisms alter soil structure and fix nitrogen, these declines in abundance may portend further ecological consequences.

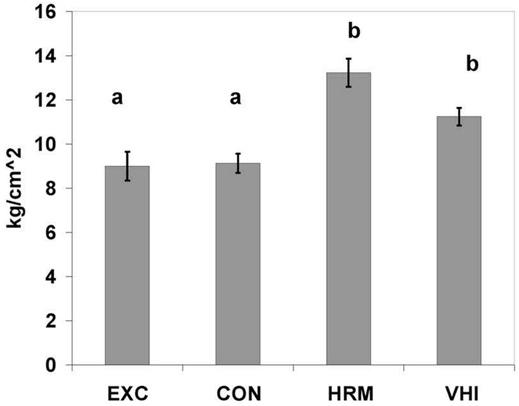

Figure 2. Soil compaction under four grazing treatments, following three years of treatment. EXC = livestock exclosure; CON = conventional, low-density, long-duration grazing; HRM = high-intensity, short-duration grazing; VHI = very high-intensity, short-duration grazing to simulate herd impact. Different letters denote significant differences in the degree of soil compaction (df=3, F=15.308, P=0.006).

Plant Cover

We found plant cover to be fairly similar among treatments, ranging from 78% to 88% (Fig. 4). Year-to-year variation in total plant cover was not significant, whereas treatment type was a significant factor (df=3, F=9.87, P<0.0001). At a finer scale of inspection, total plant cover measurements showed the HRM treatment to be consistently lower than the EXC and CON treatments by about 7-9%. Furthermore, the

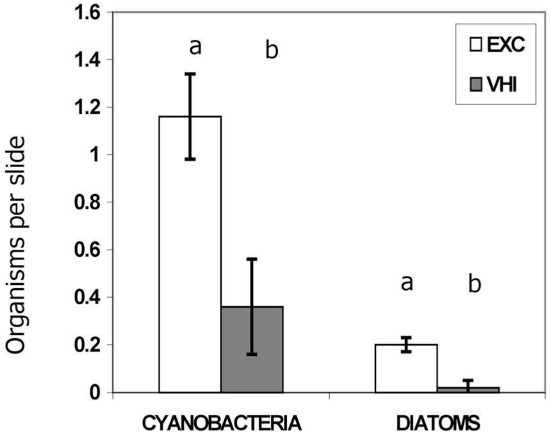

Figure 3. Abundance of cyanobacteria and diatoms in exclosures (EXC) and very high-intensity (VHI) plots following two years of treatment. Different letters denote significant differences in abundances (df=1, F=8.98, P=0.0047).

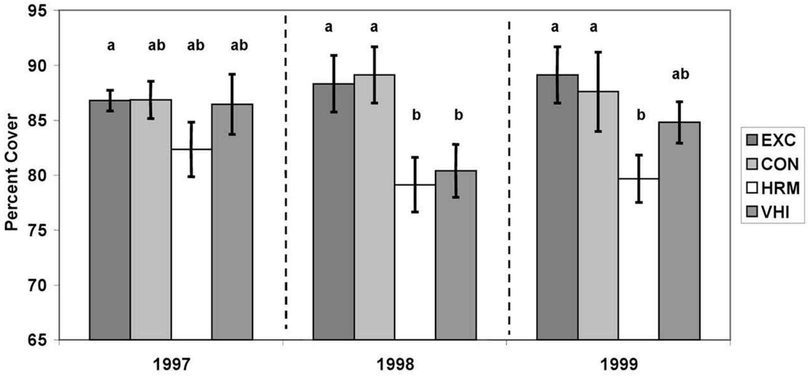

Figure 4. Percent plant cover for four grazing treatments (see Fig. 2 and text for treatment descriptions). EXC and VHI treatments were initiated following data collection in 1997, while CON and HRM treatments were put in place more than 12 years prior to initiation of this study. Between-year differences were not significant for any treatment; significant within-year differences among treatments are denoted by different letters (df=3, F=9.87, P<0.0001).

VHI treatment exhibited an 8% decline in plant cover after one year of treatment, but this difference did not persist into 1999. In general, short-term effects of treatments were measured, but their long-term implications remain unclear. Finer resolution measures, such as comparisons of community composition, are addressed in a separate paper (Loeser et al. in prep.).

Arthropods

Pre-graze and post-graze sampling of EXC and VHI plots showed a decline of greater than 50% in arthropod abundance following the VHI grazing event in 1998 (df=1, F=5.95, P=0.07; Fig. 5). In contrast to this short-term response, the pre-graze abundance, which is a measure of response since the 1997 grazing event, did not differ between treatments, suggesting that long-term effects may be negligible.

DISCUSSION

Although we are in the early stages of a long-term study, we have detected short-term differences among four treatments reflecting a gradient of grazing intensity. In general, it appears that soil properties and belowground processes are more sensitive, over the short-term, to differences in grazing treatments than are aboveground properties. This supports similar conclusions drawn by Anderson (1995) who argued that belowground organisms may be keenly susceptible to land-use change. Measurements of short-term changes in above- and belowground communities due to grazing were not unexpected, however, the more ecologically and policy relevant questions involve long-term shifts in biological diversity and ecosystem productivity.

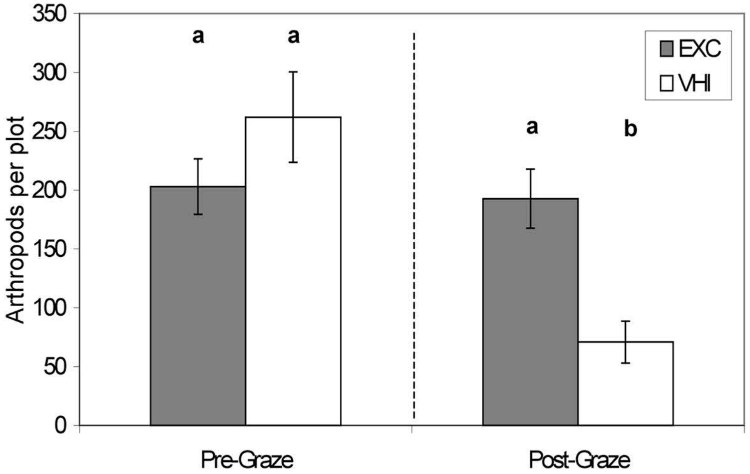

Figure 5. Arthropod abundance in exclosures (EXC) and very high-intensity (VHI) plots, before and after the 1998 grazing event, as determined by sweep net samples. Different letters denote a significant difference (df=1, F=5.95, P=0.07).

While these questions will only be answered with longer-term datasets, the short-term changes we have detected indicate that the experimental treatments have had significant, measurable effects that capture relevant impacts along a gradient of grazing intensities.

Belowground Properties

If the fundamental structure of the soil is being altered by the more intensive grazing treatments, as suggested by an increase in compaction in HRM and VHI plots, we would expect belowground soil organisms to respond. Furthermore, soil structural changes will likely affect other abiotic parameters, such as water penetration and retention. Preliminary results from our soil moisture measurements suggest that more heavily compacted sites have 1-5% less soil moisture (Loeser et al. unpub.). These alterations in soil abiotic parameters likely explain the nearly two-fold decrease in cyanobacteria and diatoms in the VHI compared to EXC treatments. Soil microorganisms in particular have limited mobility and are known to be sensitive to compaction (Whitford et al. 1995). Preliminary results from other ongoing studies at this site suggest that soil microarthropod abundance is roughly 40% lower in VHI plots than EXC plots (Loeser et al. unpub.).

Aboveground Properties

While belowground properties appear to be responding quickly to treatment effects, aboveground organisms, including plants and arthropods, have not yet demonstrated clear trends. Plots of the HRM treatment consistently showed lower ground cover than EXC plots, but because this was evident at the time that experiment began, it cannot be ascribed to the treatment itself. A treatment effect did occur in VHI plots after only one year, resulting in a loss of 10% of the live plant cover, but this difference did not persist into subsequent years. When we tested the possible relationship between arthropod samples and plant data, we did not find significant correlations ($R^2=0.01$, $P=0.12$). Arthropod samples collected shortly after the VHI grazing event showed a significant decline in total arthropod abundance, but samples from 1999, collected prior to grazing, did not differ significantly among treatments. While this suggests rapid recovery of the arthropod fauna, future collections over larger areas will be needed to determine long-term trends. Although our initial results are not conclusive, they indicate that alternative grazing treatments, such as the EXC and VHI treatments, have mixed effects on plants and arthropod communities.

Although aboveground measurements, such as plant cover and species richness, tend to dominate the grazing literature, we have demonstrated that measurements at multiple trophic levels offer additional information and provide a tractable approach for investigating grazing impacts on underlying ecosystem processes. A traditional animal- or forage-based approach would likely conclude that these treatment effects do not differ significantly, but clearly the impacts are more complicated, particularly within the soil. While additional data over an extended time period will be required to untangle grazing impacts and their ecological consequences, significant short-term differences in particular response variables between the two most extreme treatments indicate the methods that we employed to measure changes in this system are robust, and that long-term research efforts are justified.

Assessing the multi-faceted environmental implications of livestock grazing in the Southwest requires objective quantification of grazing impacts. We believe that an assessment of the environmental impacts of grazing should also examine grazing policy in the context of the increasing need for ecologically sustainable agriculture. Our research demonstrates short-term negative effects of very high grazing events on soil fauna and arthropods, but has not yet demonstrated long-term patterns in aboveground properties. As one of the very few bioregionally significant food production systems on the southern Colorado Plateau, grazing provides a significant source of edible protein that utilizes grassland communities comprised largely of native species. Efforts to generate more detailed and credible information on cattle and grassland community production levels might serve as common ground for opposing parties to discuss real-world compromises and the inclusive environmental impacts of livestock grazing versus increasing reliance on food, water, and energy imports to support the region's growing human population. We strongly believe that future research should move beyond the simplistic approach of grazed-versus-ungrazed comparisons to address a wider range of grazing practices, in order to more effectively determine whether an ecologically sustainable and socially acceptable level of grazing may exist for the publicly owned semi-arid grasslands of the Colorado Plateau.

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LITERATURE CITED

Anderson, B. 1993. Grazing management plan: Wupatki National Monument and Flagstaff areas, Arizona. National Park Service, Washington, D.C.

Anderson, J. M. 1995. The soil system. Pages 406-411 *in* H. A. Mooney, J. Lubchenco, R. Dirzo, and O. E. Sala, (eds.) Global Biodiversity Assessment. Cambridge University Press, Cambridge, MA.

Armour, C., D. Duff, and W. Elmore. 1994. The effects of livestock grazing on Western riparian and stream ecosystems. Fisheries 19: 9-12.

Bahre, C. J. 1995. Human impacts on the grasslands of southeastern Arizona. Pages 230-264 *in* M. P. McClaran and T. R. VanDevender, (eds.) The desert grassland. The University of Arizona Press, Tucson, AZ.

Belsky, A. J., A. Matzke, and S. Uselman. 1999. Survey of livestock influences on stream and riparian ecosystems in the western United States. Journal of Soil and Water Conservation 54: 419-431.

Bock, C. E., and J. H. Bock. 1998. Factors controlling the structure and function of desert grasslands: a case study from southeastern Arizona. Pages 33-43 *in* B. Tellman, D.M. Finch, C. Edminster, and R. Hamre, (eds.) Proceedings— Future of arid grasslands: identifying issues, seeking solutions, Tucson, AZ; October 9-13, 1996. U.S. Department of Agriculture, Forest Service Proceedings RMRS-P-3. Rocky Mountain Research Station, Fort Collins, CO.

Bock, C. E., and J. H. Bock. 1999. Response of winter birds to drought and short-duration grazing in southeastern Arizona. Conservation Biology 13: 1117-1123.

Bock, C. E., J. H. Bock, W. R. Kenney, and V. M. Hawthorne. 1984. Responses of birds, rodents and vegetation to livestock exclosure in a semidesert grassland. Journal of Range Management 37: 239-244.

Brady, W. W., M. R. Stromberg, E. F. Aldon, C. D. Bonham, and S. H. Henry. 1989. Response of a semidesert grassland to 16 years of rest from grazing. Journal of Range Management 42: 284-288.

Brown, D. E. 1994. Biotic Communities: Southwestern United States and Northwestern Mexico. University of Utah Press, Salt Lake City, UT.

Burgess, T. L., J. E. Bowers, and R. M. Turner. 1991. Exotic plants at the Desert Laboratory, Tucson, Arizona. Madrono 38: 96-114.

Burquez, A., and A. Martinez-Yrizar. 1997. Conservation and landscape transformation in Sonora, Mexico. Journal of the Southwest 39: 371-398.

Cox, J. R., and G. B. Ruyle. 1998. The influence of climate, soil, and grazing on the distribution of Lehmann Lovegrass. Pages 150-155 *in* B. Tellman, D.M. Finch, C. Edminster, and R. Hamre, (eds.) Proceedings— Future of arid grasslands: identifying issues, seeking solutions, Tucson, AZ; October 9-13, 1996. U.S. Department of Agriculture, Forest Service Proceedings RMRS-P-3. Rocky Mountain Research Station, Fort Collins, CO.

Davidson, E. A., and I. L. Ackerman. 1993. Changes in soil carbon inventories following cultivation of previously untilled soils. Biogeochemistry 20: 161-193.

Doerge, T. A., R. L. Roth, and B. R. Gardner. 1991. Nitrogen Fertilizer Management in Arizona. College of Agriculture, University of Arizona, Tucson, AZ.

Eden, S., and M. G. Wallace. 1992. Arizona Water: Information and Issues. University of Arizona, Tucson, AZ.

Ensminger, M. E., A. H. Ensminger, J. E. Konlande, and J. R. K. Robson. 1983. Foods and Nutrition Encyclopedia. Pegus Press, Clovis, CA.

Evans, R. D., and J. Belnap. 1999. Long-term consequences of disturbance on the nitrogen dynamics in a arid ecosystem. Ecology 80: 150-160.

Fleischner, T. L. 1994. Ecological costs of livestock grazing in western North America. Conservation Biology 8: 629-644.

Holechek, J. L., H. Gomez, F. Molinar, and D. Galt. 1999. Grazing studies: what we've learned. Rangelands 21: 12-16.

Hughes, L. E. 1996. What's in an exclosure? Rangelands 18: 201-203.

Kauffman, J. B., and W. C. Krueger. 1984. Livestock impacts on riparian ecosystems and streamside management implications...a review. Journal of Range Management 37: 430-437.

Matson, P. A., R. L. Naylor, and I. Ortiz-Monasterio. 1998. Integration of environmental, agronomic, and economic aspects of fertilizer management. Science 280: 112-115.

Mayes, H. M., and T. F. Archer. 1982. Arizona Cattle Ranches on Public Land. College of Agriculture, University of Arizona, Tucson, AZ.

McNaughton, S. J., F. F. Banyikwa, and M. M. McNaughton. 1997. Promotion of the cycling of diet-enhancing nutrients by African grazers. Science 278: 1798-1800.

Milchunas, D. G., W. K. Lauenroth, P. L. Chapman, and M. K. Kazempour. 1989. Plant communities in relation to grazing, topography, and precipitation in a semiarid grassland. Vegetatio 80: 11-23.

Milton, S. J., W. Richard, J. Dean, M. A. du Plessis, and W. R. Siegfried. 1994. A conceptual model of arid rangeland degradation. BioScience 44: 70-76.

Naeser, R., and A. St. John. 1998. Water use and the future of the Sonoita Valley. Pages 186-200 *in* B. Tellman, D.M. Finch, C. Edminster, and R. Hamre, (eds.) Proceedings- Future of arid grasslands: identifying issues, seeking solutions, Tucson, AZ; October 9-13, 1996. U.S. Department of Agriculture, Forest Service Proceedings RMRS-P-3. Rocky Mountain Research Station, Fort Collins, CO.

Pimentel, D., and M. Pimentel. 1996. Food, Energy, and Society. University Press of Colorado, Boulder, CO.

Platts, W. S. 1991. Livestock grazing. American Fisheries Society Special Publication 19: 389-423.

Rambo, J. L., and S. H. Faeth. 1999. Effect of vertebrate grazing on plant and insect community structure. Conservation Biology 13: 1047-1054.

Rossi, G., and S. Riccardo. 1927. The direct microscopical and bacteriological examination of agricultural soil. International Congress of Soil Science Proceedings and Papers 3: 9-13.

Rossi, G., S. Riccardo, G. Gesue, M. Stanganelli, and T. K. Wang. 1935. Direct microscopic and bacteriological examination of the soil. Soil Science 41: 53-66.

Rotstein, A. H. 1999. Cattle ranchers face uncertain future prices, politics imperil Arizona herds. Pages B5. Arizona Republic, Phoenix, AZ.

Savory, A. 1988. Holistic Resource Management. Island Press, Washington, D.C.

Sclove, R. E. 1998. Better approaches to science policy. Science 279: 1283.

Sisk, T. D., T. E. Crews, R. T. Eisfeldt, M. King, and E. Stanley. 1999. Assessing impacts of alternative livestock management practices: raging debates and a role for science. Pages 89-103 *in* C. van Riper, III and M. A. Stuart, (eds.) Proceedings—Fourth Biennial Conference of Research on the Colorado Plateau, Flagstaff, AZ; U.S. Geological Survey, FRESC Report Series. U.S. Geological Survey, Flagstaff, AZ.

Stohlgren, T. J., M. B. Falkner, and L. D. Schell. 1995. A modified-Whittaker nested vegetation sampling method. Vegetatio 117: 113-121.

U.S. Department of the Interior. 1994. Western Riparian Wetlands (Chapter 12). The Impact of Federal Programs on Wetlands - A Report to Congress by the Secretary of the Interior. U.S. Fish and Wildlife Service, Washington, D.C.

U.S. Fish and Wildlife. 1999. Biological opinion for Southwest region, U.S. Forest Service: Ongoing livestock grazing activities on allotments. U.S. Fish and Wildlife, Region 2, Albuquerque, NM.

van Wieren, S. E. 1991. The management of populations of large mammals. Pages 103-127 *in* I. F. Spellerberg, F. B. Goldsmith, and M. G. Morris, (eds.) The scientific mangement of temperate communities for conservation. Blackwell Scientific Publications, Oxford, England.

Whitford, W. G., G. S. Forbes, and G. I. Kerley. 1995. Diversity, spatial variability, and functional roles of invertebrates in desert grassland ecosystems. Pages 152-195 *in* M. P. McClaran and T. R. Van Devender, (eds.) The desert grassland. The University of Arizona Press, Tucson, AZ.

Computer Simulation for Rafting Traffic on the Colorado River

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Abstract. A computer program called the Grand Canyon River Trip Simulator (GCRTSim) has been developed for use by managers at the Grand Canyon National Park. GCRTSim consists of a database, simulator, and extensive analysis tools. The database will eventually contain approximately 500 trip diaries, collected in 1998 and 1999, that report stops for activities and camping along 226 miles of the Colorado River corridor within the park. The simulator provides park managers with the opportunity to set prospective launch schedules for rafting trips and simulate rafting seasons using these launch calendars. Both the trip diary database and the results of the simulations can be analyzed using graphing tools. The analysis can provide insight into use levels that could impact both the recreational experiences and resources along the Colorado River corridor.

Key words: Colorado River, Grand Canyon National Park, rafting, simulation, management, launch schedule, model.

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INTRODUCTION

The 1989 Colorado River Management Plan (National Park Service 1989) governs the recreational rafting traffic on the Colorado River within Grand Canyon National Park. This document provides guidance for park managers in charge of supervising and governing both commercial and noncommercial river rafting use. To help supplement the ability of managers to understand the complex human-environment interactions in this setting, a team of faculty and students from the University of Arizona's School of Renewable Natural Resources, and from Northern Arizona University's Department of Mathematics and Statistics (senior author's previous affiliation), have worked since April 1998 to develop the Grand Canyon River Trip Simulator Project (GCRTSim) (Bieri 2001, Cherry 1997, Gimblett et al. 2000).

The goal of GCRTSim is two fold: (1) to improve understanding of the current rafting traffic conditions, and (2) to predict possible outcomes of changes to the current set of rafting traffic regulations. To accomplish the first objective, we collected trip diaries from rafting parties, and used these data to inform the National Park Service (NPS) about the use frequency of various camping and attraction sites. The data from these trip reports, coupled with extensive expert interviews, were used to develop an artificial-intelligence and statistical-based computer simulation model of rafting traffic along the Colorado River (Brian and Thomas 1985, Jalbert 1990, 1991, O'Brien and Roberts 2000, Roberts 1998, Shelby and Nielsen 1976a, 1976b, 1976c, 1976d). The simulator can approximate the behavior of rafting trips under a wide range of natural or imposed conditions. Thus, GCRTSim can consider how a proposed set of new regulations would influence an imaginary launch schedule, and simulate river trips over multiple seasons. The resultant data can subsequently be analyzed to provide insight into the potential consequences proposed set of new regulations. The intent is to provide NPS managers with more information about existing conditions on the Colorado River, and enable them to gain insight into the potential consequences of any new proposed management actions.

Computers have provided a venue for investigating human recreational use since the mid-1970's (Bishop and Gimblett 1999, Borkan and Underhill 1989, Schechter 1975, Schechter and Lucus 1978, Underhill et al. 1986, Van Wagendonk 1979). With recent advances in computing, and the development of artificial intelligence algorithms, the potential to make real progress in this area has grown immensely. While a natural "next step" in the management of natural resources is to take advantage of the potential offered by these recent advances, to date little has been done in this arena. Some recent work has developed a related intelligent-agent based program to study the interactions between jeep tours, bicyclists and hikers in a recreational setting in Sedona, Arizona (Gimblett et al. 1996). Our efforts have been to design a computer simulation model that examines the complex interactions between humans and the natural environment. Each rafting trip is designed as an intelligent agent, imbued with the intelligence to respond dynamically to its environment and to modify its plans accordingly. This represents a new approach for managers in the National Park system, in that we are able to combine statistical analysis, artificial intelligence and tools from mathematical modeling in a cutting edge fashion.

METHODS

Data Collection Methodology

To develop a detailed picture of river use, we needed to gain an understanding of: (1) the popularity of various camping and attraction sites along the Colorado River corridor; and, (2) how various trip leaders make decisions about where to stop, when to stop, and how long to remain at a given location. To obtain this information, trip leaders were asked to complete trip itineraries during the 1998 and 1999 rafting seasons. These itineraries listed the time in and time out for each location (250 sites between the launch area at Lee's Ferry and the end of the Park's tracking of river use at Diamond Creek). The trip diaries represent trips of all lengths and propulsion types (i.e., motorized or non-motorized).

The authors worked with various constituent groups to help gain support for this data collection effort. To reach private boaters, presentations were given at the annual meetings the Grand Canyon Private Boater Association, and email notification was sent to their members, encouraging participation in our study. In addition, the permit office at the Grand Canyon National Park sent information directly to permit holders. At orientation on the day of launch, the ranger at Lee's Ferry provided our survey materials to the permit holders.

To reach the commercial trips, presentations were given at Grand Canyon River Outfitters Association meetings. The outfitters made individual decisions as to how to implement their support of this project. Some, for example, required their guides to complete trip reports. Others distributed the trip reports to their guides with a request to participate. The authors also met with the Grand Canyon River Outfitters Association to solicit support of the river guide community (a summary of the meeting dates and locations can be found at http://mathcs.holycross.edu/~croberts/research). Although completing the trip diaries was optional, we recognize that the data collected are, nonetheless, far more comprehensive than anything previously available. A statistical analysis is currently underway to more precisely determine the extent to which this database is representative and reasonable.

During 1998, more than 15 river guides were interviewed to learn as much as possible about the logic employed by a river guide when taking a trip down the Colorado River. These guides, recommended by the Grand Canyon River Outfitters Association, the Private Boaters Association and the Grand Canyon River Guides Association, collectively represented many years of experience running the Colorado River, either privately (i.e., non-commercially) or as guides for commercial outfitters. They had experience at various river flow regimes and with all types of watercraft (e.g, oars, paddle boats, dories, motor boats). Questions were open-ended and extensive. For example, to understand how a guide might choose a campsite, we asked questions such as, "When do you start thinking about camping for the evening?", "What campsites do you like and why?", "Which ones do you try to avoid and why?", and "List every factor that goes into the selection process of choosing a campsite, and explain why each factor is important." The result was a complex matrix of possibilities for campsite selection based on several scenarios or situations that might be faced by a river guide. The scenarios could either be the result of human interactions and decisions, or could be the result of responding to the natural environment. For example, a trip might avoid a campsite because a conversation earlier in the day revealed that another trip was planning to select that site (result of a human interaction and decision); alternatively, a trip might avoid a campsite because when they arrive, a recent rainfall has rendered the area too small for their group size (result of responding to the natural environment).

Simulation Engine Development

The simulation engine represents a hybrid program that uses statistical data from the trip diary database, along with artificial-intelligence algorithms developed from the expert interview process. As development of the simulation engine proceeded, additional analysis of the database, or additional querying of expert guides, has been utilized as needed. The simulation engine is constructed as an object-oriented system that uses elements of fuzzy logic in the decision structure (Gimblett et al. 2000, Manneville et al. 1989, Reghis and Raventa 1998, Tecuci and Dybala 1998). Fuzzy logic is an artificial-intelligence construct that permits a decision to be made by weighing several factors or variables in an appropriate manner. Fuzzy logic theory provides a robust and full range of decision-making tools that are suitable for capturing much of the nuances inherent in making complex decisions in the natural environment of the Colorado River. For example, when a trip is choosing a campsite, the current conditions of the river and the individual trip play a role, as does the campsite's historical popularity. Fuzzy logic takes into account all these factors and weighs them appropriately, so that each trip's campsite decision represents a reasonable outcome for that particular set of circumstances.

A launch schedule (e.g, the current launch schedule or a prospective calendar created by the user) is entered into the simulation engine, which outputs simulated trips from Lee's Ferry. These simulated trips execute days on the river by choosing attraction sites for hikes or other activities, stopping for lunch, and selecting an appropriate campsite each night. Certain trips must be at given locations on certain times (e.g., some trips exchange passengers at Phantom Ranch), and the trips are managed by the simulator to meet these fixed points as scheduled. Moreover, a sophisticated planning algorithm helps each simulated trip plan out an optimal schedule that will include stops at key attraction sites and ensure that campsite selections are appropriate. A comprehensive record is developed for each simulated trip, including where and when it encounters other trips, where it chooses to engage in an activity or to stop for camp, and the duration of time spent engaged in each activity or camp stop.

Simulation Engine Use

After running a simulation, the created database can be queried to investigate outcomes of that particular launch schedule. For example, one could query the top 10 attraction sites, and compare the simulation output with data from the real 1998 and/or 1999 trip diaries, to observe if any major differences exist. There are a number of standard and non-standard queries possible to help the user of GCRTSim judge whether the outcome of a simulation represents an improvement over the current conditions in Grand Canyon National Park.

GCRTSim has the ability to run simulations representing new prospective launch calendars. It is also possible for the user to manipulate other conditions along the river corridor. For example, the user could restrict camping or activities at any number of sites. In this instance, a user could compare data from the 1998 trip diaries, as well as from simulations run off of the 1998 launch schedule, both with or without the added camping/activity restrictions. A judgement could then be made about the possible consequences of such a management action on the dynamics of the river rafting traffic on the Colorado River.

RESULTS

The Grand Canyon River Trip Simulator Project (GCRTSim) can create numerous types of graphs and charts from a database (real or simulated) to provide insight into Colorado River rafting traffic dynamics. To help illustrate some of the uses for GCRTSim, it is important to note that the trip report database represents a wealth of valuable information. Approximately 500 trip diaries were collected, representing about a 50% return rate for the commercial and 30% return rate for private trips. To date, only the 1998 trip reports are available for analysis. Not only is it useful to examine the "real data" from trip reports, but comparisons are also possible between these "real data" and various simulation runs. Simulations were run using a launch calendar regarded as typical by the 1989 Colorado River Management Plan. Simulations were run at both 100% and 50% use levels. Comparisons were made between the simulations and real data, and the results are presented herein. It must be noted that the 1998 trip reports represent approximately 40% of the actual launches, whereas a simulation of 100% use level represents a complete launch calendar. At the 50% use level, half of the launches were removed from the standard launch calendar, the remainder of which represents an even cut of all trip types.

The authors caution the reader that the results presented here are illustrative only. It would be unwise to draw conclusions regarding management of future launch schedules based soley on data presented in this paper. First, the 100% and 50% use levels were arbitrarily created and cannot be presumed to necessarily illustrate management decision scenarios. Second, in order to evaluate the potential impact of an alternative scenario (such as a 50% use level), it is necessary to examine multiple outputs from the simulation model – only a few such indicators are presented here. The graphs simply illustrate the types of output that are available to users of the simulation model.

A user can easily compare the popularity among key attraction and camping sites along the river corridor. In Figure 1, the most popular attraction sites are presented from each of three data sets: (1) the "real" data from the 1998 trip reports, (2) the "simulated" data from 100% use level, and (3) the "simulated" data from 50% use level. Thus, it appears that key attraction sites remain popular, regardless of the number of trips on the river (Fig. 1). Simulated trips chose the same top attraction

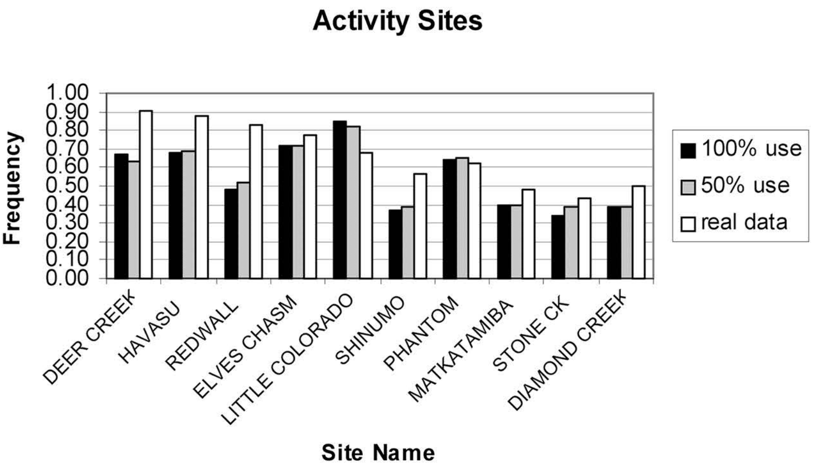

Figure 1. Comparison of recreational visitation at 10 key attraction sites along the Colorado River corridor within the Grand Canyon National Park. Real data corresponds to trip diaries collected during the 1998 river running season. The 100% and 50% results arise from simulations conducted from scenarios representing 100% use and a 50% reduction in people, boats and user days.

sites, but at a lower frequency, than that reported in the real data. Some of this error can be explained by the fact that the real data does not represent full river use. Still, efforts are underway to refine the model to better reflect current conditions on the river. Data, such as is presented in Figure 1, provides some insight into how reducing the number of launches might affect the selection of attraction sites. Again, the historical popularity of these sites keep them as key attractions, regardless of the use level, although the amount of use does change. It is interesting to note that this same dynamic does not hold for campsites. While the popularity of some campsites remain high under any use level, others fall into less use when there is less competition on the river.

Comparison between "Real" and "Simulated" Data

An important distinction between "real" and "simulated" data is illustrated in Figures 2a and b. In each case, graphs show the distribution of all trips along the river corridor on a particular day. The horizontal axis shows river mile, while the vertical axis represents the number of trips reported to be at each location on that particular day. Clearly, several trips were on the river 15 July, but we did not receive trip reports from all parties. While the complete launch schedule simulation does not match up perfectly with the trip diary data, it still provides an accurate representation for the distribution of parties along the river corridor. Note that the real data are incomplete, whereas the simulated data represent a complete scenario where every trip is repre-

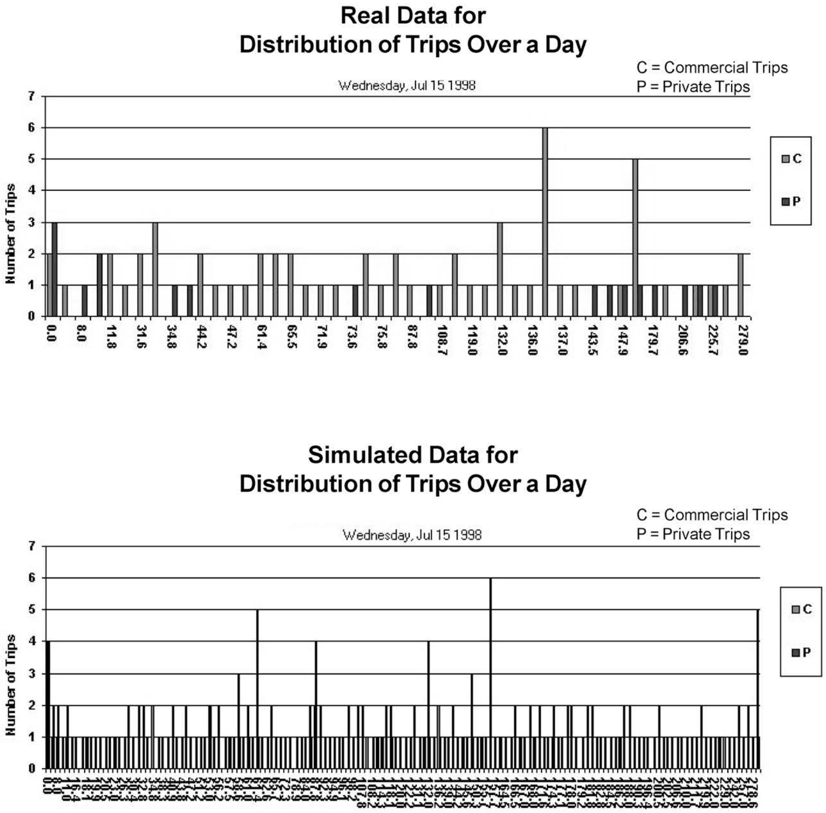

Figure 2a-b. **a**. Distribution of rafting trips along the Colorado River corridor within the Grand Canyon National Park over one day, as reported in diaries collected during the 1998 river running season ("real data"). The horizontal axis marks the river mile, and the vertical axis indicates the number of trips reported to be at that river mile on July 15, 1998. Note that not all trips on the river submitted a trip diary. **b**. Distribution of rafting trips along the Colorado River corridor within the Grand Canyon National Park over one day; results are from a simulation of a scenario that represents the typical 100% use-level ("simulated data"). The horizontal axis marks the river mile, and the vertical axis indicates the number of trips that were simulated as being at that river mile on July 15, 1998.

sented. The higher peaks represent more trips having been at those locations on that same day.

15-day Trips

All of the records for 15-day trips (using real data) were compiled to illustrate an "average" 15-day trip on the river; these data were used to generate simulated 15-day trips at both the 100% and 50% use levels (Fig. 3). The slope of the lines provides a sense of trip velocity as they travel down the river. Comparisons among the lines on this graph indicate the accuracy of our simulator. For example, the slope of the line for the real data and the 100% simulation data are closely matched. After day 10, however, the real data average trip speed is slower, and the average trip location distance is less than the simulated data. This disparity suggests that the simulation might have some error that accumulates to become obvious only after running trips of more than 10 days.

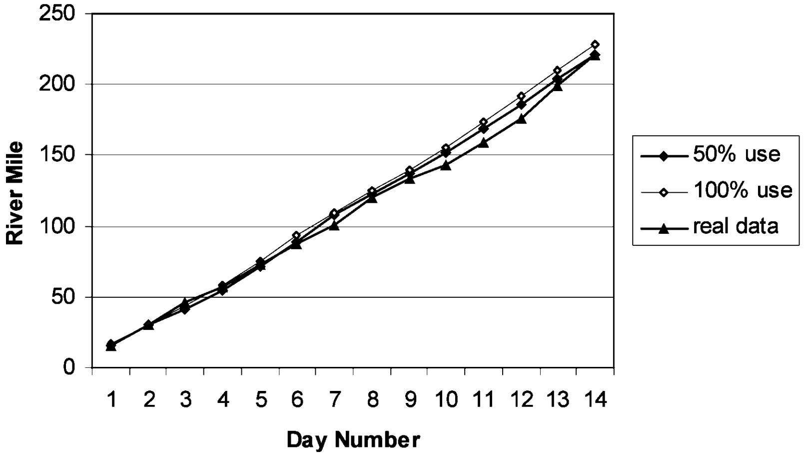

Figure 3. The average trip profile for rafting trips of 15-day duration. This graph provides a comparison between the real data and various simulated scenarios. It can be used both to calibrate the simulator in the development stage and also as a tool for interpreting outcomes of multiple scenarios.

Trips of Varying Lengths

We next provide output that takes the average of all the trips, not just those of 15-day duration (Fig. 4). Each line captures the average location of each trip on a daily basis, but also represents trips of many different lengths. The anomalous decrease after day 6 is not due to trips backtracking along the river, but rather shows the effects of shorter trip lengths that travel the entire river corridor (all 250 miles) in six or seven days. These trips, because of early completion, are then removed from the data set. A more useful query might involve separating out shorter, motorized trips for individual analysis. On day-7, only trips that are greater than or equal to seven days are shown. The simulation provides an indication that it is capturing the real data flow of rafting trips in some sort of "average" sense. The similarities between Figures 3 and 4 suggest a certain robustness in the simulator's ability to capture the basic flow of rafting traffic on the Colorado River. The simulator appears, however, to result in trip itineraries that are further down river than the real data indicates. This is another area of focus for improving the next version of our simulator.

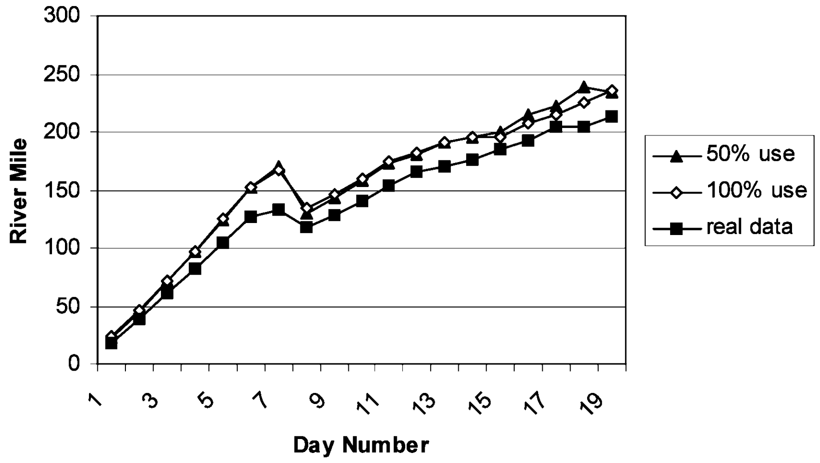

Figure 4. The average trip profile for trips of all lengths. This provides a comparison between real data and various simulated scenarios.

In addition to specific queries, GCRTSim provides a comprehensive report that can be compared to Management Objectives established in the Colorado River Management Plan (National Park Service 1989). These management objectives are the guidelines that the National Park Service employs in order to evaluate proposed launch scenarios and determine whether or not a given scenario results in acceptable river traffic conditions. For example, one management objective specifies that there should be an 80% probability that a trip will make contact with seven or fewer river parties per day, with up to 90 minutes in sight of less than 125 other people (National Park Service 1989). A simulation run based on a 100% use level, showed that this particular management objective resulted in an average probability of 54.53% that party contacts will remain within the management standards. A simulation run based on a 50% use level, resulted in an average probability of 91.09% that party contacts will remain within the management standards. Queries such as these will enable users of GCRTSim to better judge alternative management scenarios.

Discussion and Conclusions

GCRTSim, in addition to being a repository for an extensive database of trip reports completed during 1998 and 1999, is also an integrated statistical and artificial intelligence-based computer simulator that models complex, dynamic human-environment interactions in the Colorado River corridor. It will be used by managers at Grand Canyon National Park to help understand the potential impact of various alternative management scenarios for rafting trips on the Colorado River.

These results are preliminary because the 1999 trip diary data are not yet available, and additional improvements and refinements for the simulation engine are still underway. The real test will be subsequent to this, when the model is used extensively to examine potential outcomes of various alternative launch schedules. The insight that can be provided by GCRTSim is expected to be a valuable contribution to a complex situation: managing rafting traffic on the Colorado River in an optimal way for both recreators and for the natural resource itself. For up-to-date information on the status of this project, visit the websites at http://mathcs.holycross.edu/~croberts/research or http://odin.math.nau.edu/~msl.

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LITERATURE CITED

Bieri, J.A., and C.A. Roberts. 2000. Using the Grand Canyon River Trip Simulator to Test New Launch Schedules on the Colorado River. AWIS Magazine, Association for Women in Science, Washington DC. 29: 6-10.

Bishop, I.D., and H.R. Gimblett. 1999. Management of Recreational Areas: Geographic Information Systems, Autonomous Agents and Virtual Reality. Environment and Planning B. Planning and Design 2000 27: 423-435.

Borkan, R.E., and A.H. Underhill. 1989. Simulating the Effects of Glen Canyon Dam Releases on Grand Canyon River Trips. Environmental Management 13: 347-354.

Brian, N.J., and J.R. Thomas. 1984. The 1983 Colorado River Beach campsite inventory. National Park Service Division of Resource Management, Grand Canyon National Park, Grand Canyon, 56 pp.

Cherry, S. 1997. Modeling of River Trips on the Colorado River in Grand Canyon National Park. Unpublished Paper. School of Renewable Natural Resources. University of Arizona. Tucson, Arizona.

National Park Service. 1989. Colorado River Management Plan. U.S. Department of the Interior.

Gimblett, H.R., C.A. Roberts, T. Daniel, M. Mitner, S. Cherry, D. Kilbourne, M. Ratliff, D. Stallman, R. Bogle. 2000. Intelligent Agent Modeling for Simulating and Evaluating River Trip Scheduling Scenarios for the Grand Canyon National Park. Pages 245-275. *in* H.R. Gimblett H.R. (ed.) Integrating GIS and Agent based modeling techniques for Understanding Social and Ecological Processes, Oxford Press, London.

Gimblett, H.R., B. Durnota and R.M. Itami. 1996. Spatially Explicit Autonomous Agents for Modeling Recreation Use in Complex Wilderness Landscapes. Complex International Journal 3.

Jalbert, L.M. 1990. Monitoring Visitor Distribution and Use Patterns Along the Colorado River Corridor: River Contact Survey and Attraction Site Monitoring. Resource File in Grand Canyon Science Center, Grand Canyon National Park. 47pp.

Jalbert, L.M. 1991. Monitoring Visitor Distribution and Use Patterns Along the Colorado River Corridor: River Contact Survey and Attraction Site Monitoring. Resource File in Grand Canyon Science Center, Grand Canyon National Park. 32pp.

Jalbert, L.M. 1992. The Influence of Discharge on Recreational Values including Crowding and Congestions and Safety in Grand Canyon National Park. Division of Resources Management in Cooperation with Glen Canyon Environmental Studies. Grand Canyon National Park.

Jalbert. L.M. 1993. Colorado River Management; Resource Monitoring Program: Recreational Impacts to Camp and Attraction Site Quality, River Rehabilitation and Visitor Experience, Program Summary. Resource File in Grand Canyon Science Center, Grand Canyon National Park. 14pp.

Kaplinski, M., J. Hazel, M. Manone, R. Parnell and A. Dale. 1998. Colorado River sediment storage in Grand Canyon during calendar year 1997, Final Report to the U.S. Bureau of Reclamation, Grand Canyon Monitoring and Research Center, Flagstaff, AZ, 65 pp.

Kearsley, L., and R. Quartaroli. 1997. Effects of a beach/habitat building flow on campsites in Grand Canyon: Final Report of Applied Technology Associates for the Glen Canyon Environmental Studies, 18 pp.

Manneville, P., N. Boccara, G.Y. Yichniac and R. Bidaux. 1989. Cellular Automata and Modeling of Complex Physical Systems. Springer, New York.

O'Brien, G.O., J. Jansen, K.S. Thompson, A.R. Potochnik and K.J. Burke. 1997. Effects of the Effects of Continuous High Flows and Daily Fluctuating Flows from Glen Canyon Dam on Grand Canyon Beaches, 1997 and 1998: A Continuation of a Repeat Photography Study by Grand Canyon River Guides, Inc. (Adopt-a-Beach Program) Administrative report for Grand Canyon Monitoring And Research Center by the Grand Canyon River Guides Adopt-a-Beach program.

O'Brien, Gary and C.A. Roberts. 2000. Evaluation of river beach carrying capacity information utilized by the Grand Canyon River Trip Simulator: Analysis and recommendations for future study. Unpublished Paper. Northern Arizona University. Flagstaff, AZ.

Reghis, M., and E. Reventa. 1998. Classical and fuzzy concepts in mathematical logic and applications. CRC Press, Boca Raton.

Roberts, C.A, 1998. Expert Interviews with Grand Canyon River Guides. Unpublished Paper. Available at CPFS, Northern Arizona University. Flagstaff, AZ.

Schechter, M. 1975. Simulation model of wilderness area use. Resources for the Future, Washington, D.C. pp. 172.

Shelby, B., and J.M. Nielsen. 1976a. Design and Method of the Sociological Research in the Grand Canyon. Technical Report No. 1, Colorado River Research Program Report Series, U.S. Department of Interior, National Park Service.

Shelby, B., and J.M. Nielsen. 1976b. Motors and Oars in the Grand Canyon. Technical Report No. 2, Colorado River Research Program Report Series, U.S. Department of Interior, National Park Service.

Shelby, B., and J.M. Nielsen. 1976c. Use levels and Crowding in the Grand Canyon. Technical Report No. 3, Colorado River Research Program Report Series, U.S. Department of Interior, National Park Service.

Shelby, B., and J.M. Nielsen. 1976d. Private and Commercial Trips on the Grand Canyon. Technical Report No. 4, Colorado River Research Program Report Series, U.S. Department of Interior, National Park Service.

Shechter, M., and R.L. Lucus. 1978. Simulation of Recreational Use for Park and Wilderness Management. Johns Hopkins University Press for Resources for the Future, Inc., Washington, D.C. 220 pp.

Tecuci, G., and T. Dybala. 1998. Building intelligent agents: an apprenticeship multistrategy learning theory, methodology, tool and case studies. Academic Press, San Diego.

Underhill, A. H., A.B. Xaba and R.E. Borkan. 1986. The Wilderness Simulation Model Applied to Colorado River Boating in Grand Canyon National Park, USA. Environmental Management. 10: 367-374.

Van Wagendonk, J. W. 1979. Use of a wilderness simulator for management decisions. Proceedings of the 1st Conference of Scientific Research in the National Parks. Transactions and Proceedings Series 5: 1039-1040.

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The Influence of Habitat Types, Water Sources, and Movement Barriers on Pronghorn Antelope Home Ranges in Northern Arizona

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Abstract. We studied distribution and movement patterns of 17 radio-collared pronghorn antelope within the environs of Wupatki National Monument in northern Arizona. Aside from pronghorn gender differences, individual animal and herd movements were specifically influenced by fencing along main thoroughfares, historical presence of animals, forage succulence and permanently available water sources. From data analyzed and modeled with an Arc Info Geographic Information System, the extreme fragmentation that we observed in our study animals in northern Arizona leads us to believe that rights-of-way fences are a major factor affecting pronghorn movements. To facilitate movement and interchange among herds, it is imperative to reduce the effect of fenced rights-of-way so that pronghorn can freely move as perturbations occur (e.g., winter storms, droughts, fire). Another factor affecting localized movement and influencing homerange is permanently available water, particularly within Wupatki NM. Draw down of the water table by wells, along with anthropogenic manipulation of former natural watering sites, have negatively influenced locations where animals historically watered. This has resulted in no permanent water sources remaining within Wupatki NM. In fact, we found greatest movement out of the park to secure water during September, that time of year when pronghorn are most heavily harvested in northern Arizona. If wildlife managers desire to better manage and coordinate pronghorn populations over a large fragmented landscape in northern Arizona, they will have to pay closer attention to fenced transportation corridors and to the distribution of water sources.

Key words: pronghorn antelope, *Antilocapra americana*, movements, homeranges, fences, livestock grazing, GIS, highways,Wupatki National Monument.

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INTRODUCTION

Pronghorn antelope (*Antilocapra americana americana*) are widely distributed across northern Arizona and occur in isolated patches of habitat throughout the central and southern state. Historically, this species ranged over a large portion of Arizona but in the early 1900s were extirpated from many areas (Nelson 1925). Surveys found only 700 pronghorn in Arizona in 1924, but primarily due to transplants from neighboring states, this number had increased to over 10,000 by the mid 1980's. Despite increases in state-wide numbers, northern Arizona herds appear to have experienced a recent decline (Ockenfels 1994), raising concern for the long-term welfare of pronghorn in Arizona. Additional information about pronghorn home ranges, movements and habitat requirements is needed in order to better manage the present herds and to help ensure their continued survival.

Pronghorn home ranges and movement patterns have been studied in many areas of western North America (e.g., Bayless 1969, Tucker and Garner 1984). Clemente et al. (1995) found that adult pronghorn home ranges averaged 22.5 km^2 in southern New Mexico. Ockenfels et al. (1994) reported home ranges in central Arizona averaged 88 km^2 with some individual animals migrating between northern and southern areas. Based on a review of the literature, Allen et al. (1984) concluded that pronghorn movements are directly controlled by the basic habitat requirements of water and forage as affected by seasonal weather. They felt that pronghorn move large distances only if forced to do so by extreme weather or habitat conditions. O'Gara (1978) stated that "sizes of home and seasonal ranges vary so much with habitat and weather conditions that results of studies seldom have application to another area, or even another year." Thus, to better manage pronghorn in northern Arizona there is a need for research into the basic habitat requirements of these herds.

Pronghorn require a variety of habitats for their essential life activities. They use land forms typified by low, rolling expansive terrain, and although known to occur mainly in grasslands, they also use drier shrub-grass plains, steppes and deserts (Yoakum 1974). Studies of feeding habits have found that pronghorn select forbs when available, turning to browse and grass at other times of the year (Dirschl 1963, Hoover 1966, Taylor 1972, Mitchell and Smoliak 1971, Hailey 1979, Barrett 1980, Roebuck et al. 1982, Howard et al. 1982 and Koerth et al. 1984). Beale and Smith (1970) found that during summers of above average rainfall, forbs made up over 90% of the pronghorn diet. Grass is commonly utilized in early spring and occasionally at other times if new growth appears. Other summaries of dietary preference (Sundstrom et al. 1973, Autenrieth 1978, Allen et al. 1984) agree that pronghorn are opportunistic and selective, taking the most palatable and succulent forage available at each season.

In addition to necessary forage requirements, pronghorn require adequate water sources. Water distribution may restrict movements or cause animals to move into less suitable areas. Ranges that produce and maintain high pronghorn densities have water available every 1.6 km-8.0 km. In Wyoming, 95% of more than 12,000 pronghorn were within a 4.8 km - 6.4 km distance of water (Sundstrom 1968). Boyle and Alldredge (1984) found that pronghorn numbers observed within 6.4 km of water sources increased through late spring and summer to a maximum of 92% in August - just after measurements of forage moisture content were lowest. Despite the importance of water to productive antelope herds, we found only one study in Arizona that addressed permanent water sources in relation to animal distributions. Ockenfels (1994) found that the majority of pronghorn locations were within a 1.6 km radius of water; however, most of the study area was also within 1.6 km of water.

In addition to biotic factors influencing pronghorn numbers and distributions, many anthropogenic factors influence distribution and population patterns. Human encroachment, in the form of residential and commercial development, as well as road construction reduces and fragments suitable pronghorn habitat. Range management practices of livestock fencing can further fragment and isolate adjacent populations. Overgrazing and trampling from cattle reduces suitable forage and may reduce cover that would serve as pronghorn fawn shelter and seclusion from predators. In addition, overgrazing may allow more rapid tree encroachment into grassland areas, thereby reducing suitable habitat (Neff 1986, Ockenfels 1994). These various limits to pronghorn movements may result in decreased genetic interchange, ultimately leading to low genetic diversity. Populations that drop below minimum viable levels could experience lower fertility, higher fawn mortality and may be more greatly influenced by severe weather, disease or random catastrophic events.

Our study was initiated on land surrounding Wupatki National Monument, to provide much needed information on northern Arizona pronghorn antelope. Wupatki National Monument contains grassland habitats that have not been grazed for over 10 years but are immediately adjacent to currently grazed grasslands, providing a unique opportunity to study pronghorn using multiple habitat types. Monument staff have noted that pronghorn were frequently sighted within the Monument boundaries during fall and winter, but were not as often observed in the spring and summer. Since visitors have indicated that large animal sightings greatly increased their enjoyment of a trip to the Monument (Lee and Stephens, 1995), the park was interested in knowing if and why the animals were leaving. The objectives of our study were to:

- Determine pronghorn home range sizes and core use areas in and around Wupatki National Monument.
- Document the effects of roads and fences on pronghorn movement patterns.
- Determine pronghorn habitat use and their selection of vegetation, slope and aspect variables.
- Determine the effects of water distribution on pronghorn movements.
- Determine the abundance and moisture content of forbs, grasses and shrubs.
- Determine if there are monthly differences in pronghorn distributions and habitat preferences inside and outside the Monument.

STUDY AREA

Our study area was centered on Wupatki National Monument, located in north central Arizona, approximately 35 kilometers northeast of Flagstaff (Fig. 1). Terrain was flat to rolling in the north to steeper mountainous areas further south. Chinle badland formations were common in the east while basalt rock outcrops were scattered throughout the study area. Elevations range from 1300 meters north of the Monument to over 2700 meters on O'Leary Peak to the south. Elevations within Wupatki National Monument are generally between 1500 and 1800 meters.

Local climate regimes within the study area vary with elevation. Lower elevations are located in a "rain shadow," northeast of the San Francisco Peaks, where summers are hot, with average high temperatures around 30°C, and lows in the teens. Annual precipitation is 21 cm and most occurs during July and August in the form of brief, heavy but local thundershowers (monsoons). Winters are cooler with high temperatures around 5°C and lows below freezing, with one or two isolated snow showers occurring during this time. The higher elevations to the south are much cooler with considerably more precipitation, mostly in the form of winter snows.

Vegetation varied with elevation, with lower elevations characterized by Great Basin Cold Desert shrublands and grasslands, while middle elevations consisted mostly of open juniper woodlands. Coniferous forests interspersed with open grassland parks occurred in the higher elevations.

The Great Basin Cold Desert Shrub community comprised the lowest elevations (1320 to 1535 meters) of our study area. Topography was rough and broken by several major drainages. Shrubs occurred mainly on scattered hummocks separated by intervening empty areas of deep, black cinders. Dominant shrub species occurring in this community were four-wing saltbush (*Atriplex canescens*), broom snakeweed (*Gutierrezia sarothrae*), Apache plume (*Fallugia paradoxa*), shadscale (*Atriplex confertifolia*), Mormon teas (*Ephedra* spp.), sand sage (*Artemesia filofolia*) and several species of flythicket (*Brickellia* spp.). Grasses constituted less than 5% of ground cover and included galleta (*Pleuraphis* spp.), threeawns (*Aristida* spp.), and bush mulhy (*Muhlenbergia porteri*). The principal forbs were globemallow (*Sphaeralcea subhastata*), buckwheats (*Eriogonum* spp.), spurges (*Euphorbia* spp.), and prince's plume (*Stanleya pinnata*).

Grasslands within the study area were generally flat to rolling terrain. These grasslands were made up of a mixture of grasses dominated by galleta, black grama (*Bouteloua eriopoda*) and New Mexican feathergrass (*Stipa neomexicana*). Rubber rabbitbrush (*Chrysothamnus nauseosus*) and broom snakeweed were the most common shrubs. Other shrubs included threadleaf groundsel (*Senecio longilobus*) and four-wing saltbush. Winter fat (*Krascheninnikovia lanata*), an important forage plant for wildlife, occurred in low density, particularly in the ungrazed National Monument. Common forbs in this community were Russian thistle (*Salsola kali*), globemallow, spurge and several species of aster (*Aster* spp.).

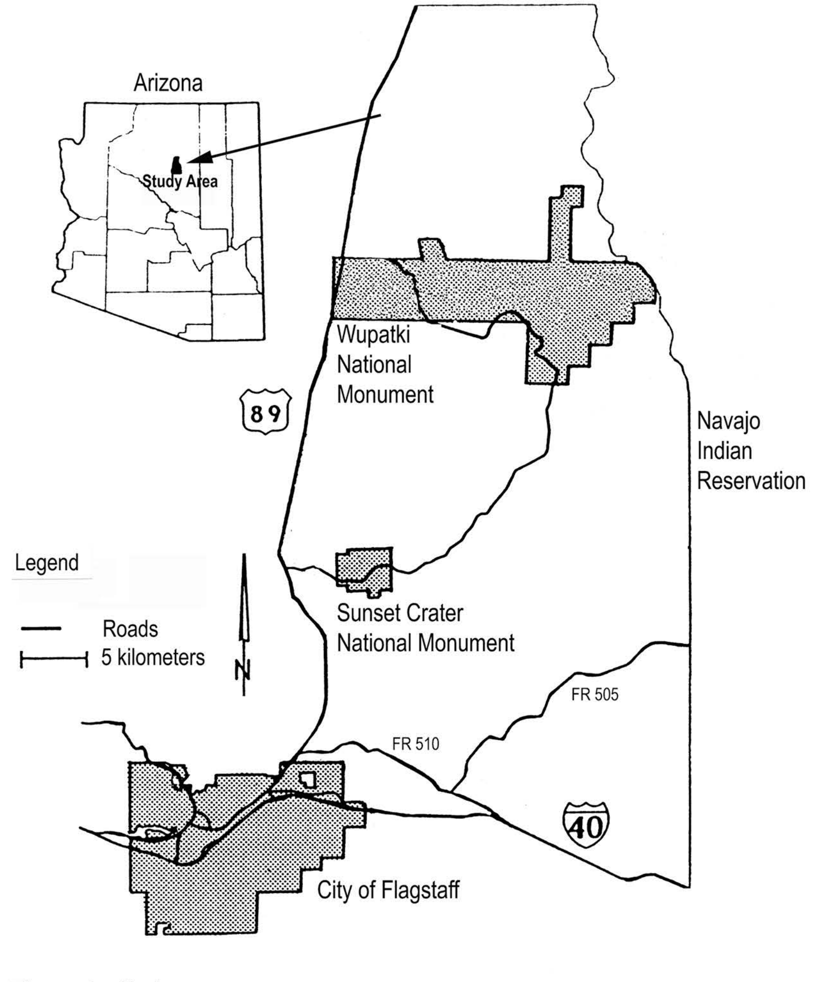

Figure 1. Study area.

Woodlands occurred on elevations above the grasslands, 1800 meters and higher, where slopes were steeper and the land broken in several areas by deep ravines. The main vegetative components were open and closed stands of one-seed juniper (*Juniperus monosperma*). Snakeweed and rabbitbrush also occurred interspersed throughout these woodlands with a variety of grasses of which galleta grass was the most dominant. Black grama, Fendler threeawn (*Aristida fendleriana*), mesa dropseed (*Sporobolus flexuosus*) and Indian ricegrass (*Oryzopsis hymenoides*) were also common.

Coniferous forests occurred at the highest elevations of our study area, dominated by ponderosa pine (*Pinus ponderosa*) with some pinyon pine (*Pinus edulis*). Cliffrose (*Purshia stansburiana*) and apache plume were common shrubs among the pines. Common grasses were little bluestem (*Andropogon scoparius*), sand bluestem (*Andropogon hallii*) and blue grama (*Bouteloua gracilis*). Several species of penstemon (*Penstemon* spp.) and skyrocket (*Gilia aggregata*) were the dominant forb species, with many other forbs present (Bateman 1976).

METHODS

Capture and Relocation

Using a net-gun fired from a helicopter, 17 pronghorn antelope were captured in October 1992,. Each animal (13 females and 4 males) was fitted with a radio transmitter collar and individually numbered eartags. Pronghorn were then aerially located twice a month until September 1994 and located on the ground from January 1993 until September 1995. Locations were plotted on 7.5' U.S.G.S. topographical maps and Universal Transverse Mercator coordinates (UTMs) derived to the nearest 0.1kilometer from mapped locations. Global Positioning System equipment was used during ground surveys to record animal locations. Data collected at each ground site included date, time, dominant vegetation type, slope, aspect, weather variables such as wind speed, temperature, and precipitation. We also recorded pronghorn group size, structure and activity. Data were entered into a computer using FoxPro, verified and then imported into an ArcView Geographic Information System.

Home Ranges and Movements

Home Ranges

Relocations of collared pronghorn were analyzed using features of the program TELEM (McKelvey 1997). Using the adaptative kernal method (Worton 1989), the 95% contour was used as an estimate of home range size while the 50% contour was used to determine core use areas. Including both aerial and ground locations, pronghorn were located once a week for home range calculations in order to reduce the possibility of auto-correlated data from more frequent observations (White and Garrott 1990). To determine if pronghorn were using the National Monument and the adjacent ranch differently throughout the year, we tested numbers of locations in and out of the Monument by month using chi-square tests. Gender related differences in home range size and differences between home range sizes of animals captured inside and outside the Monument were tested with t-tests. Interactions between gender and capture location were tested with an ANOVA.

Movements

Pronghorn movements were analyzed by calculating the distance between consecutive locations for individual animals. Consecutive locations were most often between 5 and 9 days apart, with a few more than 10 days. To determine if length of time between locations had an effect on mean distance moved, we tested the movements of a random selection of 5 (of 17) animals to determine whether there was a difference between total relocations and only those between 5 and 9 days. Distance moved was tested for gender and seasonally related differences with ANOVA. Additionally, distance moved between consecutive locations in the Monument and consecutive locations on the ranch were tested seasonally to determine if average consecutive movements differed between the Park and adjacent habitats.

Paved roads and fences were classified by type, digitized and imported into GIS coverages. Number of times pronghorn crossed these potential movement barriers was determined by sorting the data file by individual animal and date, and then counting all movements across roads and fences.

Habitat Mapping

For habitat preference analyses (vegetation, slope and aspect), in order to have adequate numbers of animal observations in each cell for chi-square tests, we divided the calendar year into three seasons based on local temperature and precipitation regimes. Spring comprised the months March through June and was characterized by warm days, cool nights and low precipitation. Average daily high was 24°C, average low 8°C, and precipitation averaged 4 cm. Summer was classified as July through October. Both day and night temperatures were considerably higher with more precipitation. Average daily high was 30°C, low 15°C and precipitation averaged 9 cm. The third seasonal category was winter (November through February), characterized by cool days and below freezing nights. Average high temperatures were 9°C , low -3°C while precipitation averaged 6 cm.

Vegetation Mapping

This portion of the study tested whether pronghorn use habitats randomly or if they preferentially select habitats, based on the premise that visibility and mobility are important selection factors. A detailed vegetation map was created for Wupatki and the surrounding area by ground-truthing an existing vegetation map for the National Monument and a map of the Babbitt (CO Bar) Ranch, taking into account shrub heights, densities, and density of juniper cover. The map was digitized into a Geographic Information System and then existing polygons corrected from field data. New vegetation polygons were created in the field, when necessary, using a Global Positioning System to produce a final vegetation coverage. The map encompassed over 90% of our pronghorn locations.

We compared the number of times radio-collared pronghorn were observed in each habitat type to expected frequencies based on the area of that vegetation class, using chi-square tests. When the null hypothesis was rejected (i.e., that all habitat types were not used equally), simultaneous 90% Bonferroni confidence intervals were made for the proportion of times animals used a specific type. To determine whether a habitat type was preferred or avoided, the confidence interval was checked for overlap with the availability proportion of the corresponding habitat type (Neu et al. 1974, Byers et al. 1984, White and Garrott 1990). Differences in preferences for habitat types were analyzed between sexes and among seasons.

Slope and Aspect Mapping

We analyzed slope and aspect preferences by creating coverages and overlaying pronghorn relocations. This was done using USGS digital elevation models and converting them to a grid. We then reclassified the grids into classes: slopes were grouped into three classes (0-9% slope, 10-19% slope and over 20% slope); aspects were grouped into nine classes, north, northeast, east, southeast, south, southwest, west, northwest and no aspect where slopes were less than one percent. These grid coverages were then converted into final polygon coverages for use in ArcView.

Number of times radio collared pronghorn were relocated within each slope and aspect class was compared to expected numbers using chi-square tests, based on the relative abundance of total area for each class. Preference or avoidance of slope and aspect classes were determined using simultaneous Bonferroni confidence intervals. Differences in preferences between sexes and seasons were also analyzed.

Forage Abundance and Succulence

During the active growing season (March through August), abundance and moisture content of forbs, grasses and shrubs within grassland habitat were collected to determine moisture content differences.

Forage Abundance

Using vegetation coverage and GIS random plotting technology, six random points a week (three in the Monument and three on adjacent habitats) were selected. We located these points using the navigator feature on the global positioning system. At each point, using a tape measure, two 50 meter straight lines were laid out along the ground in random directions from the point based on spinning a compass dial. We used the line intercept method of Canfield (1941) to determine relative abundance of forbs, grasses and shrubs, by summing up the distance (in cm) of each of these vegetation classes intercepting the tape. Total distance of each vegetation class from a line was averaged and used for analyses. At each random point, we ocularly estimated percent grass cover. Differences in abundance of each vegetation class between transects inside and outside the Monument were analyzed using t-tests. We used ANOVA to test for monthly differences in abundance, linear regressions to determine the relationship between monthly precipitation and average high temperature on the abundance of forage.

Succulence

Forage moisture content was determined by collecting one sample of each vegetation class (forb, grass, shrub) at the six points each week. Samples were clipped with scissors, placed in individual brown paper bags, weighed immediately in the field and recorded. Samples were then allowed to air dry in the bags and weight was recorded weekly until 3 consecutive weights were equal, ensuring that each sampled had dried completely, then the final dry weight was recorded. Differences between wet and dry weight, divided by wet weight was used to determine percent moisture content of each sample (Kitchen 1974, Rowlands pers. comm. 1995). Percent moisture content for each vegetation class was used to test for differences inside and outside the Monument and for monthly differences. We utilized linear regressions to determine the relationship between monthly precipitation and average high temperature on the succulence of forage.

Water Sources

A GIS coverage of available water was created by locating all water sources within our study area, determining if they were accessible to pronghorn, and if they contained seasonal or year-round water. Accessible waters were digitized in the field using a GPS. Concentric buffers of 2 km were drawn around each water source up to a distance of 10 km. This final GIS coverage was used to analyze pronghorn preferences around water sources, comparing numbers of locations by season within each buffer, to expected numbers based on relative areas of each buffer.

Using the near command in ArcView, the distance to the closest water source was calculated for every pronghorn location. These distances were analyzed by ANOVA to determine differences by sex and season. To determine significant factors affecting pronghorn distances to water, forage abundance, forage succulence, precipitation and average daily high temperature were plotted against each other and analyzed with a forward stepwise regression.

RESULTS

Capture and Relocation

Seventeen pronghorn antelope (13 females and 4 males) were captured and outfitted with radio transmitters. Four females and one male were captured inside Wupatki National Monument while nine females and three males were captured on the CO Bar Ranch. These animals were relocated a total of 1,831 times during the course of this study.

Pronghorn did not use the ranch and the Monument equally (χ^2=158, P<0.05, Fig. 2). Pronghorn were located within the Monument as often or more often from November through March. During the remainder of the year, pronghorn were significantly more common outside the Monument.

Home Ranges and Movements

Home Ranges

Analysis for normality indicated that home range and core use area size tended to come from a normally distributed population, thus t-tests and ANOVA were used to analyze these data. Home range size varied from 83.6 km^2 to 359.0 km^2.

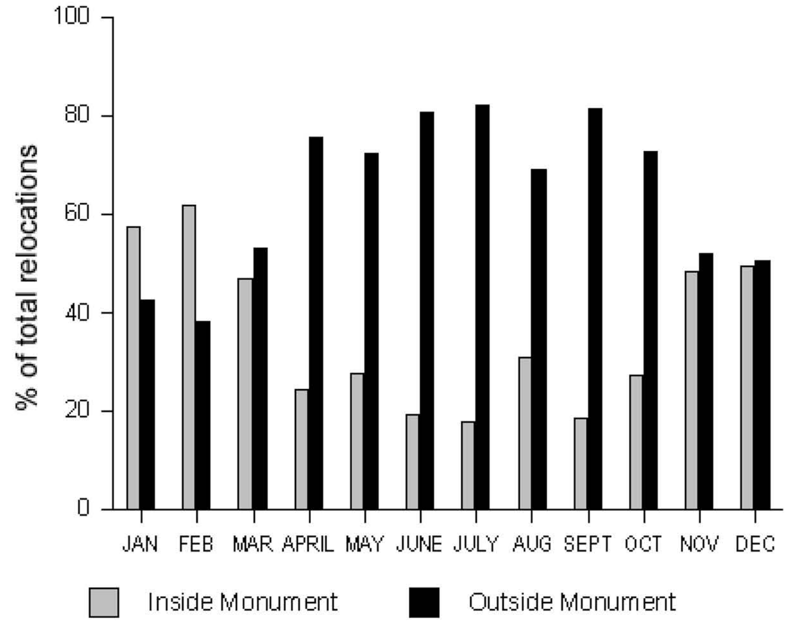

Figure 2. Pronghorn occurrences (% of total locations) inside and outside Wupatki National Monument by month.

Most home ranges were between 80 - 150 km^2 (Fig. 3a). Average home range size for all animals was 169.85 (SE 20.4) km^2. There were no differences in home range size by sex. Females tended to have larger home ranges, 181.2 (SE 25.1) km^2, versus 132.8 (SE 25.4) km^2 for males but this difference was not statistically significant (t=1.4, *P*>0.05). However, because there were only 4 male versus 13 female pronghorn, unequal sample sizes may have influenced our ability to detect differences.

Average home range size for animals captured within the Monument (n=5) was 162.6 (SE 36.6) km^2 versus 172.8 (SE 25.5) km^2 for those captured outside (n=12). However, these were not significant differences (t=0.22, *P*>0.05). Of the 17 pronghorn studied, 15 had home ranges encompassing parts of both the grazed ranch and ungrazed Monument. Two of the pronghorn had home ranges exclusively on the ranch property.

Core use areas of territories also did not differ by sex or capture location. Core use size averaged 27.68 (SE 4.5) km^2, ranging from 8.8 km^2 to 72.6 km^2, and clustered around 11 - 30 km^2 (Fig. 3b). Females tended to have larger core use areas, 31.4 (SE 5.4) km^2 compared to 15.6 (SE 3.2) km^2 for males but this was not significant (t=1.5, *P*>0.05). Animals captured outside the Monument had larger core use areas than those captured inside, 28.8 (SE 6.1) km^2 and 24.9 (SE 5.0) km^2 respectively, but this also was not a statistically significant difference (t=0.43, *P*>0.05).

Figure 3a. Frequency of home range sizes for pronghorn.

Movements

Since no significant difference was detected between using all relocations versus using only those between 5 and 9 days, all relocations were used to determine mean distance moved between consecutive locations. Normality tests revealed that mean distance moved was likely sampled from normally-distributed populations. Mean distance moved by females was 3.42 (SE 0.1) km and males 3.12 (SE 0.1) km and these distances were not significantly different (t=1.75, *P*>0.05).

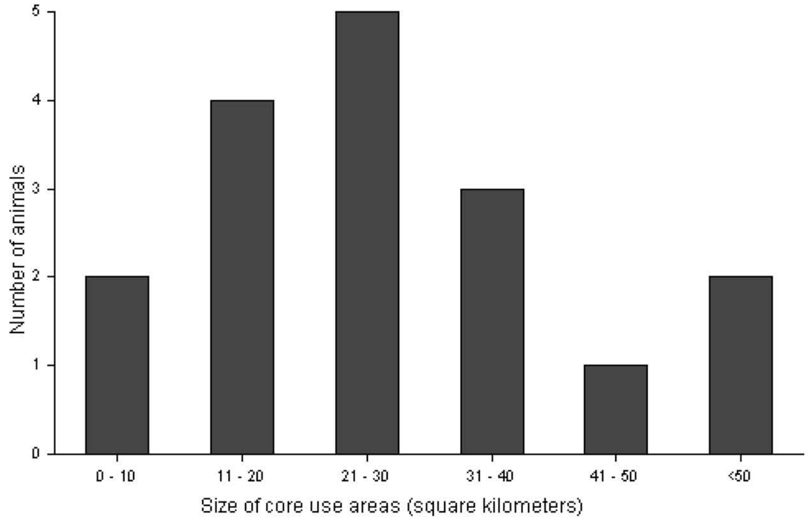

Figure 3b. Frequency of core use area sizes for pronghorn.

Mean distance moved by month of the year was tested using ANOVA and was significantly different (F=2.0, *P*<0.05). Tukey-HSD test indicated that the only significant monthly differences were between April, with the highest mean distance (3.85 km) and October with the lowest mean distance (2.54 km).

When pronghorn were in the National Monument, they did not move as far between consecutive locations during the spring and summer seasons as when on the ranch (t=2.95, *P*<0.05, t=4.43, *P*<0.05; Fig. 4). Average distance moved between consecutive locations during spring on the Monument was 2.35 (SE 0.14) km compared to 2.98 (SE 0.15) km on the ranch. During the summer season, movements on the Monument averaged 2.01 (SE 0.14) km compared to 2.90 (SE 0.14) km on the ranch. Movements between consecutive locations during the winter did not differ between animals on the ranch and Monument (t=0.14, *P*>0.05, ranch 2.82 ±0.17 km, Monument 2.85 ± 0.12 km).

Our study area was bounded on the west by US Highway 89, which is a paved two-lane highway with fenced rights-of-way. During the course of the study, no crossings of this highway were recorded for any pronghorn. In fact, several home ranges appeared to be bounded by this highway. The Wupatki-Sunset Crater loop road is a paved, two- lane road without any fences. Pronghorn crossed this road 230 times during the course of the study, and several pronghorn had home ranges straddling this road.

The livestock fence on the north of Wupatki National Monument has been modified to pronghorn standards suggested by O'Gara and Yoakum (1992). It has three strands of barb wire, with the lowest strand smooth wire, and at least 50 cm

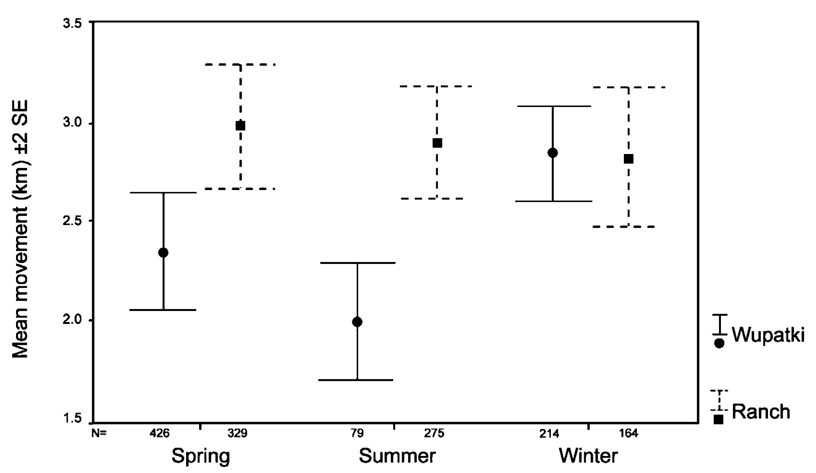

Figure 4. Average distance between consecutive locations within the Monument and consecutive locations on the Babbitt (CO Bar) Ranch by season.

above the ground. Pronghorn were located within one kilometer of this fence 189 times during the course of the study and crossed the fence 238 times. The fence on the southern boundary of Wupatki National Monument has not been modified to allow easier access for pronghorn. It is four-strand barbed wire fence with the lower strand only 32 cm above the ground. Pronghorn were located within one kilometer of this fence 117 times but crossed this fence only 75 times. Additional four strand barbed wire interior pasture fences occurred on the CO Bar Ranch, but did not appear to pose crossing problems for pronghorn.

Habitat Selection

Vegetation Selection

Using a vegetation map created for this study (Fig. 5), the following classes existed within the area encompassing more than 90% of our pronghorn relocations:

Grassland: grasses were the main component with less than 20% cover of 0-60 cm high shrubs.
Shrub-grassland: shrubs were between 20-30% cover but still less than 60 cm high. The main shrubs in this category were either rubber rabbitbrush, snakeweed or shadscale.
Open Juniper grassland: juniper cover was 5-20% and the understory was primarily grasses, with shrubs having less than 20% cover.
Open Juniper shrubland: juniper cover was 5-20% and the understory was made up of more than 20% shrub cover.
Closed juniper woodland: juniper cover was greater than 20%.
Cold Desert Shrubland: shrubs were the main vegetation (greater than 30% cover) and typically greater than 60 cm high. Common shrubs were Mormon tea, Apache plume, squawbush, snakeweed, rabbitbrush, four-wing saltbush.
Chinle Badlands/ Rock Outcrops: bare ground or deep cinders predominated.

In testing pronghorn relocations against expected numbers, based on area of each vegetation type, we found that animal use of vegetation types differed from expected based on area by sex and by season (Figs. 6 and 7). During the spring season both females and males preferred the grassland type (females $\chi^2 = 198.8$, 6 df, $P<0.05$, males $\chi^2 = 73.3$, 6 df, $P<0.05$; Tables 1a and 1b). Males and females utilized the closed juniper woodlands, cold desert shrublands and Chinle badlands less than expected. Females also preferred the shrub-grasslands, while males used this type as expected. Both sexes avoided the open juniper grasslands but used open juniper shrublands as expected.

During the summer season, pronghorn use differed from availability of habitat types (females $\chi^2 = 191.5$, 6 df, $P<0.05$; males $\chi^2 = 54.9$, 6 df, $P<0.05$; Tables 2a and 2b). Males and females preferred the grassland type. Females used shrub-grasslands more than expected while males used this type as expected. Both sexes avoided the closed juniper woodlands, cold desert shrublands and Chinle badlands. Females avoided the open juniper habitat, but males used this type as expected.

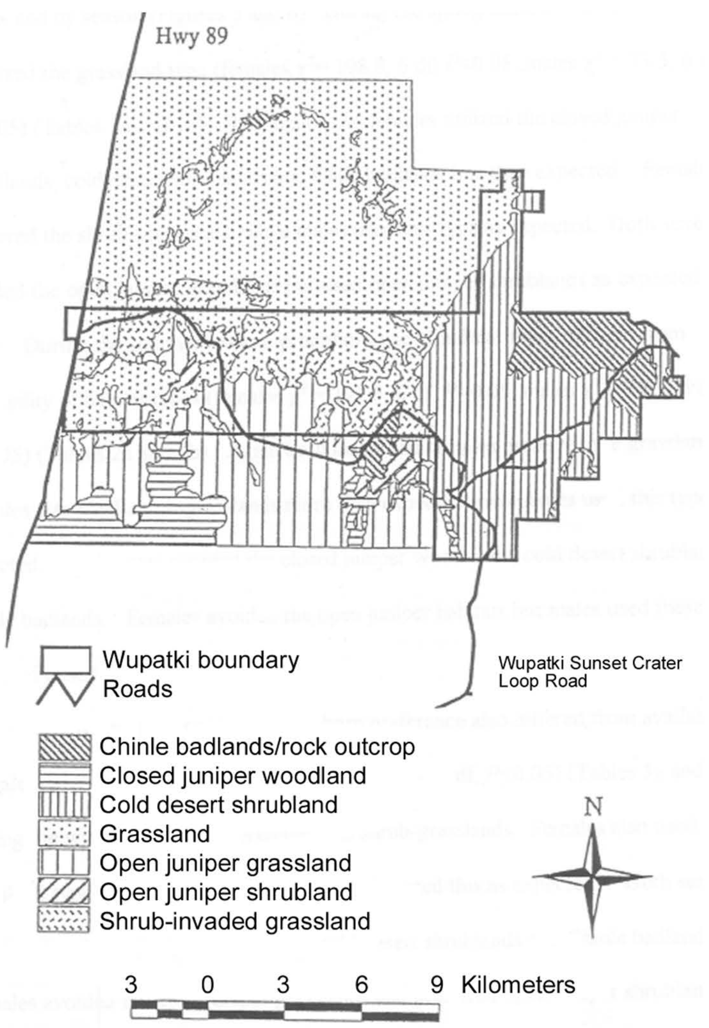

Figure 5. Vegetation map of study area.

During the winter season, pronghorn habitat preference differed from availability (females χ^2=168.1, 6 df, *P*<0.05; males χ^2=77.1, 6 df, *P*<0.05; Tables 3a and 3b), with both sexes preferring the shrub-grasslands. Females also used the grassland type more than expected, while males used it as expected. Both sexes avoided the closed juniper woodlands, cold desert shrublands and Chinle badlands. Females avoided the open juniper grasslands and preferred open juniper shrublands, while males used both types as expected.

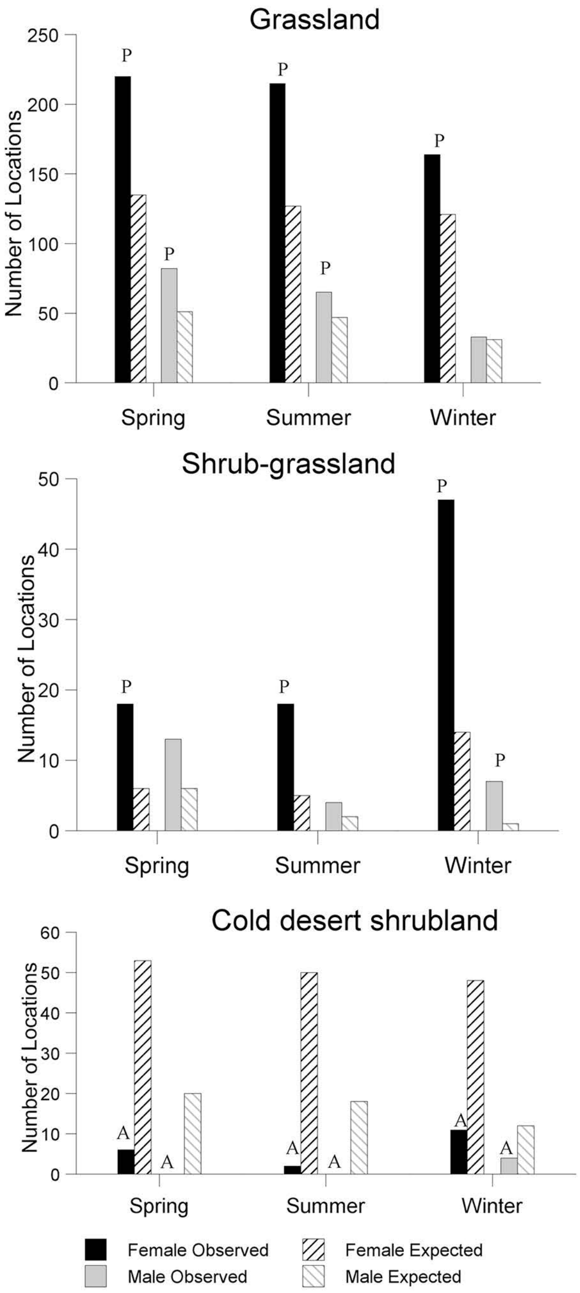

Figure 6. Number of observed pronghorn locations versus expected locations in grassland, shrub-grassland and cold desert shrubland vegetation types. P denotes use greater than expected; A denotes use less than expected.

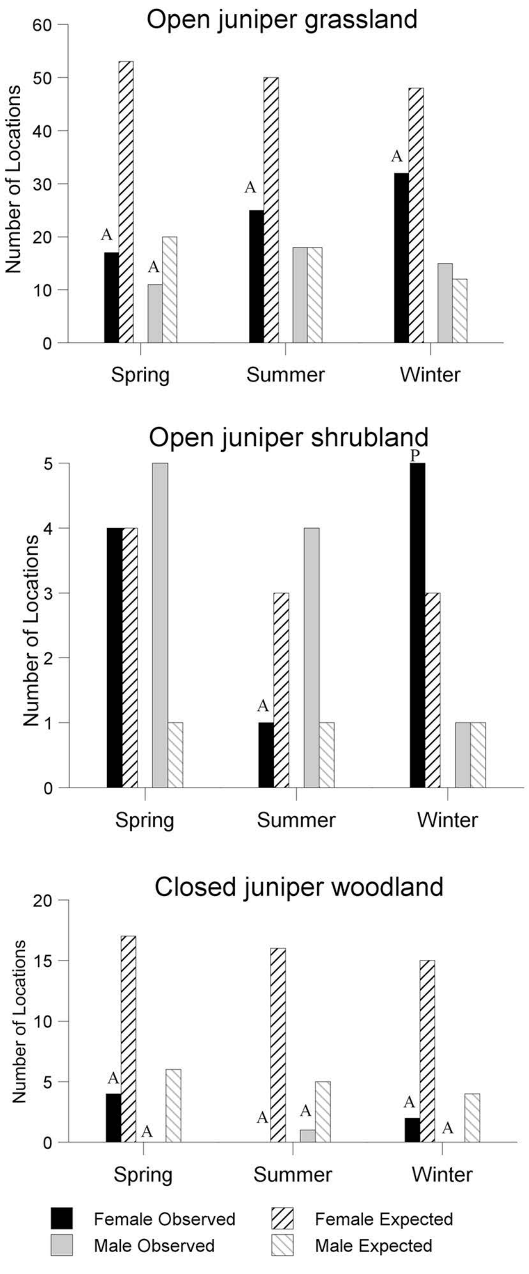

Figure 7. Number of observed pronghorn locations versus number of expected locations in open juniper grasslands, open juniper shrublands and closed juniper woodlands. P denotes use greater than expected; A denotes use less than expected.

Table 1a. Use of vegetation classes by female pronghorn compared to availability of vegetation classes in spring (March-June). Use differed from availability (χ^2=198.8, 6 df, $P<0.05$).

Vegetation Class	Observed # of locations	Expected # of locations	Proportion of area available	Bonferroni 90% CI	Preference
Grassland	220	135	0.444	0.65 - 0.79	Prefer
Shrub-grassland	18	6	0.019	0.02 - 0.09	Prefer
Open juniper grassland	17	53	0.176	0.02 - 0.09	Avoid
Open juniper shrubland	4	4	0.012	0.00 - 0.03	
Closed juniper woodland	4	17	0.057	0.00 - 0.03	Avoid
Cold desert shrubland	6	53	0.176	0.00 - 0.03	Avoid
Rock outcrops	0	16	0.053		Avoid

Slope and Aspect Selection

Pronghorn did not use slopes as expected based on availability. In addition, use of slope-classes differed by sex and season. During spring season, females preferred gentle slopes, used intermediate slopes equal to their availability, and avoided steeper slopes (χ^2=20.3, 2 df, $P<0.05$). Males avoided steeper slopes and showed no preferences for either gentle or intermediate slopes (χ^2=9.4, 2 df, $P<0.05$; Table 4a).

During the summer, females preferred gentle slopes between 0-9% and avoided intermediate (10%-19%) and steeper slopes (χ^2=45.2, 2 df, $P<0.05$). Males preferred intermediate slopes, avoided steep slopes and used gentle slopes as expected (χ^2=16.4, 2 df, $P<0.05$; Table 4b).

During the winter season, females preferred gentle while avoiding intermediate and steep slopes (χ^2=59.4, 2 df, $P<0.05$). Males avoided steep slopes but demon-

Table 1b. Use of vegetation classes by male pronghorn compared to availability of vegetation classes in spring (March-June). Use differed from availability (χ^2=73.3, 6 df, $P<0.05$).

Vegetation Class	Observed # of locations	Expected # of locations	Proportion of area available	Bonferroni 90% CI	Preference
Grassland	82	515	0.444	0.60 - 0.82	Prefer
Shrub-grassland	13	6	0.019	0.00 - 0.06	
Open juniper grassland	11	20	0.176	0.02 - 0.16	Avoid
Open juniper shrubland	5	1	0.012	0.00 - 0.09	
Closed juniper woodland	0	6	0.057		Avoid
Cold desert shrubland	0	20	0.176		Avoid
Rock outcrops	1	6	0.053	0.01 - 0.03	Avoid

Table 2a. Use of vegetation classes by female pronghorn compared to availability of vegetation classes in summer (July-October). Use differed from availability (χ^2=191.5, 6 df, P<0.05).

Vegetation Class	Observed # of locations	Expected # of locations	Proportion of area available	Bonferroni 90% CI	Preference
Grassland	215	127	0.444	0.68 - 0.81	Prefer
Shrub-grassland	18	5	0.019	0.03 - 0.09	Prefer
Open juniper grassland	25	50	0.176	0.04 - 0.13	Avoid
Open juniper shrubland	1	3	0.012	0.00 - 0.01	Avoid
Closed juniper woodland	0	16	0.057		Avoid
Cold desert shrubland	2	50	0.176	0.00 - 0.02	Avoid
Rock outcrops	0	5	0.053		Avoid

strated no preference for gentle or intermediate slopes (χ^2=13.2, 2 df, P<0.05; Table 4c, Fig. 8).

No selection of any aspect classes was detected for pronghorn during the spring season (χ^2=7.4, P>0.05; Table 5a), but they did not use aspect classes equal to availability during summer and winter seasons (χ^2=29.2 and χ^2=44.6 respectively, P<0.05; Tables 5b and 5c). During the summer season, pronghorn selected for or used, as expected, the cooler northern exposures but avoided hot and windy southerly exposures. During the winter season, pronghorn selected the northeast aspect or areas with no aspect (slope < 1%) and avoided southern aspects. All other slope aspects were used as expected.

Forage Abundance and Succulence

Forage Abundance

Forbs and grasses were significantly more abundant on our transects within

Table 2b. Use of vegetation classes by male pronghorn compared to availability of vegetation classes in summer (July-October). Use differed from availability (χ^2=54.9, 6 df, P<0.05).

Vegetation Class	Observed # of locations	Expected # of locations	Proportion of area available	Bonferroni 90% CI	Preference
Grassland	65	47	0.444	0.49 - 0.74	Prefer
Shrub-grassland	4	2	0.019	0.01 - 0.08	
Open juniper grassland	18	18	0.176	0.07 - 0.26	
Open juniper shrubland	4	1	0.012	0.01 - 0.08	
Closed juniper woodland	1	5	0.057	0.01 - 0.03	Avoid
Cold desert shrubland	0	18	0.176		Avoid
Rock outcrops	0	5	0.053		Avoid

Table 3a. Use of vegetation classes by female pronghorn compared to availability of vegetation classes in winter (November-February). Use differed from availability (χ^2=168.1, 6 df, P<0.05).

Vegetation Class	Observed # of locations	Expected # of locations	Proportion of area available	Bonferroni 90% CI	Preference
Grassland	164	121	0.444	0.52 - 0.68	Prefer
Shrub-grassland	47	14	0.019	0.03 - 0.08	Prefer
Open juniper grassland	32	48	0.176	0.07 - 0.17	Avoid
Open juniper shrubland	5	3	0.012	0.02 - 0.04	Prefer
Closed juniper woodland	2	15	0.057	0.00 - 0.02	Avoid
Cold desert shrubland	11	48	0.176	0.01 - 0.07	Avoid
Rock outcrops	0	14	0.053		Avoid

than outside Wupatki National Monument. Forbs inside were 12.3 cm (SE 1.6) while they were only 6.4 cm (SE 0.87) outside (t=3.3, P<0.05). Grasses inside were 60.5 cm (SE 1.3) and 52.4 (SE 0.9) outside (t=5.0, P<0.05). Shrubs did not differ significantly in abundance being 6.2 cm (SE 1.2) inside and 5.3 cm (SE 1.3) outside (t=0.4, P>0.05; Fig. 9).

With all vegetation classes (forb, grass and shrub), abundance differed significantly by month (F=5.8, P<0.01; F=2.4, P=0.04; F=2.5, P=0.03 respectively ; Table 6). There were significantly more forbs in March and April, while differences between other months were not significant. Grasses on our grazed transects were least abundant in May and June. However, in the Monument transects, grass abundance was lowest in March and April.

Succulence

Mean moisture content of forbs (t=1.8, P>0.05) and new growth on shrubs (t=1.6, P>0.05) did not differ inside and outside the Monument throughout the

Table 3b. Use of vegetation classes by male pronghorn compared to availability of vegetation classes in winter (November-February). Use differed from availability (χ^2=77.1, 6 df, P<0.05).

Vegetation Class	Observed # of locations	Expected # of locations	Proportion of area available	Bonferroni 90% CI	Preference
Grassland	33	31	0.444	0.31 - 0.62	
Shrub-grassland	7	1	0.019	0.01 - 0.19	Prefer
Open juniper grassland	15	12	0.176	0.09 - 0.34	
Open juniper shrubland	1	1	0.012	0.00 - 0.05	
Closed juniper woodland	0	4	0.057		Avoid
Cold desert shrubland	4	12	0.176	0.01 - 0.12	Avoid
Rock outcrops	0	4	0.053		Avoid

Table 4a. Use of slope classes by pronghorn compared with slope availability during the spring (March-June) season. Use differed from availability for females ($\chi^2 = 20.3$, 2 df, $P<0.05$) and males ($\chi^2 = 9.4$, 2 df, $P<0.05$).

Sex	Slope Class (%)	Observed # of locations	Expected # of locations	Proportion area available	Bonferroni 90% CI	Preference
Female	0 - 9	331	304	0.73	0.75 - 0.84	Prefer
	10 - 19	68	66	0.16	0.12 - 0.20	
	≥ 20	18	46	0.11	0.02 - 0.06	Avoid
Male	0 - 9	117	108	0.73	0.71 - 0.86	
	10 - 19	27	23	0.16	0.11 - 0.25	
	≥ 20	5	17	0.11	0.00 - 0.07	Avoid

Table 4b. Use of slope classes by pronghorn compared with slope availability during the summer (July-October) season. Use differed from availability for females ($\chi^2 = 45.2$, 2 df, $P<0.05$) and males ($\chi^2 = 16.4$, 2 df, $P<0.05$).

Sex	Slope Class (%)	Observed # of locations	Expected # of locations	Proportion area available	Bonferroni 90% CI	Preference
Female	0 - 9	364	305	0.73	0.83 - 0.90	Prefer
	10 - 19	42	67	0.16	0.07 - 0.13	Avoid
	≥ 20	13	47	0.11	0.02 - 0.05	Avoid
Male	0 - 9	121	122	0.73	0.64- 0.80	
	10 - 19	41	26	0.16	0.17 - 0.32	Prefer
	≥ 20	6	19	0.11	0.00 - 0.07	Avoid

Table 4c. Use of slope classes by pronghorn compared with slope availability during the winter (November-February) season. Use differed from availability for females ($\chi^2 = 59.4$, 2 df, $P<0.05$) and males ($\chi^2 = 13.2$, 2 df, $P<0.05$).

Sex	Slope Class (%)	Observed # of locations	Expected # of locations	Proportion area available	Bonferroni 90% CI	Preference
Female	0 - 9	336	273	0.73	0.86 - 0.93	Prefer
	10 - 19	37	60	0.16	0.06 - 0.13	Avoid
	≥ 20	3	42	0.11	0.00 - 0.02	Avoid
Male	0 - 9	98	92	0.73	0.69 - 0.85	
	10 - 19	27	20	0.16	0.13 - 0.29	
	≥ 20	2	14	0.11	0.00 - 0.04	Avoid

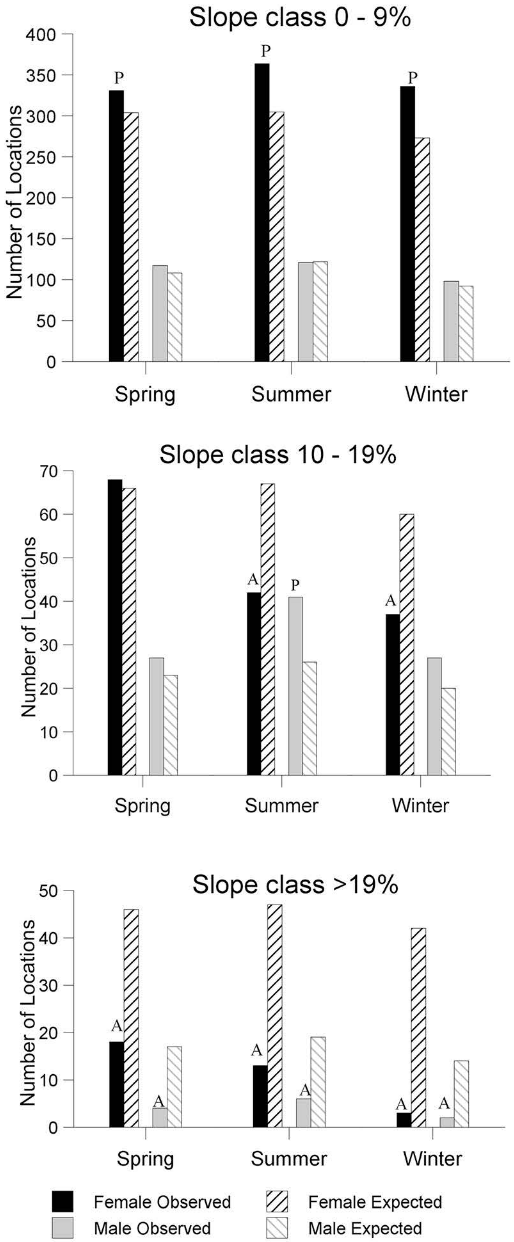

Figure 8. Number of observed pronghorn locations versus expected number of locations in slope classes 0-9%, 10-19% and >19%. P denotes use greater than expected, A denotes use less than expected.

Table 5a. Use of aspect classes by pronghorn compared witih aspect availability during the spring (March - June) season. Use did not differ from availability ($\chi^2 = 7.44$, 8 df, $P > 0.05$).

Aspect	Observed # of locations	Expected # of locations	Proportion of area available	Bonferroni 90% CI	Preference
North	115	107	0.17	0.15 - 0.22	
Northeast	122	123	0.20	0.16 - 0.24	
East	106	105	0.17	0.13 - 0.21	
Southeast	90	90	0.15	0.11 - 0.18	
South	51	59	0.10	0.05 - 0.11	
Southwest	35	31	0.05	0.03 - 0.08	
West	34	33	0.05	0.03 - 0.078	
Northwest	45	53	0.09	0.05 - 0.10	
No Aspect	18	11	0.01	0.00 - 0.07	

Table 5b. Use of aspect classes by pronghorn compared with aspect availability during the summer (July - October) season. Use did not differ from availability ($\chi^2 = 29.2$, 8 df, $P > 0.05$).

Aspect	Observed # of locations	Expected # of locations	Proportion of area available	Bonferroni 90% CI	Preference
North	136	98	0.17	0.20 - 0.29	Prefer
Northeast	118	112	0.20	0.17 - 0.25	
East	88	95	0.17	0.12 - 0.20	
Southeast	62	82	0.15	0.08 - 0.14	Avoid
South	51	54	0.10	0.06 - 0.12	
Southwest	19	28	0.05	0.01 - 0.053	
West	22	30	0.05	0.02 - 0.06	
Northwest	48	48	0.09	0.05 - 0.11	
No Aspect	16	10	0.01	0.01- 0.05	

Table 5c. Use of aspect classes by pronghorn compared with aspect availability during the winter (November - February) season. Use differed from availability ($\chi^2 = 44.6$, 8 df, $P<0.05$).

Aspect	Observed # of locations	Expected # of locations	Proportion of area available	Bonferroni 90% CI	Preference
North	79	88	0.17	0.11 - 0.20	
Northeast	137	100	0.20	0.22 - 0.32	Prefer
East	89	86	0.17	0.13 - 0.22	
Southeast	62	73	0.15	0.08 - 0.16	
South	27	48	0.10	0.03 - 0.08	Avoid
Southwest	21	25	0.05	0.02 - 0.06	
West	28	27	0.05	0.02 - 0.08	
Northwest	38	43	0.09	0.04 - 0.10	
No Aspect	22	9	0.01	0.02 - 0.07	Prefer

collection period. Average forb moisture content in the Monument was 44.8% (SE 1.6%) and outside 40.9% (SE 1.4%). New growth on shrubs averaged 37.7% (SE 0.9%) on grazed sites and 35.9% (SE 0.7%) on the ungrazed transects. Grasses were significantly more succulent in the grazed sites (27.2 SE 1.1%) than in ungrazed transects (21.2 SE 1.5%), (t=3.3, *P*<0.05; Fig. 10).

March and April forb moisture content averaged 51.9 ± 12.3%. Average succulence for the remainder of the collection period was 40.1 ± 7.9%. Differences between monthly forage succulence were significant (F=6.4, *P*<0.01). Tukey's HSD tests revealed that forbs had significantly more moisture in the early spring in the Monument and grazed sites.

Average moisture content in July for shrubs was 40.1 ± 4.0%. It was lowest in March with an average of 32.8 ± 3.6%. Moisture content for new growth on shrubs differed by month (F=4.0 *P*<0.01). Tukey's HSD test showed that new growth on shrubs had more moisture later in the summer than spring.

Grasses also differed significantly in moisture content by month (F=3.1, P=0.02). Tukey's HSD tests revealed that grasses were significantly more succulent in April (0=30.8 ± 8.9%). August had the lowest average succulence (0=19.8 ± 8.3%).

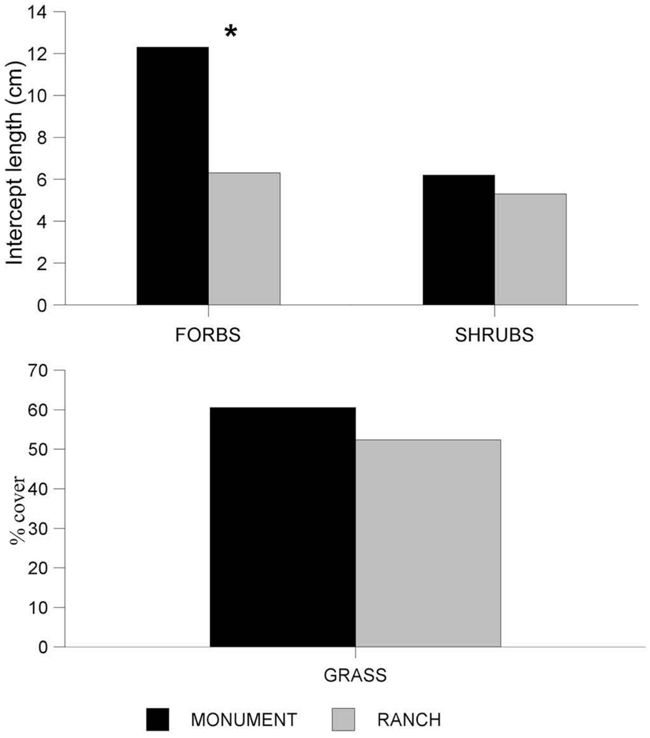

Figure 9. Forb, grass and shrub abundances in Wupatki National Monument compared to outside the Monument (in cms). * denotes significant difference.

Table 6. Monthly mean abundance of forbs, shrubs and grasses in the park and on the grazed CO Bar Ranch.

	Forbs (cm)		Shrub(cm)		Grass (%)	
Month	Park	Grazed	Park	Grazed	Park	Grazed
March	21.0	1.2	6.2	19.3	61.6	57.5
April	25.9	11.5	12.6	5.0	51.1	54.4
May	10.2	3.7	3.3	1.0	63.3	45.5
June	10.8	5.7	3.9	5.5	60.5	47.2
July	5.8	5.22	4.0	1.9	63.9	55.2
Aug	7.3	6.9	6.8	8.5	62.8	55.0

Neither average daily high temperature ($r^2 = 0.44$, $P>.05$), nor precipitation ($r^2=0.62$, $P>.05$) was significantly related to the monthly abundance of forbs. However, monthly succulence level of forbs was inversely related to the average monthly high temperatures ($r^2=0.66$, $P<.05$). As temperatures rose, succulence dropped in forbs. Precipitation levels were not statistically significant in determining succulence ($r^2=0.53$, $P>.05$).

Water Use

2 km Concentric Buffers

Pronghorn did not use the 2 km buffers around water sources as would be expected based on area within these buffers. During the year, 84% of all pronghorn locations were less than 6 km from a water source (Fig. 11). In the spring season, use of buffers differed from availability for females and males (females $\chi^2=86.5$, 4 df,

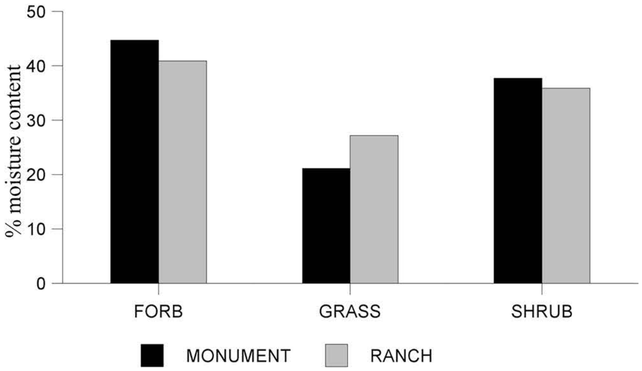

Figure 10. Forage moisture content of forbs, grasses and shrubs on Wupatki National Monument and on Babbitt Ranch. * = denotes significant difference.

$P<0.05$; males $\chi^2=103.586.5$, 4 df, $P<0.05$; Table 7a). Females preferred the 0-1.99 km buffer and avoided areas greater than 8 km, with all other buffers being used as expected. Males preferred 0-3.99 km buffers, and avoided areas greater than 6 km.

During the summer season, buffer use differed from availability for females and males (females $\chi^2=126.3$, 4 df, $P<0.05$; males $\chi^2=74.4$, 4 df, $P<0.05$; Table 7b). Throughout the summer they preferred buffers up to 3.99 km from water. Males avoided areas greater than 6 km while females avoided those greater than 8 km from water.

During the winter season (Fig. 12), buffer area use differed from availability, but females and males used the buffers similarly (females $\chi^2=122.6$, 4 df, $P<0.05$; males $\chi^2=64.4$, 4 df, $P<0.05$; Table 7c). During winter, both sexes preferred the 2-3.99 km buffer and used the 0-1.99 km and 4-5.99 km buffers as expected, but avoided areas greater than 6 km from water.

Mean Distance from Water

Mean distance of pronghorn sightings to water did not differ significantly by year during this study ($F=0.52$, $P>0.05$), but mean distance to water differed by sex and season, and by location within and outside the Monument. Female pronghorn were found farther from water sources than males during the spring season ($t = 3.43$, $P<0.01$) but there was no difference between sexes during the summer or winter. Females were significantly ($F=13.7$, $P<0.05$) closer to water during the summer (2845 SE 91 m) than spring or winter, the latter not being significantly different (spring 3,514 SE 102 m, winter 3,475 SE 106 m). Males were farther from water in the winter, (3,332 SE 145 m) than either spring or summer ($F=6.0$, $P<0.05$), which did not differ (spring 2,732 SE 123 m, summer 2,738 SE 148 m) (Fig. 13).

Pronghorn, when located within the Monument boundaries, were significantly farther from water than when located outside the Monument ($t=9.47$, $P<0.05$). Mean distance within was 4,305 ± 73.7 meters compared to 3,285 ± 78.5 meters outside the Monument.

When forb succulence, forage abundance, monthly average high temperatures, and precipitation were used to determine relationships to distance-from-water, only monthly high temperature was significant ($r^2=0.66$, $P<0.05$). As temperatures rose, pronghorn moved closer to available waters. Neither forb succulence ($r^2=0.21$, $P>.05$), forage abundance ($r^2=0.10$, $P>0.05$), nor precipitation ($r^2=0.30$, $P>.05$) were significantly correlated with distance to water.

DISCUSSION

Home Ranges, Movements and Distribution

Home range size for all radio-collared pronghorn that we studied averaged 16,900 ha and were considerably larger than the 156 - 2300 ha reported as typical home range sizes by Kitchen and O'Gara (1982). They were almost twice the size of home ranges reported by Ockenfels et al. (1994) from central Arizona. Most of our radio-

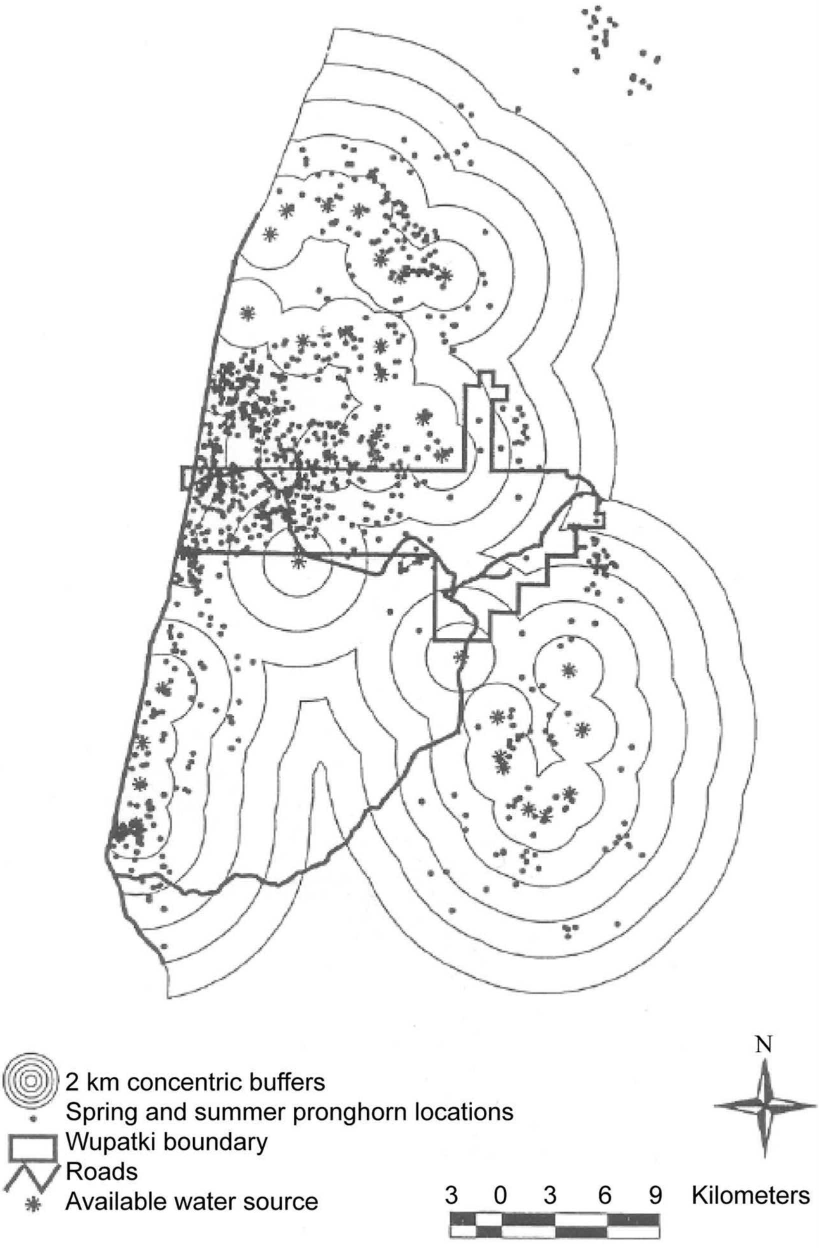

Figure 11. 2 km concentric buffers around water sources with pronghorn locations during spring and summer.

Table 7a. Distances of pronghorn locations from identified water sources compared with area within isometric 2.0 km concentric buffers around water sources during spring. Use differed from availability for females ($\chi^2 = 86.5$, 74.4, df, $P<0.05$) and males ($\chi^2 = 103.5$, 4 df, $P<0.05$).

Sex	Distance Class (km)	Observed # of locations	Expected # of locations	Proportion area available	Bonferroni 90% CI	Preference
Female	0 - 1.99	130	102	0.202	0.21 - 0.30	Prefer
	2.0 - 3.99	134	117	0.232	0.22 - 0.31	
	4.0 - 5.99	133	111	0.219	0.22 - 0.31	
	6.0 - 7.99	102	90	0.179	0.16 - 0.24	
	8.0 - 9.99	7	84	0.166	0.00 - 0.03	Avoid
Male	0 - 1.99	55	32	0.202	0.25 - 0.43	Prefer
	2.0 - 3.99	75	37	0.232	0.37 - 0.56	Prefer
	4.0 - 5.99	25	35	0.219	0.08 - 0.22	
	6.0 - 7.99	5	28	0.179	0.00 - 0.06	Avoid
	8.0 - 9.99	0	26	0.166		Avoid

collared pronghorn had home ranges encompassing parts of the grazed ranch and ungrazed Monument.

Individual pronghorn varied in their tendency to move long distances. Two females moved from the lower elevation grassland area of the National Monument to open parks in high elevation ponderosa pine forest each spring, returning to the grasslands in the late fall. One other female moved from grassland habitats on the

Table 7b. Distances of pronghorn locations from identified water sources compared with area within isometric 2.0 km concentric buffers around water sources during summer. Use differed from availability for females ($\chi^2 = 126.9$, df, $P<0.05$) and males ($\chi^2 = 74.45$, 4 df, $P<0.05$).

Sex	Distance Class (km)	Observed # of locations	Expected # of locations	Proportion area available	Bonferroni 90% CI	Preference
Female	0 - 1.99	157	91	0.202	0.29 - 0.40	Prefer
	2.0 - 3.99	133	105	0.232	0.24 - 0.34	Prefer
	4.0 - 5.99	92	99	0.219	0.16 - 0.25	
	6.0 - 7.99	67	81	0.179	0.11 - 0.18	
	8.0 - 9.99	3	75	0.166	0.00 - 0.01	Avoid
Male	0 - 1.99	50	29	0.202	0.25 - 0.44	Prefer
	2.0 - 3.99	60	33	0.232	0.31 - 0.51	Prefer
	4.0 - 5.99	27	31	0.219	0.10 - 0.26	
	6.0 - 7.99	7	25	0.179	0.00 - 0.09	Avoid
	8.0 - 9.99	0	23	0.166		Avoid

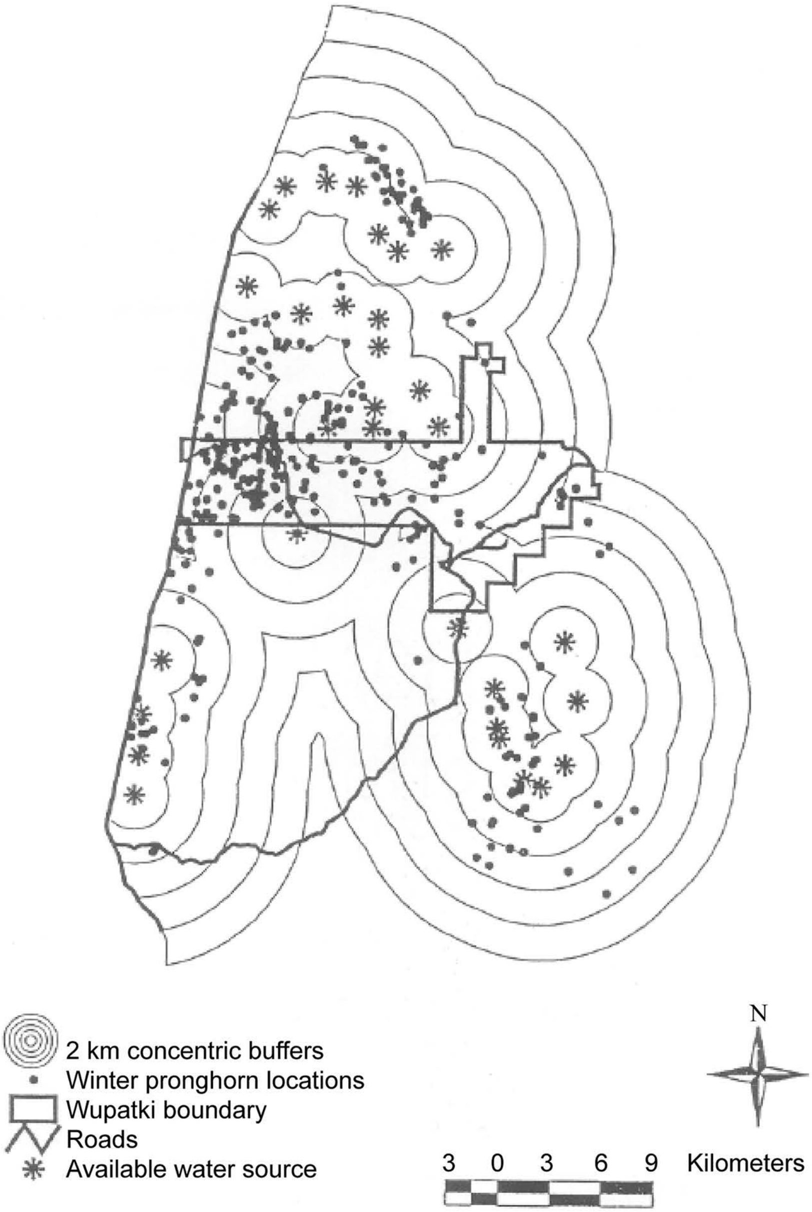

Figure 12. 2 km concentric buffers around water sources with pronghorn locations during the winter season.

Table 7c. Distances of pronghorn locations from identified water sources compared with area within isometric 2.0 km concentric buffers around water sources during winter. Use differed from availability for females (χ^2 = 122.6, df, $P<0.05$) and males (χ^2 = 64.3, 4 df, $P<0.05$).

Sex	Distance Class (km)	Observed # of locations	Expected # of locations	Proportion area available	Bonferroni 90% CI	Preference
Female	0 - 1.99	91	82	0.202	0.17 - 0.27	
	2.0 - 3.99	168	95	0.232	0.35 - 0.46	Prefer
	4.0 - 5.99	94	90	0.219	0.18 - 0.28	
	6.0 - 7.99	53	73	0.179	0.08 - 0.17	Avoid
	8.0 - 9.99	4	68	0.166	0.00 - 0.02	Avoid
Male	0 - 1.99	26	25	0.202	0.12 - 0.29	
	2.0 - 3.99	63	29	0.232	0.39 - 0.60	Prefer
	4.0 - 5.99	26	27	0.219	0.12 - 0.29	
	6.0 - 7.99	12	22	0.179	0.03 - 0.15	Avoid
	8.0 - 9.99	0	21	0.166		Avoid

ranch, across the Little Colorado River, to desert shrubland habitat on the Navajo Reservation each spring prior to fawning, returning to the ranch in late summer. All of the other pronghorn showed migratory behavior but did not tend to move such large distances, having maximum movements between 10 km and 20 km, comparable to movements reported by Ockenfels (1994) in central Arizona.

We found that the mean distance moved by pronghorn between consecutive locations averaged 3.3 km. Hailey (1979) reported mean distance moved as 1.2 km,

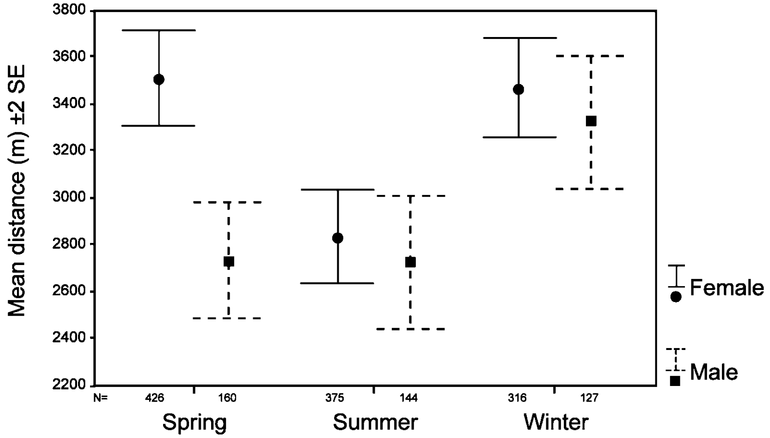

Figure 13. Mean distances to water (in meters) for male and female pronghorn, by season.

and Ockenfels (1994) found average distance moved in central Arizona herds to be 2.5 km, somewhat smaller than found in this study. However, pronghorn herds in central Arizona are much more confined by man-made barriers (e.g., roads, fences, housing developments), than are animals in the more remote area of our study. Ockenfels (1994) reported that the area he studied was "well watered" with very few areas farther than 1.6 km from water, while over 80% of our study area was greater than 1.6 km from water.

Some fences (i.e., net wire or fences with a low bottom wire), highways and railroads may pose barriers to pronghorn movement, thereby fragmenting habitat, restricting movement and isolating populations (Buechner 1950, O'Gara and Yoakum 1992, van Riper and Ockenfels et al. 1998). Pronghorn move within habitats in response to drought, forage and water availability, winter storms, human disturbances and other changing conditions. Highway 89, a paved and fenced two-lane road was an effective movement barrier separating herds to the east and west. At no time, during the 3 years of this study, did we document any pronghorn crossing this highway. However, the paved but unfenced two-lane Monument road did not appear to pose movement problems for pronghorn. Pronghorn commonly crossed, and several home ranges straddled, this road.

Livestock fences at Wupatki National Monument, with lower strands modified for pronghorn, as described by O'Gara and Yoakum (1992), did not appear to deter pronghorn from crossing pasture boundaries. Pronghorn did not cross a fence without lower strand modifications as often, but several pronghorn had home ranges encompassing both sides of these fences. However, we simply counted the number of times pronghorn crossed these fences. If pronghorn came to the fence and had trouble or decided not to cross, this would not be revealed by our data. In times of stress, such as pursuit by a predator or deep winter snow cover, these fences may still pose problems.

Although pronghorn used the ranch and Monument, they used these habitats differently during the course of the year. During winter months animals were frequently located within the National Monument boundaries, but during the rest of the year were far more common on Babbitt Ranch property. From these distribution patterns, it is apparent that the pronghorn in this study need to utilize components of habitats on both the ranch and Monument in order to meet their annual essential life requirements.

Aside from the grazing regimes, there are two main differences between Babbitt Ranch and the Monument: (1) the ranch has several water sources available to the pronghorn while the Monument has none; and (2) the Monument has more diverse habitat types. The ranch consists mostly of grassland (92%) with a few patches of shrub-grassland (6%) and juniper habitats (1%) while the Monument contains grasslands (25%), shrub-grasslands (12%) and open juniper habitats (13%). Within the grassland vegetation type, we found that the Monument had significantly more forbs available during the spring and summer.

Forage Succulence

Pronghorn are considered to be opportunistic and selective, taking the most palatable and succulent forage available at all seasons (Sundstrom et al. 1973, Authenreith 1978, Allen et al. 1984). Beale and Smith (1970) and Baker (1953) found that forbs, which provide high quality nutrition, digestibility and moisture, represent 86% or more of pronghorn summer diets in the Great Basin. Other authors have reported that forbs are the main component of pronghorn diets, with browse becoming increasingly important as forbs decrease in abundance (Mitchell and Smoliak 1971, Koerth et al. 1984). Abundance of forage classes in our study differed between the grazed Babbitt Ranch and the ungrazed Wupatki National Monument. Throughout the collecting period, forbs were significantly more abundant within the Monument. Forbs were also more abundant in spring and early summer than in other months. Forbs are particularly important at this critical time of the year for late gestation, lactation and growth of fawns.

Despite the fact that the Monument had more forbs available during late spring and summer, this is the time of the year that pronghorn are found more frequently on the ranch, perhaps needing to remain closer to permanent water sources. During the spring and summer seasons, pronghorn utilizing the ranch moved larger distances between consecutive locations than when the animals were in the Monument. This may be due to lower forb production on the ranch, forcing the pronghorn to move greater distances to find adequate forage.

Besides abundance, succulence of forage is an important consideration for pronghorn. Beale and Smith (1970) found that water consumption of pronghorn in Utah varied inversely with the quantity and succulence of available forage. Although forbs were more abundant on the Monument, moisture content did not differ between the Monument and ranch. Forbs and grasses were significantly more succulent during the spring season. Shrubs provided more succulence during the late summer as forbs dried out.

Water Use

Although consumption of succulent forage can help pronghorn meet water requirements, the importance of dependable and accessible water sources is not disputed, especially in the arid Southwest. Beale and Holmgren (1975) concluded that pronghorn cannot live without water during hot weather, even if forage succulence is above average, and that fawns are most affected by a lack of water. Texas droughts brought about a reduction in vitality of antelope which resulted in decreased fertility (Autenreith 1978). Whisler (1984) states that diurnal, xeric-dwelling ungulates such as pronghorn must tolerate large solar radiation heat loads, since they are less able to behaviorally avoid daily and seasonal temperature extremes in the open, often windswept, habitats that they typically occupy.

Placement of water sources plays an important role in determining pronghorn distributions and daily and seasonal movements. Boyle and Alldredge (1984) found that pronghorn in Wyoming began dispersing from winter ranges as snow cover receded in spring and by June concentrated on adjacent summer ranges where drinking water was more abundant and dependable. In this study, pronghorn began moving onto the Babbitt Ranch in late spring, as forbs became available and were most succulent, and remained on the ranch where water sources were available throughout the summer months.

Kindschy et al. (1978) stated that the optimal water distribution was for all pronghorn areas to be within 1.6 km of water, although Sundstrom (1968) found ranges that produced and maintained high pronghorn densities had water available every 1.6 - 8.0 km. In Wyoming Sundstrom (1968) found that 95% of more than 12,000 pronghorn locations were within 6.4 km of water. Ockenfels et al. (1994) found that nearly all pronghorn locations in central Arizona occurred < 1.6 km from water; however, there were very few areas in their study area that were more than 1.6 km from water.

In our study, the majority of pronghorn locations in all seasons (83% in spring, 87% in summer and 85% in winter) were within a 6 km radius of a water source. However, during spring and summer, both male and female pronghorn used areas only up to 4 km from a water source more often than expected. During the spring and summer, water demands are most likely the greatest for pronghorn. Females need increased water for late gestation, fawning, and lactation. Later in the summer, temperatures rise and forage dries out, creating an increased need for free standing water for male and female pronghorn. We found that areas greater than 6 km were avoided by males, and females avoided areas greater than 8 km from water.

During the winter, temperatures are much lower, and pronghorn became less dependant on permanent water sources. Both sexes ranged from 0 - 6 km from water as expected based on area. Again, areas greater than 6 km from water were avoided.

Although female pronghorn were located within 2 km of a water source more frequently than expected during the spring season, average distance to water for females was greater in spring than either summer or winter. Females need increased water for lactation during the spring. Forb production and moisture content were also highest at this time, and the need for free standing water may be lessened by the consumption of succulent forage. Beale and Smith (1970) found that pronghorn in Utah did not drink water when forbs were abundant and moisture content 75% or greater. Moisture content in this study hovered around 52%, so pronghorn would most likely still need additional water. However, if water requirements during spring were met mostly by forage consumption, females with young fawns may have ranged farther from water sources to avoid increased predation around the denuded vegetation closer to water sources.

Both male and female pronghorn were closest to water sources during the summer, when temperatures were high and forage less succulent. Both sexes ranged farther from water during the winter. During the winter, temperatures were much lower in this area, and thus the need for free standing water was decreased. In addition, brief snow showers provided ephemeral sources of drinking water from snowmelt. During the hot summer, as forb production decreased and the plants lost moisture, pronghorn were most likely driven closer to water due to an increased need for free standing water.

When pronghorn were located within the National Monument boundaries, they were significantly farther from water sources than when they were located outside the Monument. However, forage production was significantly higher on the National Monument. The fact that there are no permanent sources of drinking water available to supplement the pronghorns' water requirements in the Monument may force them into areas outside the Monument that have lower forage production. Once pronghorn leave the Monument seeking water, they have to move greater distances in order to find sufficient quantities of nutritious forage, as evidenced by their larger consecutive movements on the ranch when compared to the Monument. These trade-offs between forage quality and water availability may help explain the large home range sizes and movements between the ranch and Monument made by the pronghorn in our study. This may also explain why pronghorn have home ranges and core use areas encompassing both the ranch and Monument, as components of both are necessary for this animal to meet its life requirements.

Habitat Selection

In this study, pronghorn moved from Monument to ranch habitats in early spring, remained on the ranch throughout the summer, then returned to Monument habitat in the late fall and winter. During the winter, forb production is low and pronghorn must turn to browse and evergreen forage for food. Shrub and juniper habitats which provide this food source are much more common on the National Monument than the ranch. Additionally, temperatures are lower and snow provides an ephemeral source of water, lessening the need for free-standing water. Thus the pronghorn utilize Monument habitats more during the winter portion of the year.

In spring, forbs become abundant and are at their greatest succulence in grassland habitats. Pronghorn move to these grasslands at the north edge of the Monument and the ranch to utilize forbs. However, as summer approaches and temperatures rise drastically, water from the forage is insufficient to satisfy pronghorn water needs. The National Monument does not have any available permanent water sources. However, water impoundments for cattle that are accessible to pronghorn, are common on the ranch. Thus, during the summer pronghorn move onto the ranch in order to remain closer to water sources, which may leave them in areas of less desirable forage. As winter approaches, the animals move back toward the Monument for winter browse.

Because forb production is lower on the ranch during the spring and summer, pronghorn may need to range farther on the ranch to find adequate forage supplies. In fact, we documented larger consecutive movements when on the ranch at this time of the year, when compared to movements on the Monument. Making long movements and utilizing areas of lower quality forage could likely contribute to the large home ranges seen in this study, and may also result in decreased pronghorn productivity and increased mortality.

In addition to forage and water needs, pronghorn utilize specific habitats throughout the year for other life requirements, such as mating and birthing, predator detection and avoidance and shelter from weather. Vegetation composition and structure have been long known to influence pronghorn use of an area (Yoakum 1980). Since vision and mobility contribute to predator detection and avoidance, pronghorn are thought to avoid tall, dense vegetation (Sundstrom et al. 1973, Kindschy et al. 1978, 1982). Pronghorn typically inhabit open grasslands, shrub-grasslands, steppes and deserts that provide adequate forage supplies, shelter, and hiding cover for fawns (Yoakum 1974). Numerous studies have determined that pronghorn do not use vegetation types in proportion to their availability. Yoakum (1974, 1979, 1980) found that pronghorn prefer vegetation less than 60 cm high. He considered vegetation over 60 cm as suboptimal because it obstructs views of the surrounding area. In addition, he found that areas with a dense ground cover of shorter shrubs was less preferred because it reduces the mobility of pronghorn and increases their vulnerability to predation. Willis et al. (1988) also reported that pronghorn select areas of low shrub volume.

Pronghorn in this study did not use vegetation classes based on their availability, with males and females selecting different habitat classes at different times of the year. As expected, pronghorn avoided the taller, closed juniper woodlands and cold desert shrublands, during all seasons, where shrub and tree height and density greatly reduce visibility and mobility. Chinle badland and rock outcrop classes where bare ground dominated were also avoided. Additionally, during all seasons, pronghorn preferred the grassland type, where shrubs made up less than 20% of the vegetation.

Pronghorn preferences for shrub-grasslands (shrubs 20-30%) varied by sex and season. Females selected the shrub-grasslands during the spring and summer, when fawning is occurring in northern Arizona. The heavier shrub component in the grassland may provide better access to good quality fawning areas for females and more fawn hiding cover. The presence of numerous, rather than a few isolated shrubs may make fawn detection by predators more difficult, thereby allowing for higher fawn survival.

During the winter, males and females used shrub-grasslands more than expected. This is most likely due to the fact that forb abundance was decreasing, and the pronghorn were turning to browse for forage. The importance of browse for pronghorn during the winter has been documented by numerous authors (Hoover 1966, Bayless 1969, Mitchell and Smoliak 1971, Taylor 1972, Barrett 1980). In all these studies, browse made up at least 80% of the pronghorn winter diet. Hailey (1979) noted movements of pronghorn in winter to brushy areas in Texas. Beale and Smith (1970) contend that browse is required to sustain pronghorn during winters or droughts.

Although open juniper is considered suboptimal habitat for pronghorn, because visibility and mobility are reduced (Yoakum 1980), female pronghorn used open juniper shrublands during the spring and winter. Although these habitats increase risk of predation, Goldsmith (1989) found that pronghorn compensate for obstructed visibility and reduce the risk of predation by increasing vigilance. Pronghorn use of areas with taller vegetation in winter or early spring, when forb availability is low, has been documented in previous studies (Bayless 1969, Beale and Smith 1970, Sundstrom et al. 1973, Neff and Woolsey 1979, Barrett 1980). Dirschl (1963) found that pronghorn were concentrated during winter in areas where sagebrush and junipers provided evergreen forage for the animals. In northern Arizona, Gay (1984) found areas with taller vegetation to be winter and early spring feeding sites.

The female pronghorn in our study also used juniper shrublands during spring when fawning is occurring. The higher percentage of shrub cover may provide important fawning sites and hiding cover for developing fawns. Clemente et al. (1995) found that female pronghorn in southern New Mexico occupied mesquite vegetation classes, which would be considered suboptimal vegetation based on reduced visibility and mobility, in early spring and continued to occupy this type for 2-3 months coinciding with the fawning period.

Pronghorn typically inhabit open, gentle terrain because it provides enhanced visibility and mobility. Studies point out that the species is adapted to flat or undulating terrain of less than 20% slopes (Yoakum 1980, Kindschy et al. 1982). Pronghorn antelope in our study did not use slope classes equal to their availability. Male and female pronghorn avoided steep slopes (over 19%) during all seasons of the year. Female pronghorn preferred gentle slopes between 0 - 9% during all seasons. Males used both the gentle and intermediate slopes equal to their availability in all seasons, with the exception of summer when they favored the intermediate slopes, perhaps looking for cooler temperatures and shade from the intense summer sun.

No selection of aspect classes was detected for pronghorn during our spring season. During the summer season, pronghorn either selected for, or used as expected, the cooler northern exposures and avoided the hot and windy southern exposures. During winter, pronghorn selected the northeast aspect and avoided the southern aspects, again most likely avoiding the prevailing southwesterly winds.

SUMMARY AND MANAGEMENT RECOMMENDATIONS

We found that pronghorn in northern Arizona had larger than average home ranges, and displayed longer than average movements than reported in the literature. Most of the pronghorn had home ranges utilizing the grazed Babbitt (CO Bar) Ranch property and the ungrazed Wupatki National Monument, but focused use of these areas at different times of the year. During the winter, pronghorn utilized the Monument as often or more frequently than the CO Bar Ranch. However during spring and summer, animals were more common on the ranch property. The ranch had permanent water sources available to animals while the Monument had none. Ranch vegetation was predominately grassland while the Monument contained grasslands, shrub-grasslands and open juniper habitats. These two differences and the seasonal requirements of pronghorn can readily explain movements between the ranch and Monument that we observed.

It appears that pronghorn are utilizing the ranch as summer range in a large part due to the availability of free-standing water. However, they must also use the Monument for winter range, exploiting its browse habitats. Constructing permanent water sources in the National Monument, in areas frequented by the pronghorn, would likely reduce long range movements. This may also increase fawn survival, as shrub habitats needed for fawn hiding cover are more abundant on the Monument. In addition, pronghorn might stay in or nearer the Monument boundaries during the early fall hunting season and during the summer months, which would enhance visitor's enjoyment of the Monument and perhaps increase visitor knowledge and appreciation for this animal.

Management Implication

There are several water sources on the CO Bar Ranch that are inaccessible to pronghorn due to fencing. These fences could be modified to allow pronghorn access in order to increase numbers of available water sources. One tank, just north of the Wupatki boundary, if made accessible to pronghorn, would provide essential water much closer to areas of superior forage within the Monument.

The grazing status on National Forest lands south of Wupatki National Monument should be reviewed. Currently there are no cattle using this area and thus no need for the barbed wire fence along the southern park boundary. If it is determined that cattle may use this area in the future, the fence should be modified to pronghorn standards (as described by 0'Gara and Yoakum 1992) in order to enhance pronghorn movement.

Park resource managers should coordinate with highway planners to reduce the impacts of Highway 89 on pronghorn populations in this area. Removing, modifying, or moving the fence further back from the highway are possible options that should be examined in order to allow pronghorn movement between isolated herds on both sides of this highway. The use of underpasses and overpasses constructed to facilitate pronghorn crossing of roadways would be a preferred alternative. Although Ward et al. (1980) found that pronghorn did not use underpasses along I-80 in Wyoming, modifications such as widening an existing underpass to allow better visibility may prove successful to enhancing movement across Highway 89.

Other possible mitigation features that could be undertaken by the national park service in northern Arizona could be: (1) removing fences along rights-of-way; (2) expanding rights-of-way dimensions by placing fences further away from the transportation corridor (e.g., road or railroad), then modifying the fences to permit better movement of pronghorn between fenced areas; (3) relocating rights-of-way out of pronghorn habitat; (4) consider relocating animals, particularly to isolated areas where pronghorn have been extirpated; (5) providing permanent water sources in Wupatki and Sunset Crater NM; and, (6) provide signs on unfenced park roads warning visitors of wildlife movement corridors. Careful attention should also be given to preventing any fencing of presently unfenced roads.

The issues confronting national park areas in dealing with pronghorn management in northern Arizona, is only an indication of a much larger problem facing managers of protected areas around the world. If managers wish to have their protected areas function as species reservoirs (i.e., 'sources' instead of 'sinks'), they have to: 1) begin to forge active partnership with contiguous land owners to manage resources on an ecosystem basis; 2) then decide to what degree they are willing to allow active management to occur when their managed lands can not adequately support a species; and finally, 3) standardize (or partition) the degree of management among managers of all lands within each ecosystem.

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LITERATURE CITED

Autenrieth, R., (ed.). 1978. Guidelines for the management of pronghorn antelope. Proc. Pronghorn Antelope Workshop 8: 473-526.

Allen, A.W., J.G. Cook and M.J. Armbruster. 1984. Habitat suitability index models: Pronghorn. USDA Fish and Wildlife Service, FWS/OBS-82/10.65. Fort Collins, CO 22 pp.

Baker, T. 1953. Antelope movement and migration studies. Wyoming Wildlife 17: 31-36.

Barrett, M.W. 1980. Seasonal habitat associations of pronghorn in Alberta. Proceedings of the Pronghorn Antelope Workshop 9: 174-195.

Bateman, G.C. 1976. Natural Resource Survey and Analysis of Sunset Crater and Wupatki National Monuments. Office of Resource Management, Southwest Region, National Park Service.

Bayless, S.R. 1969. Winter food habits, range use and home range of antelope in western Montana. Journal of Wildlife Management 33: 105-118.

Beale, D.M. and R.C. Holmgren. 1975. Water requirements for antelope fawn survival and growth. Utah Department of Natural Resources Division Wildlife Federal Aid Project W-65-D23. Salt Lake City. 27 pp.

Beale, D.M. and A.D. Smith. 1970. Forage use, water consumption and productivity of pronghorn antelope in western Utah. Journal of Wildlife Management 34: 124-136.

Boyle, S.A. and A.W. Alldredge. 1984. Pronghorn summer distribution and water availability in the Red Desert, Wyoming. Proceedings of the Pronghorn Antelope Workshop 11: 103-104.

Buechner, H.K. 1950. Life history, ecology and range use of the pronghorn antelope in Trans-Pecos, Texas. American Midland Naturalist 43: 257-355.

Byers, C.R., R.K. Steinhorst and P.R. Krausman. 1984. Clarification of a technique for analysis of utilization-availability data. Journal of Wildlife Management 48: 1050-1053.

Canfield, R.H. 1941. Application of the line intercept method in sampling range vegetation. Journal of Forestry 39: 388-394.

Clemente, F., R. Valdez, J.L. Holechek, P.J. Zwank and M. Cardenas. 1995. Pronghorn home ranges relative to permanent water in southern New Mexico. The Southwestern Naturalist 40: 38-41.

Dirshcl, H. 1963. Food habits of pronghorn in Saskatchewan. Journal of Wildlife Management 21: 55-67.

Gay, S.M. 1984. Winter range forage availability and utilization of range forage by pronghorn (*Antilocapra americana*) near Anderson Mesa. M.S. Thesis, Northern Arizona Univ., Flagstaff, AZ. 164pp.

Goldsmith, A.E. 1989. Vigilance behavior of pronghorn in different habitats. Journal of Mammalogy 71: 460-462.

Hailey, T.L. 1979. A Handbook for pronghorn antelope management in Texas. Texas Parks Wildlife Department Federal Aid Wildlife Report Series 20, Austin. 59pp.

Hoover, R.L. 1966. Antelope food habits and range relationships in Colorado. Proceedings of Antelope States Workshop 2: 75-85.

Howard, V.W., S.L. Beasom, A.R. Lara and L. LaPlant. 1982. A preliminary evaluation of forage preferences for pronghorn in east central New Mexico. Proceedings of the Pronghorn Antelope Workshop 10: 86-105.

Kindschy, R., C. Sundstrom, and J, Yoakum. 1978. Range/wildlife interrelationships-pronghorn antelope. Proceedings of the Pronghorn Antelope Workshop 8: 216-269.

Kindschy, R., C. Sundstrom, and J, Yoakum. 1978. 1982. Wildlife habitats in managed rangelands—the Great Basin of southeastern Oregon: pronghorns. U.S. Forest Service General Technical Report PNW-145. 18pp.

Kitchen, D.W. 1974. Social Behavior and Ecology of the Pronghorn. Wildlife Monographs 38. The Wildlife Society, Washington, D.C. 96 pp.

Kitchen, D.W. and B.W. O'Gara. 1982. Pronghorn. Pages 960-971 *in* Wild Animals of North America (J.A. Chapman and G.A. Feldhamer eds.) John Hopkins Univ. Press. Baltimore, MA.

Koerth, B.H., L.J. Krysl, B.F. Sowell and F.C. Bryant. 1984. Estimating seasonal diet quality of pronghorn antelope from fecal analysis. Journal of Range Management 37: 560-564.

Lee, M.E. and D. Stephens. 1995. Anasazi cultural park study. Colorado Plateau Field Station Technical Report NPS/NAUCPFS/NRTR-95/07. 260pp.

McKelvey, K. 1997. TELEM: Unpublished software. Redwood Sciences Lab, Arcata, CA.

Mitchell, G.J. and S. Smoliak. 1971. Pronghorn antelope range characteristics and food habits in Alberta. Journal of Wildlife Management 35: 152-164.

Neff, D.J. 1986. Pronghorn habitat description and evaluation: a problem analysis report. Arizona Game and Fish Department Federal Aid Wildlife Restoration Project W-78-R Final Report Phoenix, AZ. 15pp.

Neff, D.J. and N. Woolsey. 1979. Effects of predation by coyotes on antelope fawn survival on Anderson Mesa. Arizona Game and Fish Department Special Report 8. Phoenix, AZ. 36 pp.

Nelson, E.W. 1925. Status of pronghorn antelope: 1922-1924. USDA Bulletin. 1346. Washington, D.C. 64pp.

Neu, C.W., C.R. Byers and J.M. Peek. 1974. A technique for analysis of utilization-availability data. Journal of Wildlife Management 38: 541-545.

Ockenfels, R.A. 1994. Factors affecting adult pronghorn mortality rates in central Arizona. Arizona Game and Fish Department Wildlife Digest 16. Phoenix, AZ.

Ockenfels, R.A., A.A. Alexander, C.L. Dorothy Ticer and W.K. Carrel. 1994. Home ranges, movement patterns and habitat selection of pronghorn in central Arizona. Arizona Game and Fish Department Technical Report 13. 80pp.

O'Gara, B.W. 1978. *Antilocapra americana*. Mammalian Species 90: 1-7.

O'Gara, B.W. and J.D. Yoakum. 1992. Pronghorn Management Guides. Proceedings of the Pronghorn Antelope Workshop 15 (Suppl.). 101pp.

Roebuck, C.M., C.D. Simpson and B.E. Dahl. 1982. Food habits and preference of pronghorn in three habitats of the Texas panhandle. Proceedings of the Pronghorn Antelope Workshop 10: 71-85.

Sundstrom, C. 1968. Water consumption by pronghorn antelope and distribution related to water in Wyoming's Red Desert. Proceedings Antelope States Workshop 3: 39-46.

Sundstrom, W.G. Hepworth and K.L. Diem. 1973. Abundance, distribution and food habits of the pronghorn. Wyoming Game and Fish Community Bulletin 12. Cheyenne, WY. 61pp.

Taylor, E.R. 1972. Food habits and feeding behavior of pronghorn in the Red Desert of Wyoming. Proceedings of the Antelope States Workshop 5: 211-299.

Tucker, R.D. and G.W. Garner. 1984. Home range and diel movements of pronghorn antelope fawns in Brewster County, Texas. Proceedings of the Pronghorn Antelope Workshop 11: 71-89.

van Riper III, C. and R.A. Ockenfels. 1998. The influence of transportation corridors on the movement of pronghorn antelope over a fragmented landscape in northern Arizona. Pages 241-248, *In*: Process of the 2nd International Conference Transactions and Wildlife Ecology. Ft. Meyers, FL, D. Zeigler (ed.).

Ward, A.L., N.E. Farnwalt, S.E. Henry, and R.A. Hodorff. 1980. Effects of highway operation practices and facilities on elk, mule deer and pronghorn antelope. Federal Highway Administration Report FHWA-RD-79-143. Washington. D.C. 48pp.

Whisler, L.S. 1984. Seasonal adaptations of pronghorn antelope to water deprivation. M.S. Thesis, University of Wyoming., Laramie, WY. 81pp.

White, G.C. and R.A. Garrot. 1990. Analysis of Radio Tracking Data. Academic Press Inc. San Diego, CA.

Willis, M.J., G.P. Keister and D.P. Sheehy. 1988. Pronghorn habitat selection in southeast Oregon. Proceedings of the Pronghorn Antelope Workshop 13pp.

Worton, B.J. 1989. Kernal methods for estimating the utilization distribution in home range studies. Ecology 70: 164-168.

Yoakum, J.D. 1974. Pronghorn habitat requirements for sagebrush grasslands. Proceedings of the Pronghorn Antelope Workshop 6: 16-24.

Yoakum, J.D. 1979. Managing rangelands for pronghorn. Rangelands 1: 146-148.

Yoakum, J.D. 1980. Habitat Management guides for the American pronghorn antelope. U.S. Bureau of Land Management Technical Note 347. Denver, CO. 78pp.

Mule Deer Demographic Responses to Select Climatic Variables in Arizona

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Abstract: To determine what effect climate has potentially had on recent demographic shifts and population declines of mule deer in Arizona, I studied the relationship of monthly precipitation and Palmer Drought Severity Index (PDSI) values with Arizona Game and Fish Department winter mule deer (*Odocoileus hemionus*) survey fawn:doe (FDR) and buck:doe (BDR) ratio data. Seven of 37 Game Management Units (GMUs) had no relationship between measured climatic variables and FDR, while 22 other GMUs had relationships with adjusted R^2 of < 0.350. Thirteen of 37 GMUs had no relationship between measured climatic variables and BDR, while 19 GMUs had relationships with adjusted R^2 of < 0.350. Pooling GMUs into similar habitats did not improve the modeled fit of relationships between demographic parameters and climatic variables. Habitats at climatic extremes (i.e., desertscrub and montane conifer habitats) demonstrated a predictable and superior model fit with FDR, more so than other habitats (i.e., Mohave desertscrub, chaparral and desertscrub, and grassland-woodland habitats), suggesting climate has a greater influence on recruitment in less moderate climates.

Statewide mule deer population estimates showed a relationship with PDSI data with an adjusted R^2 of 0.446. This apparent weak explanatory ability is probably the result of some combination of: (1) mule deer demographics responding to other confounding factors such as predation, habitat alterations or succession, or sport harvest, (2) climatic variation not driving population declines across Arizona, (3) other climatic variables, such as temperature, having a greater influence than precipitation or PDSI, (4) demographic parameters responding to a combination of climatic factors in addition to those I evaluated either directly or through vegetative influences (nutrition or cover), or (5) survey data is not accurately representative of the population. However, the explanation of 40-50% of the variation in statewide mule deer population numbers does suggest that climatic variables do have a strong influence in determining deer numbers throughout the state.

Key words: Arizona, climate, mule deer, *Odocoileus hemionus*, Palmer Drought Severity Index, precipitation.

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INTRODUCTION

Mule deer in Arizona have suffered population declines during the past two decades (Arizona Game and Fish Department, unpub. data). Resource managers have attributed much of this decline to either ultimate or proximate causal agents. In fact, the decline in mule deer numbers has occurred across the West, and the Western Association of Fish and Wildlife Agencies (WAFWA) established an ad hoc committee in June 1998 specifically to examine this phenomenon. At their initial meeting, this committee identified climatic changes as one of eight factors (climatic changes, habitat alterations or succession, nutrition, disease, competition, predation, sport harvest, or urbanization) that likely has had substantial influence on mule deer populations across the West (WAFWA Mule Deer Ad Hoc Committee, unpub. data). Connolly (1981*a*, *b*) identified similar putative causes for a West-wide decline in the 1960s and 1970s.

Various climatic factors influence ungulate populations. Precipitation in desert regions may influence mule deer productivity (Leopold and Krausman 1991, Smith and LeCount 1979) and movements (Kucera 1992, Rautenstrauch and Krausman 1989). Low temperature may influence habitat occupation, as certain habitats provide needed thermal cover (Parker and Gillingham 1990). High temperatures influence mule deer during summer, and deer respond by altering activity patterns (Leopold and Krausman 1987). Yet the impact of many climatic variables on ungulates is realized through vegetative influences on nutrition and carrying capacity (Feldhamer et al. 1989, Langvatn et al. 1996, Leopold and Krausman 1991, Smith and LeCount 1979). Winter snow accumulations can also dramatically influence survival (Mech et al. 1987, Picton 1984).

Because climate has the potential to influence mule deer populations, I studied climatic relationships in regard to demographic parameters measured routinely by the Arizona Game and Fish Department (AGFD). My objective was to compare mule deer demographic components with monthly precipitation data and Palmer Drought Severity Index (PDSI) (Palmer 1965), in an attempt to determine if these climatic variables had an influence on Arizona's mule deer population.

METHODS

The AGFD conducts winter deer surveys from ground (foot, vehicle, or horseback) or air (helicopter or fixed-wing) during winter (months of December and January). During these surveys, observers record the number of observed male, female, and young. Population estimates are then derived using annual buck:doe ratios (BDR), fawn:doe ratios (FDR), harvest estimates from mail out questionnaires, estimates of mean annual non-hunt mortality based on change-in-ratio estimates, and an initial estimate of the population size (Fig. 1). Sampling efforts were not equal among years. Consequently, I did not search for relationships in non-ratio data (raw counts) despite acknowledged inherent problems with ratio data (Atchley et al. 1976, Packard and Boardman 1988). I was also unable to separate survey data by technique.

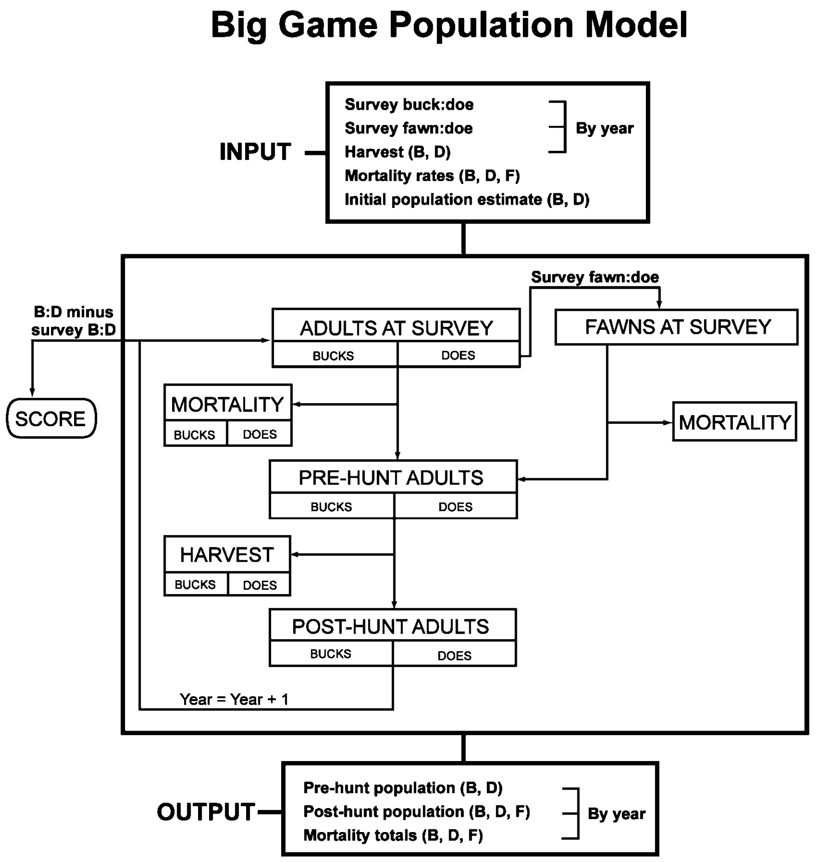

Figure 1. Conceptual framework of the Arizona Game and Fish Department model for estimating mule deer population numbers in Arizona.

I examined relationships between mule deer demographic parameters using data from the AGFD, and climatic variables from the National Oceanic and Atmospheric Administration data base. Specifically, I calculated FDR and BDR from AGFD winter surveys from 1957 to 1996. Monthly precipitation and Palmer Drought Severity Index (PDSI) data were taken from the most central and representative weather station of each individual GMU. I also included monthly weather data, including two years prior to mule deer surveys, to examine lag effects on populations. Because GMUs have been changed over the years, all surveys were pooled to the largest common unit (i.e., GMUs 1-10, 12, 13, 15-24, 27-45). I used these data in an exploratory, forward step-wise, multiple linear regression (*P* to enter = 0.05, *P* to remove = 0.10) analysis to determine which climatic factors best predicted mule deer demographic parameters and population responses.

Cluster analysis was used to group similar GMUs based on proportions of habitat associations (Brown et al. 1979). I then pooled mule deer observations across similar GMUs and recalculated FDR and BDR. Climatic data were averaged across similar GMUs. Each pooled group of GMUs with similar habitat was then reanalyzed using forward step-wise, multiple linear regressions.

Finally, I used statewide mule deer population estimates from 1970-1996 and climatic factors to examine larger scale relationships. For statewide climatic data, I averaged climatic data across the state. Again, I used forward step-wise multiple linear regression to evaluate this relationship. Because these analyses were exploratory in nature, I consciously ignored the potential for autocorrelation among climatic variables.

RESULTS

Monthly precipitation and PDSI values explained little of the variation in FDR and BDR data (Table 1). In addition, I found little consistency among GMUs in climatic factors that explained variation in demographic parameters. Seven of 37 GMUs demonstrated no relationship with FDR and weather variables. Adjusted R^2 on FDR models ranged from 0.148-0.562, although 22 models had adjusted $R^2<0.350$. Thirteen of 37 GMUs demonstrated no relationship with BDR and weather variables. Adjusted R^2 on BDR models ranged from 0.096-0.520, although 19 models had adjusted $R^2<0.350$ (Table 1).

Cluster analysis grouped GMUs into 5 categories: (1) montane conifer GMUs (1-14, 19, 23, 25-27), (2) Mohave desertscrub GMU (15), (3) chaparral and desertscrub GMUs (17, 18, 20-22, 24, 37), (4) grassland-woodland GMUs (28-36), and (5) desertscrub GMUs (16, 38-46) (Figs. 2 and 3). Multiple linear relationships from the analysis of pooled GMUs yielded dissimilar relationships among categories, with relatively low adjusted R^2 values. These relationships were generally dissimilar from many of the individual GMUs within each category (Table 2). The statewide mule deer population estimate was best described by greater PDSI values in the September before surveys and greater PDSI values in the October 2 years before surveys. The adjusted R^2 value for this relationship was 0.446.

DISCUSSION

Relatively little variation in mule deer population parameters measured by AGFD was explained by multiple linear relationships with monthly precipitation or PDSI values. Several possible explanations exist for this lack of explanation: (1) mule deer demographics are responding to other confounding factors such as predation, habitat alterations, or sport harvest, (2) climatic variation is not driving population declines across Arizona, (3) other climatic variables, such as temperature, might have a greater influence than precipitation or PDSI, (4) demographic parameters might respond to a combination of climatic factors in addition to those that I evaluated, either directly or through vegetative influences (e.g., nutrition or cover), or (5) survey data does not accurately represent the true mule deer population numbers.

Table 1. Significant climatic variables and adjusted R^2 values for multiple linear regression equations explaining fawn:doe ratios (FDR) and buck:doe ratios (BDR) in each Arizona Game Management Unit (GMU).

GMU	FDR[a]	R^2	BDR[a]	R^2
1	No relationship	--	+Oct ppt, +P Oct ppt., -P Oct PDSI	0.395
2	-Jul PDSI	0.235	-Jan ppt, -P Jan ppt	0.392
3	+Jul PDSI, -Aug PDSI	0.224	-PP Jan PDSI	0.108
4	-P Jun ppt	0.148	No relationship	--
5	-Feb ppt, -Sep ppt, +P Jul ppt	0.360	-Feb PDSI	0.164
6	+Jan PDSI, -Aug ppt, -Feb ppt, +PP Jan ppt	0.382	+P Aug ppt, -May PDSI	0.244
7	No relationship	--	+P Apr ppt, -Mar ppt, +P Aug PDSI	0.299
8	+Jul ppt, +P Jul ppt, +Nov PDSI, -P Dec ppt, -Mar ppt, -P Jun ppt	0.562	-P Aug PDSI	0.255
9	+Nov ppt, +P Apr ppt, +P May ppt	0.276	-Aug PDSI	0.236
10	-Feb ppt, -P Feb PDSI	0.319	No relationship	--
12	+P Dec PDSI, -Jan PDSI	0.246	-P Jul PDSI	0.116
13	+Dec ppt, +P Apr ppt	0.375	-Dec ppt, -P Oct PDSI	0.297
15	-P Jan ppt	0.171	+Jan ppt, +Feb ppt, +P Nov ppt, -Apr PDSI	0.520
16	+Nov PDSI, -P Jan ppt	0.342	+P Sep ppt	0.252
17	+Nov PDSI	0.171	No relationship	--
18	+P Jun ppt, -Mar PDSI	0.235	+P Dec ppt, -P Apr ppt, -May PDSI	0.319
19	+Jul ppt	0.136	-Feb ppt	0.150
20	+Jul ppt	0.083	No relationship	--
21	+Jul PDSI, -May PDSI	0.271	+Jul PDSI, -P Dec ppt	0.372
22	+Oct ppt, +P Dec ppt	0.217	-P Jul PDSI	0.183
23	+Sep ppt, +P Jun ppt, +P Jan PDSI, -Aug PDSI	0.392	No relationship	--
24	+Mar ppt, +P Apr ppt, +Jan PDSI, -Apr ppt, -May ppt, -P Aug ppt	0.554	No relationship	--
27	+Jul PDSI, +P Jul PDSI, -P Aug PDSI	0.297	+P Oct ppt, +P Nov ppt, -Jul PDSI	0.464
28	+Dec ppt, +P Apr ppt	0.278	No relationship	--
29	No relationship	--	+P Sep ppt	0.135
30	No relationship	--	-May ppt	0.126
31	+Oct ppt, -P Apr PDSI	0.153	No relationship	--
32	+Jan PDSI, -Aug ppt, -P Aug PDSI	0.329	No relationship	--
33	No relationship	--	-P Apr PDSI	0.205
34	No relationship	--	-Jan PDSI	0.127
35	+Aug ppt, +Sep PDSI	0.259	No relationship	--
36	-Oct ppt, -Apr ppt, -P Nov ppt, -P Apr ppt, -P Mar ppt	0.447	-Apr PDSI	0.254
37-38	+Oct ppt, -Jun ppt, -P Jul ppt, -P Apr ppt	0.370	+P Sep ppt	0.133
39-40	No relationship	--	No relationship	--
41	-Jan ppt, -P Sep ppt, -P Feb PDSI	0.341	No relationship	--
42	+Nov ppt, -P Mar PDSI	0.184	No relationship	--
43-44-45	-P May PDSI	0.159	+P Sep PDSI	0.096

[a] Abbreviations: ppt refers to precipitation, PDSI refers to Palmer Drought Severity Index, + refers to positive effect of factor, - refers to negative effect of factor, no modifier on month refers to data from during or immediately preceding the survey, P as a modifier on month refers to the year prior to the survey, and PP as a modifier on month refers to 2 years prior to the survey.

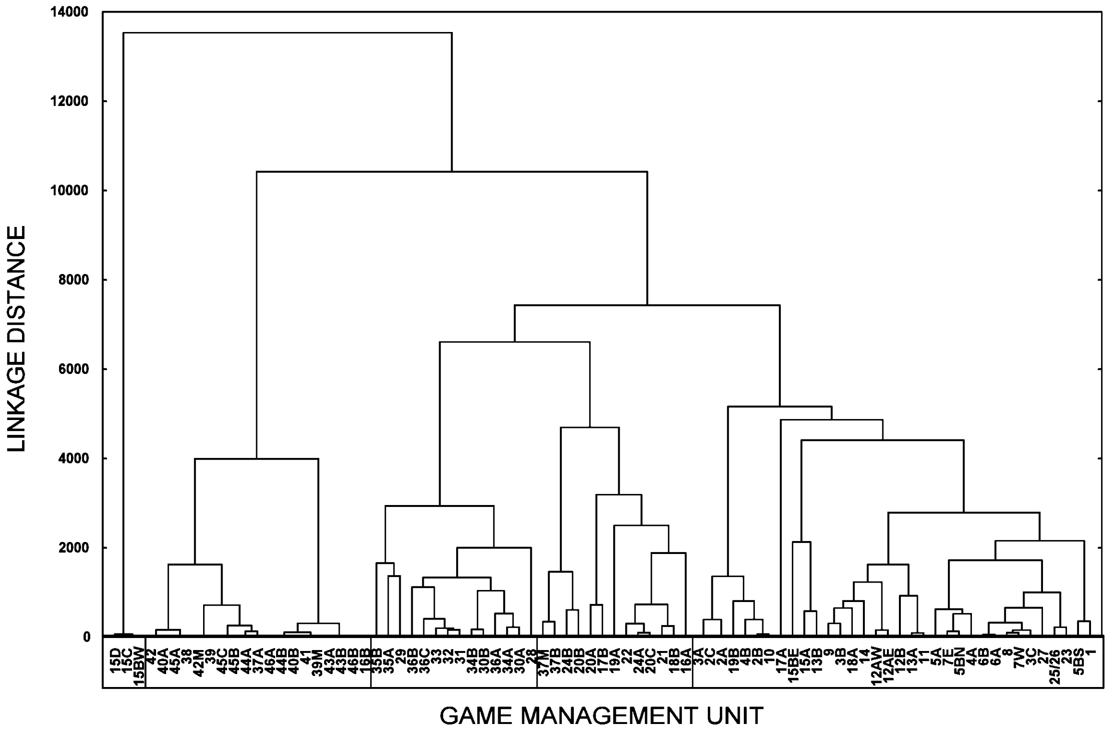

Figure 2. Cluster diagram of Arizona Game Management Units, based on similarities of habitat associations (Brown et al. 1979). Clusters (from left to right) are (1) Mohave desertscrub, (2) desertscrub, (3) grassland-woodland, (4) chaparrel and desertscrub, and (5) montane conifer habitats.

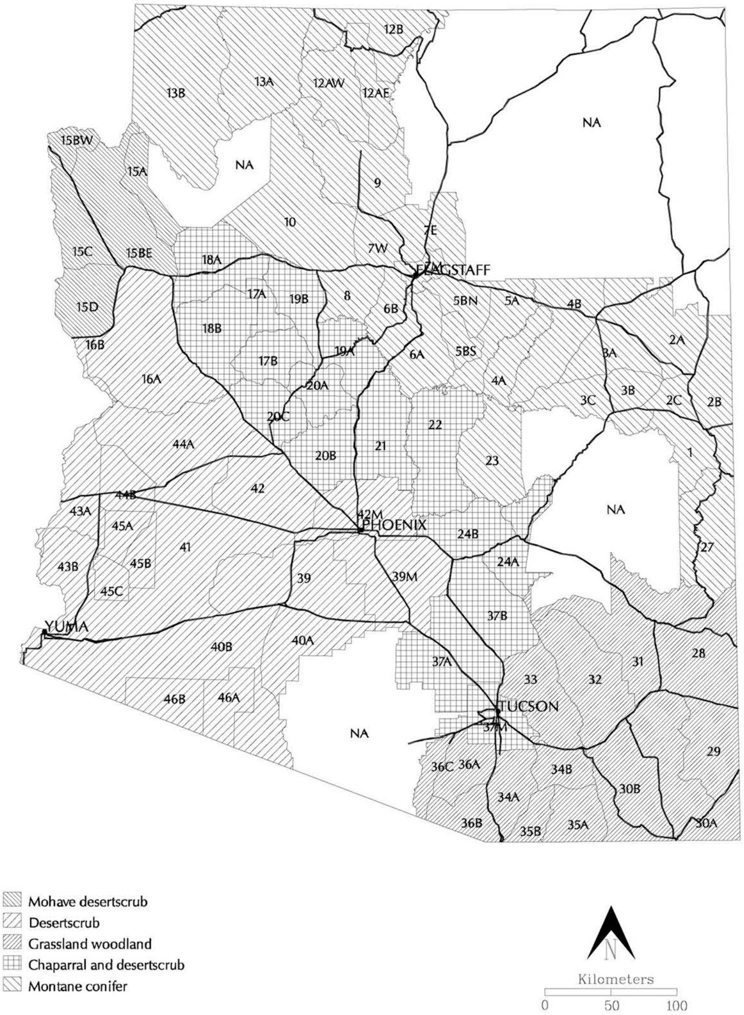

Figure 3. Arizona map indicating Game Management Units, pooled by cluster analysis, used in the evaluation of relationships among mule deer ratio and climatic data.

Mule deer populations, like most wildlife, probably respond both directly and indirectly to many climatic factors, although developing consistent predictive relationships across their occupied range is virtually impossible. However, PDSI may be an important factor influencing statewide mule deer populations. PDSI values can be more indicative of favorable conditions for forage growth and development of suitable fawn hiding cover. Precipitation may be favorable in some habitats, such as the warmer portion of the state, whereas it may be detrimental where snow accumu-

Table 2. Significant climatic variables and adjusted R^2 values for multiple linear regression equations explaining fawn:doe ratios (FDR) and buck:doe ratios (BDR) across similar Game Management Units in Arizona.

Category	FDR[a]	R^2	BDR[a]	R^2
Montane conifer	-Feb ppt, -Nov PDSI	0.312	-Jul PDSI, -P Jun PDSI	0.292
Mohave desertscrub	-P Jan ppt	0.171	+Jan ppt, +Feb ppt, +P Nov ppt, -Apr PDSI	0.520
Chaparral and desertscrub	-PP Jan PDSI	0.083	No relationship	—
Grassland-Woodland	+Dec PDSI, -P Jun PDSI	0.210	-Aug PDSI	0.115
Desertscrub	+Nov ppt, +Mar ppt, -P Feb PDSI, -P Jan PDSI	0.410	+P Sep ppt	0.092

[a] Abbreviations: ppt refers to precipitation, PDSI refers to Palmer Drought Severity Index, + refers to positive effect of factor, - refers to negative effect of factor, no modifier on month refers to data from during or immediately preceding the survey, P as a modifier on month refers to the year prior to the survey, and PP as a modifier on month refers to 2 years prior to the survey.

lations adversely impact mule deer populations. Rainfall in a given habitat is known to induce migration (Kucera 1992), whereas humidity may be the factor that induces movements in another habitat (McCullough 1964). In yet another ungulate species, increased rainfall can correlate with decreased population density (Latham et al. 1997). Each of these factors may be useful in understanding wildlife habitat relationships within a given community, however when applied to habitats beyond where the relationships were discovered, the relationships may be spurious. However, PDSI values may be better suited to indexing statewide populations.

Environmental relationships tend to be complex, although simple models may approximate our understanding of animal-environment relationships. Climatic variables, in addition to those I used in my evaluation, influence vegetative development, succession, nutritive quality, and cover components of the habitat (Singer et al. 1997, Post and Stenseth 1999). Mule deer densities in themselves have the potential to influence survival of young (Clutton-Brock et al. 1987). Prey densities influence predator densities, and ultimately habitat structure that both occupy. Neither habitat nor climate may be succinctly represented in a single, concise variable.

When examining population responses to climate, winter FDR may be a better variable than BDR because winter surveys occur after fall hunting seasons. Sport harvests influence BDR and may obscure, or be difficult to separate from, climatic effects. Yet, even with FDR, GMUs within each pooled habitat category did not exhibit consistent relationships among themselves or with pooled data sets.

Desertscrub habitats were favorably influenced by winter precipitation, probably for reasons elucidated by Smith and LeCount (1979). Similarly, decreased drought conditions and increased precipitation should create favorable forage and hiding cover within grassland-woodland and chaparral and desertscrub habitats. Conversely, explanations supporting the negative influence of winter precipitation in Mohave desertscrub are difficult to develop. Montane conifer habitats were negatively influenced by winter precipitation, presumably as a result of snow accumulations and resulting physiological stress. The superior fit of the regression models to the desertscrub and montane conifer habitats suggests that climate is more influential in determining FDRs within these potentially more extreme Arizona habitats.

Mule deer survey data may in itself be problematic, in that small sample sizes are not uncommon within GMUs, and misclassification of sex and age classes can substantially alter estimated ratios. The probability of misclassification can increase with observer inexperience, survey speed, distance, and inclement weather. However, explaining 40-50% of the variation within mule deer population estimates, using measured climatic variables, may be adequate for large-scale modeling. This is particulary true if climate is proven to have the largest influence on mule deer populations. Predation, habitat structure, and relation to carrying capacity may be unable to explain as much of the variation in Arizona's mule deer population as does the climatic variables that were analyzed in this paper.

ACKNOWLEDGEMENTS

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LITERATURE CITED

Atchley, W. R., C. T. Gaskins, and D. Anderson. 1976. Statistical properties of ratios. I. Empirical results. Systematic Zoology 25: 137-148.

Brown, D. E., C. H. Lowe, and C. P. Pase. 1979. A digitized classification system of the biotic communities of North America, with community (series) and association examples for the Southwest. Journal of the Arizona-Nevada Academy of Science 14 (supplement 1): 1-16.

Clutton-Brock, T. H., M. Major, S. D. Albon, and F. E. Guinness. 1987. Early development and population dynamics in red deer. I. Density dependent effects on juvenile survival. Journal of Animal Ecology 66: 53-67.

Connolly, G. E. 1981*a*. Trends in populations and harvest. Pages 225-244 *in* O. C. Wallmo, (ed.) Mule and black-tailed deer of North America. University of Nebraska Press, Lincoln.

Connolly, G. E. 1981*b*. Limiting factors and population regulation. Pages 245-286 *in* O.

C. Wallmo, (ed.) Mule and black-tailed deer of North America. University of Nebraska Press, Lincoln.

Feldhamer, G. A., T. P. Kilbane, and D. W. Sharp. 1989. Cumulative effect of winter on acorn yield and deer body weight. Journal of Wildlife Management 53: 292-295.

Kucera, T. E. 1992. Influences of sex and weather on migration of mule deer in California. Great Basin Naturalist 52: 122-130.

Langvatn, R., S. D. Albon, T. Burkey, and T. H. Clutton-Brock. 1996. Climate, plant phenology and variation in age of first reproduction in a temperate herbivore. Journal of Animal Ecology 65: 653-670.

Latham, J., B. W. Staines, and M. L. Gorman. Correlations of red (*Cervus elaphus*) and roe (*Capreolus capreolus*) deer densities in Scottish forests with environmental variables. Journal of the Zoological Society of London 242: 681-704.

Leopold, B. D., and P. R. Krausman. 1987. Diurnal activity patterns of desert mule deer in relation to temperature. Texas Journal of Science 39: 49-53

Leopold, B. D., and P. R. Krausman. 1991. Factors influencing desert mule deer distribution and productivity in southwestern Texas. Southwestern Naturalist 36: 67-74.

McCullough, D. R. 1964. Relationships of weather to migratory movements of black-tailed deer. Ecology 45: 249-256.

Mech, L. D., R. E. McRoberts, R. O. Peterson, and R. E. Page. 1987. Relationship of deer and moose populations to previous winters' snow. Journal of Animal Ecology 56: 615-627.

Packard, G. C., and T. J. Boardman. 1988. The misuse of ratios, indices, and percentages in ecophysiological research. Physiological Zoology 61: 1-9.

Palmer, W. C. 1965. Meterologic drought. U. S. Weather Bureau Research Paper 45. 48pp.

Parker, K. L., and M. P. Gillingham. 1990. Estimates of critical thermal environments for mule deer. Journal of Range Management 43: 73-81.

Picton, H. D. 1984. Climate and the prediction of reproduction of three ungulate species. Journal of Applied Ecology 21: 869-879.

Post, E., and N. C. Stenseth. 1999. Climatic variability, plant phenology, and northern ungulates. Ecology 80: 1322-1329.

Rautenstrauch, K. R., and P. R. Krausman. 1989. Influence of water availability and rainfall on movements of desert mule deer. Journal of Mammalogy 70: 197-201.

Singer, F. J., A. Harting, K. S. Symonds, and M. B. Coughenour. 1997. Density dependence, compensation, and environmental effects on elk calf mortality in Yellowstone National Park. Journal of Wildlife Management 61: 12-25.

Smith, R. H., and A. LeCount. 1979. Some factors affecting survival of desert mule deer fawns. Journal of Wildlife Management 43: 657-665.

Herpetofauna Survey of Petrified Forest National Park, Arizona

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Abstract. We present the results of an amphibian and reptile inventory conducted in 1997-1998 at Petrified Forest National Park. Using visual encounter surveys, pitfall trapping, artificial cover boards, and night driving techniques, we recorded 1,628 individual amphibians and reptiles (exclusive of larval amphibians) of 23 species. The species total includes seven amphibians, nine lizards, and seven snakes. Two of the lizard species (both of them whiptail lizards, genus *Cnemidophorus*) are new to the park. Small populations of the little striped whiptail are the first records for Petrified Forest, and also the first reported occurrences in Navajo and Apache counties. The New Mexico whiptail (probably introduced) is the first report for the state of Arizona. Petrified Forest National Park has a diverse herpetofauna, with species from varied biogeographic regions (Great Plains, Great Basin, and southern deserts and grasslands) occurring together in the park. The park is one of the few remaining large protected areas of grassland habitat on the southern Colorado Plateau, and supports regionally rare grassland amphibians and reptiles.

Key words: amphibians, reptiles, Petrified Forest National Park, Arizona, Little Colorado River basin, grasslands, inventory, habitat associations, biogeography.

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INTRODUCTION

Accurate inventory data, including information on the occurrence of plant and animal species, their distribution, abundance, and habitat relationships, is one of the essential starting points for informed protection and management of natural resources. In spite of long-standing policy (e.g. NPS-75; National Park Service 1992) and discussion on the importance of resource inventory, many National Park Service areas remain seriously deficient in even basic inventory data (e.g. Stohlgren and Quinn 1992). The need for baseline natural resource data is especially acute in areas and habitats that have been extensively disturbed, as is the case with grassland habitats on the southern Colorado Plateau (Kearney and Peebles 1960, Lowe 1964, Brown 1994).

Despite protecting a large area of native grassland and other habitats important to amphibians and reptiles, Petrified Forest National Park has never had a herpetofauna inventory. The grassland and grass-shrub habitats of the Petrified Forest area are known to support regionally rare species, such as Couch's spadefoot (*Scaphiopus couchii*) and the milk snake (*Lampropeltis triangulum*) (Stebbins 1985). For the southern Colorado Plateau region, there have been no previous intensive studies of grassland amphibian and reptile assemblages. The few published reports on amphibians and reptiles in the region only document species occurrence within a general area (e.g. Eaton 1935, Harris 1963).

The goal of this study was to conduct a complete species inventory (after Scott 1994) of amphibians and reptiles at Petrified Forest, compare sampling methods in grassland and grass/shrub habitats, and describe the herpetofauna in terms of relative abundance, habitat associations, and biogeography. In addition to providing inventory data to park resource managers, this study is important for its contribution to understanding the distribution and ecology of amphibians and reptiles in the region. Because Petrified Forest is both geologically and floristically characteristic of a large portion of the southern Colorado Plateau, and in particular of the Little Colorado River basin of northeastern Arizona, results of this study contribute to understanding the fauna of the wider geographic region.

METHODS

Study Area

Petrified Forest National Park is located on the south-central Colorado Plateau, straddling the border of Navajo and Apache counties east of Holbrook, Arizona (Fig. 1). The park encompasses 38,133 ha, and lies within the Little Colorado River basin. Elevations vary from 1,617 m along the Puerco River, which bisects the park, to 1,900 m at the summit of Pilot Rock in the extreme northwestern corner of the park (USGS 1981, 1982). Topographically, the park ranges from rolling, sandy grasslands to mesas and extensively eroded badlands.

Petrified Forest has warm summers and moderately cold winters. Average summer (July) high temperature is 33.6°C, with overnight lows averaging 15.6°C. In January, average daytime high temperature is 8.4°C, with an average low of -6.6°C. Mean annual precipitation is 24.4 cm, much of it coming in the form of monsoon

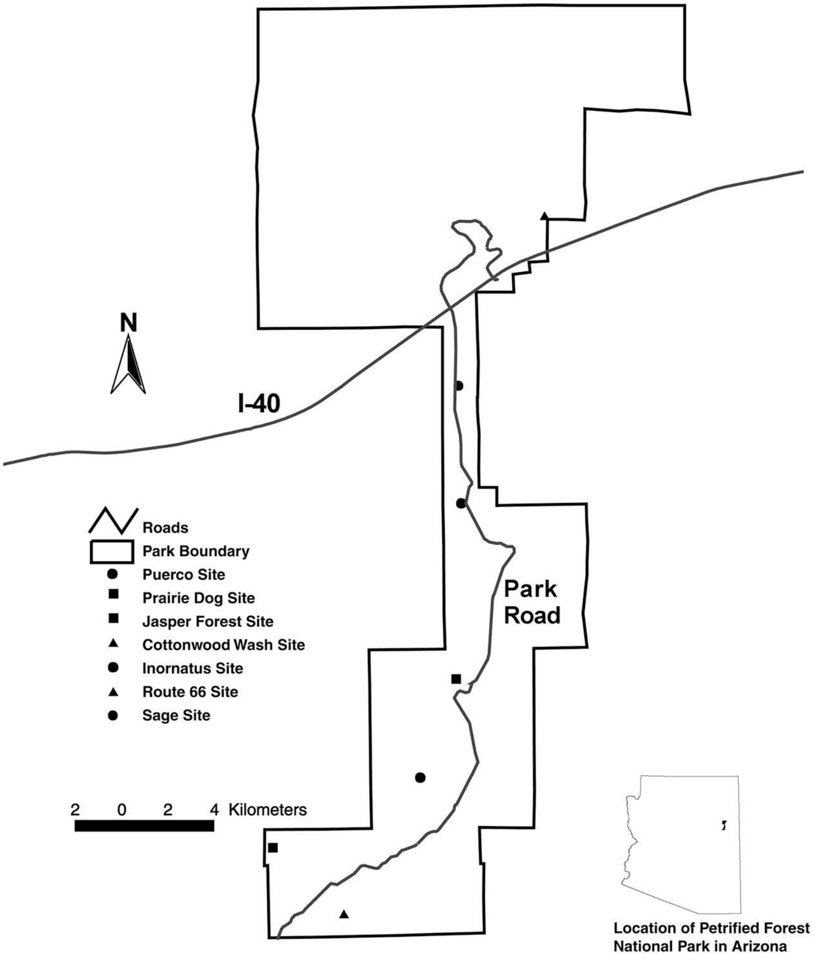

Figure 1. Outline map of Petrified Forest National Park, showing major roads and location of sampling sites during a herpetological inventory from May 1997 - September 1998.

thunderstorms in July-September. Spring and early summer are dry, and often extremely windy.

Petrified Forest lies within the Plains and Great Basin Grassland biome of Brown and Lowe (1980). Park vegetation is a complex interdigitation of arid grasslands, grass-shrublands, dune communities, and badlands and other barren habitats. Areas of juniper woodland and riparian trees and shrubs are limited in area, but add significantly to the park's biological diversity. For analysis of amphibian and reptile distribution, we recognized a number of broad vegetation types: grasslands, shrub communities (primarily shrub-grasslands), dune communities, riparian communities (Puerco River), and juniper woodland. Dominant and characteristic perennial plant species of these habitat types are described in Appendix 1. Two additional habitats for amphibians and reptiles – rocky areas (including rock outcrops and boulder fields) and developed areas – are not based on vegetation associations, but may support distinctive associations of amphibians and reptiles. We do not cover in detail badlands, desert pavement, and saline flats because of their limited amphibian and reptile fauna.

Field Methods

We used a variety of field survey methods at Petrified Forest during the spring, summer, and early fall, when amphibians and reptiles are most active. Sampling was initiated in July 1997 and completed in September 1998. We trapped amphibians and reptiles using four-liter (one gallon) pitfall traps (Fellers and Drost 1991), 19-liter (five gallon) pitfall arrays with drift fences (Campbell and Christman 1982, Jones 1986, Corn 1994), and artificial cover boards (Fellers and Drost 1994). We placed combinations of traps and cover boards at seven sites located in different habitats throughout the Park. A typical installation consisted of an array of four 19-l pitfall traps arranged in a 'Y' shape, with a metal flashing drift fence connecting the four traps (Jones 1986). The Y-array was paired with a 135 m transect of five 4-l pitfall traps, alternating with five cover boards, each measuring 60 cm x 120 cm x 2 cm (¾-inch plywood). Spacing between traps and boards was 15 m. We sampled trap sites twice a month. During each session, pitfalls and arrays were open (lids removed) for four consecutive nights, and checked at least every other day. Cover boards were checked once per sampling session.

We conducted night driving surveys (Mendelson and Jennings 1992, Rosen and Lowe 1994, Shaffer and Juterbock 1994) on the main park road, which runs the entire length of the Park from north to south (Fig. 1). Surveys generally consisted of driving the length of this road (45 km one way), but occasionally included other paved and unpaved roads. Start time of surveys varied from official sunset to about 10 p.m., with most surveys completed by 11 p.m. We completed at least eight night surveys each month, except in the early and late season, when amphibian and reptile activity was low.

Visual encounter surveys (VES; Crump and Scott 1994) were primarily used to survey for diurnal lizard species. We selected areas for these surveys that would sample the range of habitats and geographic regions within the Park, with particular attention being given to searching areas not sampled by other methods. For example, we did not extensively trap sites or conduct night drives in much of the northern section of the Park because of its remoteness as part of a large wilderness area. Time-constrained searches and general surveys comprised our VES. Time-constrained searches covered relatively small, predefined areas in single habitat types, each of which was searched for a period of about an hour. General surveys typically covered larger areas, were not restricted to single habitat types, and were not time-limited. These surveys were conducted in areas away from roads and away from our main sampling areas. All areas covered by visual encounter surveys were recorded on 1:24,000 scale maps, along with data on time, habitat, and species.

Besides these specific sampling methods, we also recorded data from general field observations, which included turning natural and artificial cover, animals seen on the park roads during the day, and observations of amphibians and reptiles during the course of other fieldwork. We also solicited observations from personnel working in the park, including National Park Service staff and other field researchers.

RESULTS

Sampling Effort

Distribution of sampling effort varied by month for the different sampling techniques (Table 1). Sampling effort for pitfall and array traps is measured in trap-days ((number of traps open) x (number of days they were open for)), and for artificial cover boards, number of times the boards were checked (i.e., turned to look for animals underneath). Sampling effort totaled 1,811 trap-days for 4-l pitfalls, 1,657 trap-days for 19-l array traps with drift fences, and 915 checks of artificial cover boards.

We spent 135 hours conducting visual encounter surveys, including general surveys and time-constrained searches (TCS). During the first year, we concentrated on general surveys of large areas of the park on foot, to provide a broad overview of the geographic extent of Petrified Forest National Park, and its range of habitats. Some of the more remote areas sampled by general surveys included Digger Wash and Pilot Rock in the northwest corner of the park, the area north of old Route 66 on the northeast park boundary, the Blue Mesa area along the park's eastern boundary, and the south Petrified Forest Wilderness area in the southeast corner of the park.

Table 1. Monthly sampling effort for a survey of amphibians and reptiles at Petrified Forest National Park, Arizona, between July 1997 and September 1998. Sampling effort for pitfall and drift fence arrays is recorded as trap-days, and sampling effort for cover boards is measured as number of times the boards were checked (see text). Effort for visual encounter surveys, including time-constrained searches (TCS) and general surveys, is measured in hours. Effort for night driving is number of km driven.

	Jul 97	Aug 97	Sep 97	Oct 97	May 98	Jun 98	Jul 98	Aug 98	Sep 98
Pitfall traps	0	55	199	0	320	320	319	469	159
Drift fence arrays	0	60	199	0	288	284	285	421	144
Cover boards	0	0	30	10	145	160	240	210	120
TCS	0.0	0.0	0.0	0.0	4.5	12.7	5.0	8.5	0.0
General survey	13.9	17.7	5.6	0.4	6.3	24.4	14.0	8.4	14.2
Night driving	222	968	1,022	142	87	713	628	1,161	625

TCS were initiated in the second year of the project. Just over 30 hours of time-constrained searches were conducted in 1998.

We began night drive surveys in July 1997, with a total of 2,354 km driven in 1997, mostly along the main north-south park road. We drove a total of 3,214 km from May through September of 1998, primarily along the main park road. Over the 2-year study period, total road survey sampling amounted to 5,567 km.

Amphibian and Reptile Diversity

We sighted or captured 1,628 individual amphibians and reptiles during this study, of 23 species. These included seven amphibians (one salamander and six spadefoot and true toads), nine lizards, and seven snakes (Table 2; nomenclature follows the federal interagency Integrated Taxonomic Information System or ITIS; see http://www.itis.usda.gov/access.html). We found all but one of these 23 spe-

Table 2. Amphibians and Reptiles of Petrified Forest National Park, based on an inventory study conducted in 1997 and 1998. Names follow ITIS (see text). Some familiar names have been changed recently, including: *Pituophis melanoleucus* changed to *P. catenifer*, and *Scaphiopus multiplicatus* and *Scaphiopus bombifrons* changed to *Spea multiplicata* and *Spea bombifrons*.

AMPHIBIANS

Salamanders

- Tiger Salamander (*Ambystoma tigrinum*)

Frogs and Toads

- Couch's Spadefoot (*Scaphiopus couchii*)
- Plains Spadefoot (*Spea bombifrons*)
- Southern Spadefoot (*Spea multiplicata*)
- Great Plains Toad (*Bufo cognatus*)
- Red-spotted Toad (*Bufo punctatus*)
- Woodhouse's Toad (*Bufo woodhousii*)

REPTILES

Lizards

- Collared Lizard (*Crotaphytus collaris*)
- Lesser Earless Lizard (*Holbrookia maculata*)
- Short-horned Lizard (*Phrynosoma douglasii*)
- Sagebrush Lizard (*Sceloporus graciosus*)
- Eastern Fence Lizard (*Sceloporus undulatus*)
- Side-blotched Lizard (*Uta stansburiana*)
- Little Striped Whiptail (*Cnemidophorus inornatus*)
- New Mexico Whiptail (*Cnemidophorus neomexicanus*)
- Plateau Striped Whiptail (*Cnemidophorus velox*)

Snakes

- Glossy Snake (*Arizona elegans*)
- Night Snake (*Hypsiglena torquata*)
- Common Kingsnake (*Lampropeltis getula*)
- Milk Snake (*Lampropeltis triangulum*)
- Striped Whipsnake (*Masticophis taeniatus*)
- Gopher Snake (*Pituophis catenifer*)
- Western Rattlesnake (*Crotalus viridis*)

cies in the first month and a half of field work, by mid-August 1997. The last species found was the New Mexico whiptail (*Cnemidophorus neomexicanus*), which has a very restricted distribution in the park. This species was first discovered early in the second year, in mid-June 1998. The little striped whiptail (*Cnemidophorus inornatus*) and the New Mexico whiptail represent first reports of these species in the Petrified Forest region, and the occurrence of the New Mexico whiptail at Petrified Forest is the first record of that species anywhere in the state of Arizona (Persons and Wright 1999a; Fig. 2).

Comparison of Methods

The different field techniques used in this study varied widely in their effective-

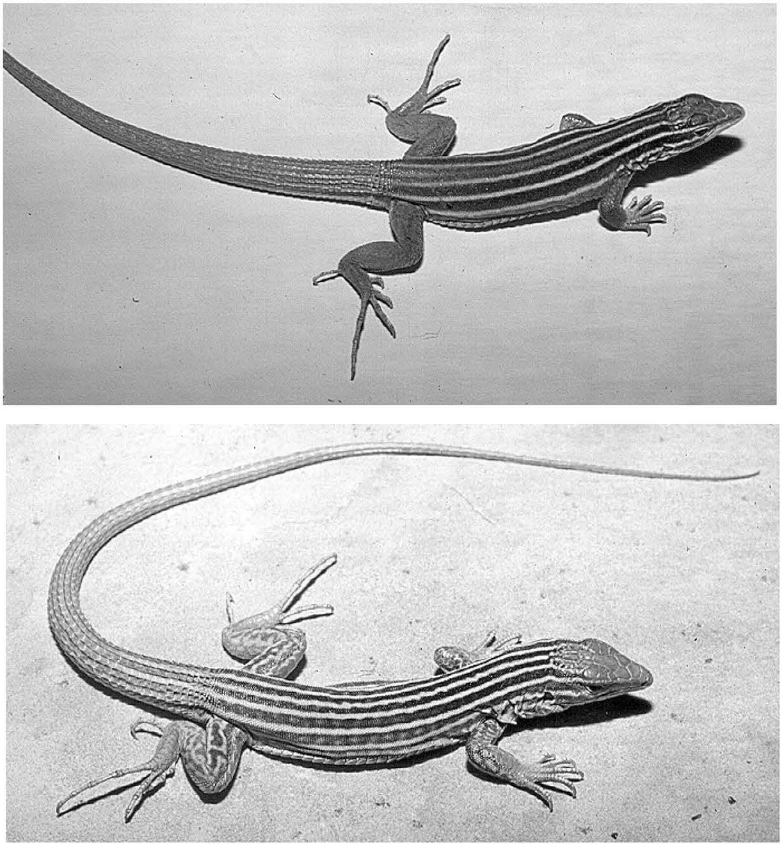

Figure 2. *Cnemidophorus inornatus* (above), and *C. neomexicanus* (below), two additions to the known herpetofauna of Petrified Forest National Park and the surrounding region (photos by T. B. Persons).

ness in sampling different species of amphibians and reptiles (Table 3). In general, lizards were most effectively sampled by pitfall and array trapping and cover boards, and by visual encounter surveys (time-constrained searches and general surveys). Moderate numbers of some amphibian species were captured in array traps, though the highest numbers of all species were recorded during night driving surveys. Except for the striped whipsnake (*Masticophis taeniatus*), nearly all of the snakes were

Table 3. Comparison of capture totals of different amphibian and reptile sampling methods at Petrified Forest National Park in 1997 and 1998. Methods and sampling effort are as listed in Table 1. Number of species and total number of individuals accounted for with each sampling method are listed for amphibians, lizards, and snakes. Animals not identified to species (e.g., *Spea* sp.) are not listed in the species total, unless they were the only members of that taxon recorded.

	Pitfall	**Array**	**Cover**	**TCS**	**General**	**Night**
Tiger Salamander	0	1	0	0	0	5
Couch's Spadefoot	0	1	0	0	0	24
Plains Spadefoot	1	14	0	0	0	53
New Mexico Spadefoot	0	30	0	0	1	191
Spadefoot, *Spea* species	0	8	0	2	7	1
Great Plains Toad	0	8	1	0	2	70
Red-spotted Toad	0	0	0	0	0	12
Woodhouse's Toad	0	0	0	0	0	3
Amphibian species:	**1**	**5**	**1**	**1**	**2**	**7**
Total amphibians:	**1**	**62**	**1**	**2**	**10**	**359**
Collared Lizard	2	5	8	9	23	2
Lesser Earless Lizard	0	7	3	4	22	4
Short-horned Lizard	0	0	3	1	2	2
Sagebrush Lizard	31	45	41	1	19	0
Eastern Fence Lizard	3	9	8	30	125	0
Fence Lizards, *Sceloporus* sp.	0	0	2	1	15	0
Side-blotched Lizard	1	1	7	15	8	0
Little Striped Whiptail	0	0	0	0	11	0
New Mexico Whiptail	0	0	0	0	5	0
Plateau Striped Whiptail	26	28	2	32	186	0
Whiptails, *Cnemidophorus* sp.	0	0	0	8	8	0
Lizard species:	**5**	**6**	**7**	**7**	**9**	**3**
Total lizards:	**63**	**95**	**74**	**101**	**424**	**8**
Glossy Snake	0	0	0	0	0	15
Night Snake	0	0	0	0	0	33
Common Kingsnake	0	0	0	1	2	6
Milk Snake	0	0	0	0	0	7
Striped Whipsnake	0	1	0	0	2	2
Gopher Snake	0	0	0	1	2	47
Western Rattlesnake	0	0	0	0	0	28
Snake species:	**0**	**1**	**0**	**2**	**3**	**7**
Total snakes:	**0**	**1**	**0**	**2**	**6**	**138**
Total species:	**6**	**13**	**9**	**12**	**17**	**18**
Total numbers:	**64**	**158**	**75**	**105**	**440**	**505**

found during night driving surveys. Species recorded only during night driving surveys included the red-spotted (*Bufo punctatus*) and Woodhouse's toad (*B. woodhousii*), and glossy snake (*Arizona elegans*), night snake (*Hypsiglena torquata*), and milk snake (*Lampropeltis triangulum*). No other species were detected with only one sampling method, except for the isolated populations of little striped whiptail and New Mexico whiptail, which were only encountered during general surveys.

Small (4-1) pitfall traps, drift fence arrays with large (19 l) pitfall traps, and artificial cover boards were all set out in the same areas, and generally sampled the same fauna. The arrays were much more effective in sampling amphibians, however (Table 3), presumably because the drift fences intercepted individuals moving from place to place. Artificial cover boards were about as effective as array traps for lizards, capturing as many or more individuals of all species except plateau striped whiptail, and recording one species not captured in the arrays (short-horned lizard, *Phrynosoma douglasii*). For approximately equal effort, the 4-l pitfall traps were less effective than arrays or cover boards, capturing fewer species and fewer individuals.

Habitat and abundance

Table 4 lists capture data for the most common species captured at each of the pitfall/array/coverboard sampling sites at Petrified Forest, and Figure 3 shows "capture" (i.e., encounter) rates for the most common species recorded on visual encounter surveys (combined time-constrained searches and general surveys). Both data sets are grouped into habitats as grassland, shrubland, sand/shrub habitat, rock habitat (rocky cliffs and slopes, boulder fields), and riparian habitat. Capture rates varied among the different grassland sampling sites, probably due to wide variation in height and density of grass in the different areas. Jasper Forest and the Prairie Dog

Table 4. Capture rates of amphibians and reptiles at pitfall and drift fence array sites at Petrified Forest National Park, Arizona, in 1997-98. Rates are captures per 1,000 trap-nights (see text). Site codes are: COWA-Cottonwood Wash; INOR-Inornatus; JAFO-Jasper Forest; PRDO-Prairie Dog; PUER-Puerco River; RT66-Route 66; and SAGE-Sagebrush. Habitat at the site is in parentheses below the site code. For some sites, a secondary habitat is listed after the first, "main" habitat (e.g. Grass/Rock).

	JAFO (Grass/Rock)	PRDO (Short grass)	RT66 (Tall grass)	SAGE (Shrub)	COWA (Sand/Shrub)	INOR (Rock)	PUER (Riparian)
Plains Spadefoot	0.0	0.0	0.0	2.1	13.2	0.0	4.7
Southern Spadefoot	0.0	5.6	8.3	1.0	17.6	2.8	33.0
Collared Lizard	0.0	0.0	0.0	1.0	2.2	11.1	0.0
Lesser Earless Lizard	0.0	16.7	2.8	0.0	0.0	0.0	0.0
Sagebrush Lizard	0.0	5.6	0.0	48.5	28.7	2.8	0.0
Eastern Fence Lizard	2.8	0.0	0.0	0.0	3.3	0.0	37.7
Side-blotched Lizard	5.6	0.0	0.0	0.0	0.0	0.0	0.0
Plateau Striped Whiptail	2.8	0.0	0.0	23.7	29.8	5.6	4.7

site are relatively open areas of short grass, while the Route 66 site has much taller, denser grassland. In addition, Jasper Forest has scattered surface rocks, and the presence of extensive burrows at the Prairie Dog site may be important to existing amphibian and reptile populations. Among all of the grassland sites, lesser earless lizard (*Holbrookia maculata*) at the Prairie Dog site had the highest capture rate (Table 4). For visual encounter surveys in grassland, the highest encounter rates were for plateau striped whiptail (*Cnemidophorus velox*), followed by lesser earless lizard (Fig. 3).

At the Sagebrush sampling site, sagebrush lizards (*Sceloporus graciosus*) had the highest capture rate, followed by plateau striped whiptails. The same two species were most numerous in visual encounter surveys in shrub habitats. The Cottonwood Wash sampling site, in deep sand with scattered shrubs in the southern part of the park, was the most productive trapping site at Petrified Forest. We captured four lizard species and two spadefoot toad species at the site, with nearly equal numbers of plateau striped whiptails and sagebrush lizards. In visual encounter surveys in old dune and other sand substrate habitats, plateau striped whiptails and lesser earless lizards were encountered most frequently, and eastern fence lizards (*Sceloporus undulatus*) were somewhat less common.

Collared lizards were captured most often in the rock habitat sampling site, while eastern fence lizards were most numerous in visual encounter surveys in rock habitats, followed by plateau striped whiptails and collared lizards. At the riparian sampling site, eastern fence lizards and southern spadefoots (*Spea multiplicata*) were the most common captures, while plateau striped whiptails were numerous in visual encounter surveys in riparian habitat (the highest numbers of any species we recorded in any habitat), and eastern fence lizards were also common.

DISCUSSION

Sampling Effort

We conducted fieldwork at Petrified Forest for one week every other week, so that sampling was spread uniformly across the active period for amphibians and reptiles, with approximately two sampling sessions per month. Except for the project start-up period, sampling effort was consistent across months (Table 1). Sampling effort for visual encounter surveys and night driving surveys was more variable, with effort concentrated during the times when observed amphibian and reptile activity was greatest (Table 5). In particular, night-time temperatures in May and June at Petrified Forest are relatively cold, and we observed very little activity at night, so we concentrated night driving sampling effort in the warmer months, from July through September. This also corresponded to the general time period of monsoon rains at Petrified Forest, which markedly increased amphibian activity.

Amphibian and Reptile Diversity

Petrified Forest has moderate numbers of amphibian and reptile species, and is of particular interest for its grassland species. Noteworthy aspects of the fauna include three species of spadefoot toads: the plains spadefoot, which is near the western extent of its range in the Petrified Forest area; the New Mexico spadefoot;

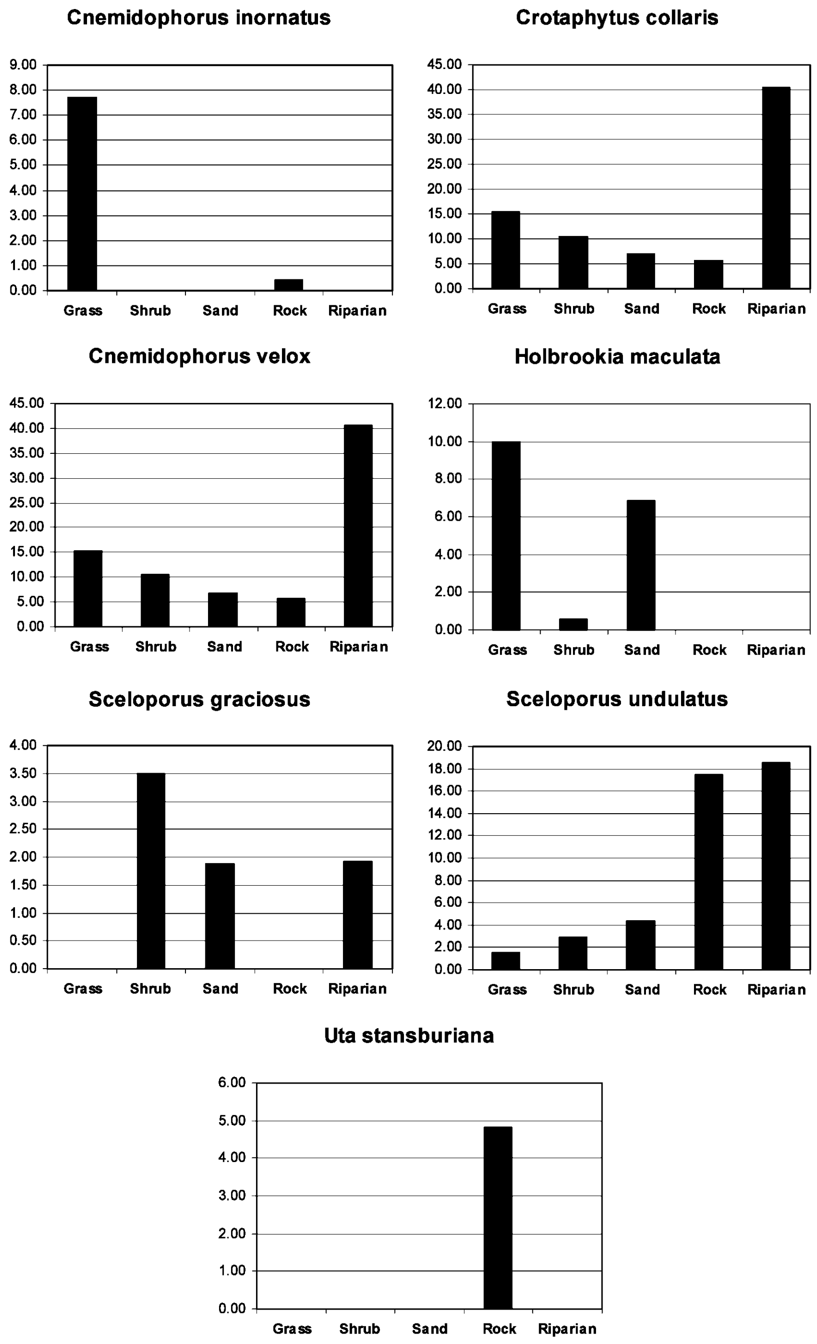

Figure 3. Encounter rates, by habitat, of lizard species at Petrified Forest National Park, in visual encounter surveys conducted in 1997 and 1998. Numbers are individuals seen per 10 hours search time.

Table 5. Night drive sampling of amphibians and reptiles at Petrified Forest National Park, by month and year, in 1997-1998. Distance driven varied among different months, so data have been adjusted to number of individuals per 1,000 km of driving.

	1997				1998				
SPECIES	**JUL**	**AUG**	**SEP**	**OCT**	**MAY**	**JUN**	**JUL**	**AUG**	**SEP**
Tiger salamander	0.0	1.0	1.0	7.0	0.0	0.0	1.6	0.9	0.0
Total:	**0.0**	**1.0**	**1.0**	**7.0**	**0.0**	**0.0**	**1.6**	**0.9**	**0.0**
Plains spadefoot	9.0	6.2	2.0	0.0	0.0	0.0	49.4	9.5	1.6
Couch's spadefoot	0.0	2.1	1.0	0.0	0.0	0.0	27.1	3.4	0.0
New Mexico spadefoot	99.1	10.3	10.8	21.1	0.0	0.0	189.5	12.9	17.6
Great Plains toad	36.0	13.4	4.9	7.0	0.0	0.0	38.2	15.5	1.6
Red-spotted toad	18.0	2.1	0.0	0.0	0.0	0.0	6.4	0.9	1.6
Woodhouse's toad	0.0	0.0	1.0	0.0	0.0	0.0	1.6	0.9	0.0
Total:	**162.2**	**34.1**	**20.5**	**28.2**	**0.0**	**0.0**	**313.7**	**43.9**	**22.4**
Glossy snake	0.0	4.1	2.9	0.0	0.0	2.8	1.6	0.9	6.4
Night snake	9.0	8.3	4.9	7.0	11.5	7.0	8.0	4.3	1.6
Common kingsnake	0.0	3.1	0.0	0.0	0.0	0.0	0.0	0.9	3.2
Milk snake	0.0	4.1	0.0	0.0	0.0	0.0	0.0	1.7	1.6
Striped whipsnake	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.9	1.6
Gopher snake	4.5	8.3	14.7	28.2	0.0	0.0	1.6	5.2	19.2
Western rattlesnake	9.0	6.2	7.8	14.1	0.0	1.4	1.6	5.2	3.2
Total:	**22.5**	**34.1**	**31.3**	**49.3**	**11.5**	**11.2**	**12.7**	**18.9**	**36.8**

and the Couch's spadefoot, which occurs as a disjunct population at Petrified Forest, well north of the main part of the species' range in Arizona. Also of note are three species of whiptail lizards. One of these (the little striped whiptail) is bisexual, while the other two (plateau striped whiptail and New Mexico whiptail) are unisexual and reproduce by parthenogenesis. Only the plateau striped whiptail was known from Petrified Forest or the northeastern Arizona area prior to our study. The little striped whiptail was probably once more widespread in the region, as it has declined in other parts of its range where grassland habitats have been lost or degraded (Bogan et al. 1998, Wright and Lowe 1965, 1968). The two small populations that we found at Petrified Forest are the only ones known from Apache and Navajo Counties in northeastern Arizona, and are separated from the nearest other populations by a distance of approximately 107 km (Persons and Wright 1999b).

The small population of New Mexico whiptails along the Puerco River floodplain within Petrified Forest is far west of the species' range along the Rio Grande drainage in New Mexico (Persons and Wright 1999a). Skin-grafting studies indicate that the lizards at Petrified Forest are genetically identical to populations in New Mexico (Persons and Wright, in prep.). Since the New Mexico whiptail is parthenogenetic, the population at Petrified Forest could have arisen from a single individual transported on the Atchison-Topeka and Santa Fe railroad (an east-west line that runs just north of the Puerco River through the park), or escaped from a vehicle

(Interstate Highway 40 links Petrified Forest with the heart of the New Mexico whiptail's range in central New Mexico).

From a conservation standpoint, the population of milk snakes at Petrified Forest is of interest. This small snake is very rare in the state of Arizona, known from only a few restricted locations scattered across the state. As with some of the other amphibians and reptiles at Petrified Forest, the occurrence of the milk snake at this location may be linked to the isolated area of healthy grassland protected within the park. This species and the little striped whiptail stand out as the two rarest and most restricted species protected within Petrified Forest National Park.

Completeness of Inventory

That this study resulted in a nearly complete species inventory is supported by the fact that 22 of the 23 species documented (96%) were found after the first month and a half of field work, with varied field methods, intensive sampling effort, and extensive geographic coverage of the park. While there are a few additional species that could possibly occur at Petrified Forest (e.g., the many-lined skink, *Eumeces multivirgatus*, in the Puerco River floodplain, and the secretive southwestern black-headed snake, *Tantilla hobartsmithi*), only one species seems likely to have been missed during our surveys. The northern leopard lizard, *Gambelia wislizenii*, is known to occur in the general region of Petrified Forest (Stebbins 1985), and has been seen by one of us (TBP) 8 km west of the park boundary, in contiguous habitat (Puerco River flood plain). If this species occurs in the park, it is evidently rare and locally distributed. We surveyed many areas of suitable open shrub and shrub-grassland habitat, and found only the related collared lizard, a species usually associated with rocky situations.

Comparison of Methods

To be most meaningful, comparisons of survey methods should include measures of cost. This provides a standard basis for comparison, and also reflects the fact that most surveys are conducted under limited budgets. The most expensive component of any survey is typically personnel time (e.g., Burbidge 1991), and that is particularly true of the observer-intensive methods used in this survey. For each sampling method, we recorded the amount of time that field personnel were actively engaged in that sampling method. We spent approximately 137 person-hours of effort on pitfall/array/coverboard sampling sites (including 25 hours for installation of the traps and boards), 136 hours on visual encounter surveys (combined time-constrained searches and general surveys), and 182 hours on night-driving surveys. If travel time to and from sampling sites is added in for pitfall/array/coverboard and visual encounter surveys (we did not record this precisely, because we were frequently engaged in more than one activity at a time), the amount of time we spent on the different methods is relatively close, with a slight bias toward night-driving.

Of the survey methods we used for amphibians and reptiles at Petrified Forest, the two most effective were visual encounter surveys and night driving. Night driving was by far the most effective method for amphibians and snakes (Table 3). Night driving surveys found all of the seven species of amphibians that we documented at Petrified Forest, including two (red-spotted toad and Woodhouse's toad) that were not found with any other survey technique. Likewise, night driving recorded nearly five times as many individuals as all of the other techniques combined. The only other method that captured appreciable numbers of amphibians was drift fence arrays, in which we captured five amphibian species and just over 60 individuals. We recorded more individuals of each amphibian species during night-driving surveys than we did with all other methods combined.

The significant advantage of night-driving surveys for snakes was even more pronounced. Again, all seven species of snakes that we documented at Petrified Forest were recorded on night drives, including road-killed individuals of the diurnal striped whipsnake. By comparison, all other methods combined recorded only three snake species (Table 3). In terms of numbers of animals, we recorded 138 individual snakes on night drives, compared to a total of nine with all other methods combined.

Visual encounter surveys (combining time-constrained searches and general surveys) were most effective for lizards (Table 3). VES documented all nine lizard species known from Petrified Forest National Park, including two (little striped whiptail and New Mexico whiptail) that were not found with any other method. The drift fence/pitfall arrays and artificial coverboards provided comparable or better results for two relatively secretive species (the short-horned lizard and sagebrush lizard), but for most species we recorded substantially higher numbers of individuals during visual encounter surveys. This was especially true for the conspicuous, active, and wide-ranging whiptail lizards.

Besides their effectiveness for survey purposes, a significant advantage of visual surveys is that they have almost no other associated cost, compared to the significant materials cost and installation and maintenance time required for pitfalls, drift fences, and coverboards. However, there are problems associated with visual encounter surveys that must be taken into account. Because most animals observed are not caught, some individuals may be misidentified, or individuals may not be identified to species level (e.g., *Sceloporus* sp. and *Cnemidophorus* sp. in Table 3). With adequate training and experience, this should not be a serious problem for inventory purposes. More serious, if one wishes to quantify numbers of different species, is observer bias. This is a notorious problem with visual surveys (e.g., McDonald 1981), and extends both to differences among observers in the numbers of animals seen, and also (in unconstrained general surveys) to differences in the areas that different observers choose to focus their search efforts.

Habitat and Abundance

Sampling methods that we used for amphibians and reptiles at Petrified Forest provide information on relative abundance, but the different methods have their own distinct biases. Inferences about relative abundance are strongest when different sampling methods yield the same rank order of species. Night driving provided the most extensive information on amphibians and snakes. For amphibians, rank abundance of the different species was similar between night driving and drift-fence arrays (the only other method that yielded appreciable numbers of amphibians; Table 3). New Mexico spadefoots were the most abundant species encountered, followed by either Great Plains toad (night driving) or plains spadefoot (arrays). For snakes, no other method yielded more than six individuals, so night-driving data are the only yardstick that we have for species abundance. The four most numerous snakes encountered on night drives were, in order: gopher snake; night snake; western rattlesnake; and glossy snake. Relative abundance information from night driving has the important caveat that we do not know the propensity of different species to move onto the road, or to remain on the road for extended periods of time (one evident bias is that small, dark species such as the night snake are more likely to be overlooked than larger, lighter-colored species). Still, with appropriate caution in interpreting results, our night-driving data provides a good basis of comparison for future night-driving surveys. Night-driving surveys were not stratified by habitat, so we cannot discuss habitat associations for amphibians and snakes.

Our VES provided the most extensive data for lizards, but a comparison with data from trapping methods (pitfalls, drift fence arrays, and artificial cover) showed a conspicuous difference for the sagebrush lizard. Otherwise, VES and trapping yielded the same rank abundance. For VES this was, in order: plateau striped whiptail; eastern fence lizard; collared lizard; lesser earless lizard; and sagebrush lizard.

We broke down the data from VES and trapping by habitat (Table 4 and Fig. 3), and all species showed pronounced patterns of abundance in relation to habitat. Plateau striped whiptail, eastern fence lizard, and collared lizard had broad distributions across habitats, while side-blotched lizard was quite restricted. There were evident differences in abundance between the two methods, primarily for sagebrush lizard and plateau striped whiptail (Table 6).

Table 6. Most numerous amphibian and reptile species recorded by trapping methods (including pitfall traps, drift fence arrays, and artificial cover) and visual encounter surveys in different major habitats at Petrified Forest National Park in 1997-98. See also Table 4 and Figure 3.

	Trapping	VES
Grass	Lesser earless lizard, Southern spadefoot	Plateau striped whiptail, Lesser earless lizard
Shrub	Sagebrush lizard, Plateau striped whiptail	Plateau striped whiptail, Sagebrush lizard
Sand	Plateau striped whiptail, Sagebrush lizard	Lesser earless lizard, Plateau striped whiptail
Rock	Collared lizard	Eastern fence lizard, Plateau striped whiptail
Riparian	Eastern Fence Lizard, Southern spadefoot	Plateau striped whiptail, Eastern fence lizard

Biogeography

Northeastern Arizona, including Petrified Forest, lies within a broad area of overlap of Great Basin and Great Plains biotic communities (Brown 1994). In addition, the region incorporates habitat elements derived from grasslands and deserts more characteristic of southern Arizona and northern Mexico. This mixing of biogeographic elements is reflected in the park's herpetofauna. The 23 species that we recorded can be categorized as having the main part of their range in either the Great Basin, Great Plains, the desert and grassland regions of the Southwest, eastern North America, or some combination of these (Table 7; Stebbins 1985). Species with more southern ranges dominate the fauna, while species characteristic of the Great Basin (sagebrush lizard), Great Plains (plains spadefoot), and eastern U.S. (milk snake) are near the limits of their range. Two of the species listed under "Other" in Table 7 have unique distributions: the New Mexico whiptail lizard is likely introduced (Persons

Table 7. Biogeographic patterns of the amphibian and reptile fauna of Petrified Forest National Park, Arizona. Species are categorized as occurring primarily in the Great Basin, Great Plains, southern deserts and grasslands, or eastern North America. Species listed as "other" have distributions that are widespread in western North America (tiger salamander, short-horned lizard, gopher snake, western rattlesnake), more restricted (Plateau Striped Whiptail on the southern Colorado Plateau), or probably introduced in the Park (New Mexico Whiptail). Species with distributions that are distinctly associated with two different areas are noted in both columns.

Species	Great Basin	Plains	Southern	Eastern	Other
Tiger Salamander					X
Couch's Spadefoot			X		
New Mexico Spadefoot			X		
Plains Spadefoot		X			
Woodhouse's Toad				X	
Red-spotted Toad			X		
Great Plains Toad		X	X		
Collared Lizard	X		X		
Short-horned Lizard					X
Lesser Earless Lizard		X	X		
Sagebrush Lizard	X				
Eastern Fence Lizard				X	
Side-blotched Lizard	X		X		
Little Striped Whiptail			X		
Plateau Striped Whiptail					X
New Mexico Whiptail					X
Striped Whipsnake	X		X		
Gopher Snake					X
Common Kingsnake			X	X	
Milk Snake				X	
Glossy Snake			X		
Night Snake	X		X		
Western Rattlesnake					X
TOTAL	**5**	**3**	**12**	**4**	**6**

and Wright 1999a), and the plateau striped whiptail lizard is largely restricted to the Colorado Plateau, having originated in this region through interspecific hybridization (Wright 1993).

In contrast to the predominance of southern amphibian and reptile species in the region, the flora of the Petrified Forest area is generally considered to be most closely allied with the Great Basin (Kearney and Peebles 1960, Gleason and Cronquist 1964, Brown 1994). This points to the role that other mechanisms, besides vegetation and climate, have played in the distribution of amphibians and reptiles that occur in the park. The most obvious factor is topographic barriers, such as the mountains of central Utah and the canyon of the Colorado River, which separate Great Basin species from northeastern Arizona. Hence, although the vegetation is primarily derived from Great Basin and Great Plains floras (Brown 1994), the close geographic proximity of Petrified Forest to the grasslands and deserts to the south has evidently been more important in determining the current composition of the park's herpetofauna.

Conservation

Petrified Forest National Park protects a large area of native grassland, and aside from a portion of Wupatki National Monument north of Flagstaff, contains the only federally protected grasslands in the Little Colorado River basin of northeastern Arizona. Livestock grazing has had a profound impact on grasslands in the Southwest (e.g., Lowe 1964), and through exclusion of grazing Petrified Forest may also play an important role in the conservation of a number of regionally rare amphibian and reptile species, including Couch's spadefoot, little striped whiptail, and milk snake. Besides exclusion of livestock grazing, the current policy of night-time road closure at Petrified Forest may also play an important role in protecting the park's herpetofauna. Road mortality can have significant impacts on amphibians and reptiles, even in National Park areas (Rosen and Lowe 1994). Although the policy of night-time road closure at Petrified Forest was initiated to protect the park's significant geologic and cultural resources, local populations of nocturnal amphibians and reptiles also benefit.

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LITERATURE CITED

Bogan, M., C. Allen, E. Muldavin, S. Platania, J. Stuart, G. Farley, P. Mehlhop, and J. Belnap. 1998. The Southwest. Pages 543-592 *in* Mac, M., P. Opler, C. Puckett Haecker, and P. Doran (eds.) Status and trends of the nation's biological resources. 2 vols. U.S. Department of the Interior, U.S. Geological Survey, Reston, VA.

Brown, D. E. 1994. Biotic Communities, Southwestern United States and Northwestern Mexico. University of Utah Press, Salt Lake City.

Brown, D. E., and C. H. Lowe. 1980. Biotic Communities of the Southwest. USFS General Technical Report (Map) GTR RM-78.

Burbidge, A. A. 1991. Cost constraints on surveys for nature conservation. pp. 3-6 *in*: C. Margules and M. P. Austin (eds.), Nature conservation: cost effective biological surveys and data analysis. CSIRO, Australia.

Campbell, H. W., and S. P. Christman. 1982. Field techniques for herpetofaunal community analysis. Pages 193-200 *in*: Scott, N. J. (ed.) Herpetological Communities. USFWS Wildlife Research Report 13.

Corn, P. S. 1994. Straight-line drift fences and pitfall traps. Pages 109-117 *in*: Heyer, W. R., M. A. Donnelly,, R. W. McDiarmid, L. C. Hayek, and M. S. Foster (eds.) Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians. Smithsonian Institution Press, Washington, D.C.

Crump, M., and N. Scott. 1994. Visual encounter surveys. Pages 84-92 *in*: Heyer, W. R., M. A. Donnelly, R. W. McDiarmid, L. C. Hayek, and M. S. Foster (eds.) Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians. Smithsonian Institution Press, Washington, D.C.

Eaton, T. H. 1935. Report on Amphibians and Reptiles of the Navajo Country. Bulletin 3, Rainbow Bridge-Monument Valley Expedition, Berkeley, California.

Fellers, G. M., and C. A. Drost. 1991. Ecology of the Island night lizard, *Xantusia riversiana*, on Santa Barbara Island, California. Herpetological Monographs 5: 28-78.

Fellers, G. M., and C. A. Drost. 1994. Sampling with artificial cover. Pages 146-150 *in*: Heyer, W. R., M. A. Donnelly, R. W. McDiarmid, L. C. Hayek, and M. S. Foster (eds.) Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians. Smithsonian Institution Press, Washington, D.C.

Gleason, H. A., and A. Cronquist. 1964. The Natural Geography of Plants. Columbia University Press, New York.

Harris, A. H. 1963. Ecological distribution of some vertebrates in the San Juan Basin, New Mexico. Museum of New Mexico Papers in Anthropology 8: 1-64.

Jones, K. B. 1986. Amphibians and reptiles. Chapter 14 *in*: Cooperider, A. Y., R. J. Boyd, and H. R. Stuart (eds.) Inventory and Monitoring of Wildlife Habitat. U.S. Department of the Interior, Bureau of Land Management Service Center, Denver, Colorado.

Kearney, T. H., and R. H. Peebles. 1960. Arizona Flora with Supplement by J. Howell, E. McClintock and collaborators. University of California Press, Berkeley.

Kierstead, J. R. 1981. Flora of Petrified Forest National Park, Arizona. Unpublished master's thesis, Northern Arizona University, Flagstaff.

Lowe, C. H. 1964. Arizona landscapes and habitats. Pages 1-132 *in*: Lowe, C. H. (ed.) The Vertebrates of Arizona. University of Arizona Press, Tucson.

McDonald, L. L. 1981. Summarizing remarks: observer variability. Pages 388-389 *in*: Ralph, C. J., and J. M. Scott (eds.), Estimating numbers of terrestrial birds. Studies in Avian Biology no. 6, Cooper Ornithological Society.

Mendelson,, J. R., and W. B. Jennings. 1992. Shifts in the relative abundance of snakes in a desert grassland. Journal of Herpetology 26: 38-45.

National Park Service. 1992. NPS-75. Natural Resources Inventory and Monitoring Guidelines. U.S. Department of the Interior, National Park Service. U.S. Government Printing Office.

Persons, T. and J. W. Wright. 1999a. Discovery of *Cnemidophorus neomexicanus* in Arizona. Herpetological Review 30: 207-209.

Persons, T. and J. W. Wright. 1999b. Geographic distribution: *Cnemidophorus inornatus.* Herpetological Review 30: 109.

Rosen, P. C., and C. H. Lowe. 1994. Highway mortality of snakes in the Sonoran desert of southern Arizona. Biological Conservation 68: 143-148.

Scott, N. J. 1994. Complete species inventories. Pages 78-84 *in*: Heyer, W. R., M. A. Donnelly, R. W. McDiarmid, L. C. Hayek, and M. S. Foster (eds.) Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians. Smithsonian Institution Press, Washington, D.C.

Shaffer, H. B., and J. E. Juterbock. 1994. Night driving. Pages 163-166 *in*: Heyer, W. R., M. A. Donnelly, R. W. McDiarmid, L. C. Hayek, and M. S. Foster (eds.) Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians. Smithsonian Institution Press, Washington, D.C.

Stebbins, R. C. 1985. Western Reptiles and Amphibians, Second Edition. Houghton Mifflin Co., Boston.

Stohlgren, T. J., and J. F. Quinn. 1992. An assessment of biotic inventories in western U.S. National Parks. Natural Areas Journal 12: 145-154.

Treadwell, B. D., and D. A. Miller. 1978. Generalized vegetation map of Petrified Forest National Park. GIS map and accompanying summary descriptions of vegetation categories. Applied Remote Sensing Program, Office of Arid Lands Studies, University of Arizona, Tucson.

USGS. 1981. Petrified Forest National Park. 1:50,000 scale metric topographical map.

USGS. 1982. Adamana. 1:24,000 scale topographical map.

Wright, J. W. 1993. Evolution of the lizards of the genus *Cnemidophorus.* Pages 27-81 *in*: Wright J. W., and L. J. Vitt (eds.) Biology of Whiptail Lizards (Genus *Cnemidophorus*). Oklahoma Museum of Natural History, Norman, Oklahoma.

Wright, J. W., and C. H. Lowe. 1965. The rediscovery of *Cnemidophorus arizonae* Van Denburgh. Journal of the Arizona Academy of Science 3: 164-168.

Wright, J. W., and C. H. Lowe. 1968. Weeds, polyploids, parthenogenesis, and the geographical and ecological distribution of all-female species of *Cnemidophorus*. Copeia 1968: 128-138.

Changes in Water Temperature of Backwaters During Fluctuating vs. Short-Term Steady Flows in the Colorado River, Grand Canyon

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Abstract. Discharge from Glen Canyon Dam, Arizona, fluctuates in a diel pattern which may affect native fishes and their habitats in the Colorado River, Grand Canyon. Differences in water temperature, turbidity, dissolved oxygen (DO) and pH in main channel and backwater habitats were compared between fluctuating and short-term (3-day) steady discharge regimes. Mean temperature in the main channel and backwaters displayed regular diel fluctuations, but mean temperatures were warmer under steady flows in both habitats ($P<0.01$). Mean main channel temperature was 8.36° C under fluctuating flows and increased to 8.92° C under steady flows. In backwaters, mean temperature increased from 11.91° C to 14.18° C, and minimum, maximum and diel temperature range were higher under steady flows ($P<0.01$). Mean and minimum DO decreased and range of DO increased ($P\leq 0.03$), while mean, maximum and range of pH ($P\leq 0.03$) increased in backwaters under steady flows. Mean turbidity did not significantly change ($P\geq 0.35$). These water quality changes may affect native fish populations through their influence on primary and secondary production and the potential for a change in non-native fish community. These factors should be more closely examined before implementation of a steady flow regime, construction of a temperature control structure or other changes that might increase water temperature in the Colorado River in Grand Canyon.

Key words: temperature, dam discharge, fluctuating flow, steady flow, Colorado River, Glen Canyon Dam.

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INTRODUCTION

The flow of water in the Colorado River through Grand Canyon is predominantly regulated by hypolimnetic discharge from Glen Canyon Dam. The closure of Glen Canyon Dam, in 1963, turned a seasonally warm, muddy river into one that is typically clear and constantly cold. This change has greatly affected the river corridor biota, particularly native fishes. Alteration of spawning and rearing habitat, blockage of migration and introduced non-native species have contributed to the extirpation of four of the original eight native species (Minckley 1991). Reproducing populations of only four native species remain: humpback chub, *Gila cypha* (listed as endangered; U. S. Fish and Wildlife Service 1990), flannelmouth sucker, *Catostomus latipinnis*, bluehead sucker, *Catostomus discobolus* and speckled dace, *Rhinichthys osculus*. As many as 17 exotic fish species, most of which are predators and/or competitors of native species, have been found within the Grand Canyon (Maddux et al. 1987, Valdez and Ryel 1995, Arizona Game and Fish Department 1996).

Glen Canyon Dam is operated as a peaking power hydropower facility. From 1963 through July 1991, daily discharge fluctuated widely, with no restrictions on ramping rates. During this period, discharge peaked as high as 893 m^3/s (31,500 cfs) in the early afternoon, while discharge during the early morning could be as low as 28 m^3/s (1,000 cfs) or 85 m^3/s (3,000 cfs), depending on the time of year. On 1 August 1991, interim operations were implemented which restricted discharge to a maximum of 567 m^3/s (20,000 cfs) and a minimum of 227 m^3/s (8,000 cfs) from 07:00 to 15:00, and 142 m^3/s (5,000 cfs) at night. Ramping rates were also restricted to 71 m^3/s (2,500 cfs) per hour up and 43 m^3/s (1,500 cfs) per hour down.

Changing from an unregulated to a regulated stream has caused backwaters to become increasingly important as rearing areas for native fishes in the Colorado River system (Holden 1978, Valdez and Clemmer 1982, Carter et al. 1985, Maddux et al. 1987, Arizona Game and Fish Department 1996). Backwaters, quiet pockets connected to the main channel (but with greatly reduced flow), are formed in areas of eddies where scouring occurs under higher flows. As water levels drop, a reattachment sand bar is exposed, partially isolating the eddy return channel and forming the backwater (Rubin et al. 1990). Not only do backwaters provide calm, sheltered water, they are also warmer and contain greater densities of aquatic invertebrates than the main channel (Cole and Kubly 1976, Arizona Game and Fish Department 1996). However, fluctuations in dam releases cause inundation and/or dewatering of backwaters, reducing their ability to support larval and juvenile fish (Kennedy 1979).

In an effort to improve habitat for native fish, a regimen of steady releases from Glen Canyon Dam has been proposed (U.S. Fish and Wildlife Service 1994). Stabilized river levels would prevent the daily loss and creation of backwaters. The present diel cycle of flow fluctuations forces juvenile fish to move into or out of many backwaters each day as these habitats are inundated and/or dewatered with changes in river stage. Jourdonnais and Hauer (1993) speculated that forced movement, caused by alterations in river discharge, may increase predation on juvenile fish. Eliminating fluctuations could improve conditions for juvenile fishes. It is likely that backwaters, under steady flow conditions, would support increased planktonic and benthic invertebrate communities as a result of increased temperature and decreased daily flushing (Kennedy 1979). A dramatic increase in benthic invertebrate populations has been seen in backwaters sampled under reduced fluctuations (Arizona Game and Fish Department 1996) when compared to those sampled under flow regimes designed to maximize power production (Cole and Kubly 1976, Haury 1986, 1988). Conversely, turbidity, which is used as cover by native Colorado River fishes (Valdez and Ryel 1995, Arizona Game and Fish Department 1996), will likely decrease under steady flows. This would make backwaters and other near shore areas less hospitable to larval and juvenile native fishes. Additionally, other water quality parameters in backwaters, such as dissolved oxygen and pH will also be affected by steady flows and, subsequently, primary and secondary production.

This study was conducted to determine differences in diel temperature changes in backwaters and the main channel between fluctuating vs. steady flow regimes in the Colorado River, Grand Canyon. Herein, I provide initial data concerning the effect of steady flows on temperature, pH, dissolved oxygen and turbidity of backwater and main channel larval and juvenile native fish habitat. I also examine the effects that any changes might have on native fishes should a steady flow be implemented in the Colorado River, Grand Canyon, Arizona.

STUDY AREA

This study was conducted on the Colorado River, in Grand Canyon National Park, near the confluence of the Colorado and Little Colorado (LCR) rivers (RK 99; RK = river kilometers in the Colorado River below Lees Ferry; Fig. 1). This reach was selected because of its importance to native fishes, as all four remaining native species reproduce in the LCR and rear in backwaters and the main channel of the Colorado River in this reach (Arizona Game and Fish Department 1996). The reach between Kwagunt Rapid (RK 90.1) and Lava Chuar Rapid (RK 105.4) was explored for suitable backwaters.

Four backwaters, RK 94.6L, 95.9L, 97.8L and 102.5R ('L' and 'R' denote side of river when facing downstream), were selected based on the likelihood that they would persist under fluctuating vs. steady flow regimes (Fig. 1). The backwaters varied in many physical characteristics which affect warming and water chemistry, including surface area, depth, mouth dimensions, amount of algae and/or aquatic vegetation and exposure to solar radiation.

METHODS

My sampling period was four days of fluctuating flows (25-28 May 1994) and three days of steady flows (29 - 31 May 1994). Fluctuating flows ranged from 219.6-370.2 m^3/s (7756-13075 cfs) while steady flows were approximately 236 m^3/s (8,325 cfs). Steady releases from Glen Canyon Dam began at approximately 06:00 28 May 1994 and reached my backwater sites, at the confluence of the Colorado and Little Colorado rivers, at approximately 00:00 on 29 May 1994. Sampling was completed on 31 May 1994 when normal fluctuations resumed.

One temperature gauge (Ryan Tempmentor^{TM}) was placed in the middle of each backwater on 24 May 1994. In one backwater (RK 97.8L) a HydroLab DataSonde

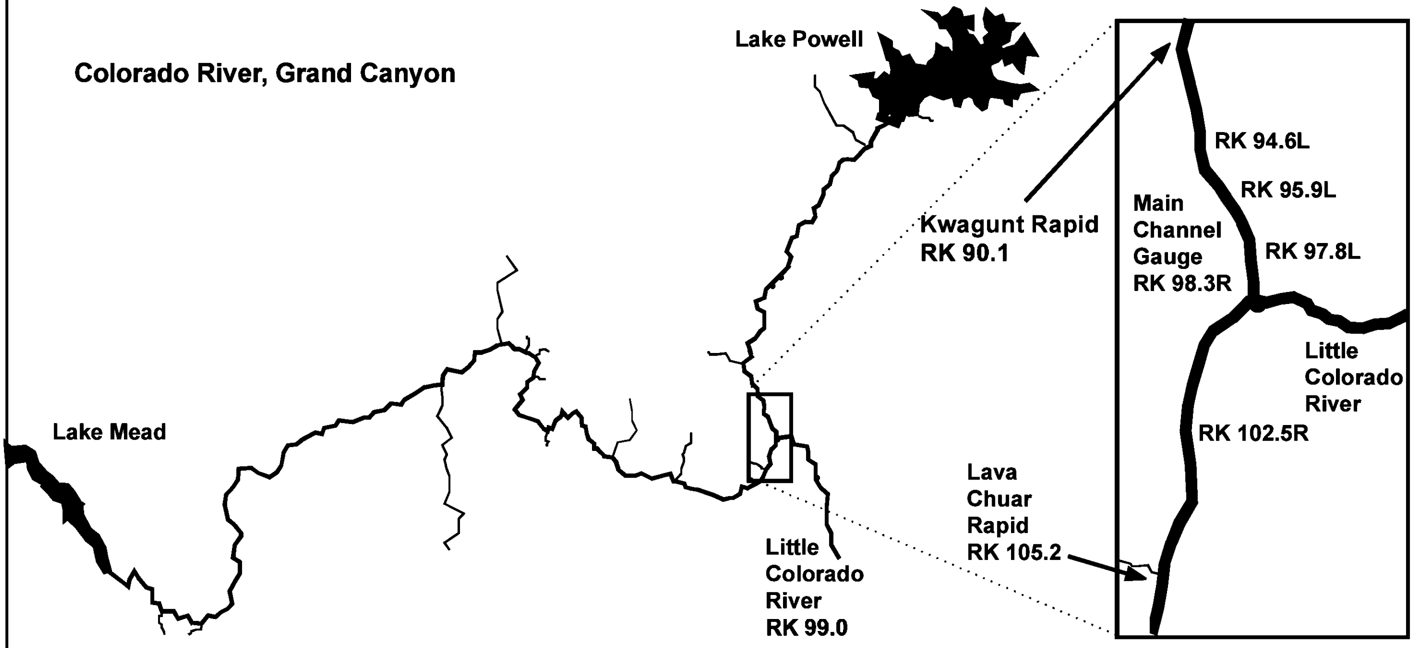

Figure 1. Colorado River, Grand Canyon, Arizona, and the location of the backwater and main channel sites sampled in this study. Locations are given as river kilometers downstream from Lees Ferry and side of river when facing downstream.

II™ was used which also recorded dissolved oxygen (DO) and pH. Each gauge was shaded from direct sunlight and suspended approximately 25 cm below the water surface. Turbidity was measured once each day in each backwater and the main channel using a Hach™ nephelometer. Main channel temperature and discharge data were obtained from the U.S. Geological Survey gauge on the Colorado River at RK 98.3R, above the mouth of the LCR. All instruments were set to record at 30 minute intervals from 25 May - 1 June 1994. Available direct solar radiation (hours) for each site at the end of May was later measured using a Solar Pathfinder™. Differences in diel mean, minimum, maximum and range of temperature (°C), DO, pH and mean turbidity between steady vs. fluctuating river discharges in backwaters vs. the main channel were tested using a t-test. Probability was accepted when $P \leq 0.05$.

RESULTS

Flows and Backwater Sites

Two backwaters, RK 94.6 L and RK 97.8 L, were well established. They had been sampled regularly by Arizona Game and Fish Department (unpub. data) and contained aquatic, emergent and terrestrial vegetation in and around them. The remaining two backwaters, RK 95.9L and RK 102.5 R, were bounded by clean sand bars and were more ephemeral.

The backwater at RK 94.6 L was long (up to 61 m), wide (up to 7 m) and mostly shallow. Its size varied greatly with water elevation (Table 1). It also received the

Table 1. Representative and maximum depth (cm), surface area (m^2) and hours of direct solar radiation in late May, for each backwater sampled, 25-31 May 1994, during fluctuating and steady flow regimes in the Colorado River, Grand Canyon, Arizona. Backwater location is given as river kilometer and side (left or right).

	Backwater Location			
Parameter	**94.6L**	**95.9L**	**97.8L**	**102.5R**
Representative Depth (cm)				
Fluctuating Flow	21-66	28-35	72-116	58-76
Steady Flow	64	52	73	54
Maximum Depth (cm)				
Fluctuating Flow	32-85	56-61	107-170	70-94
Steady Flow	124	81	112	70
Surface Area (m^2)				
Fluctuating Flow	178-335	32-19	140-248	40-67
Steady Flow	324	57	165	145
Maximum Length (m)				
Fluctuating Flow	52-58	12-14	28-31	10-16
Steady Flow	61	19	34	18
Maximum Width (m)				
Fluctuating Flow	6-7	2	5-8	7-8
Steady Flow	6	6	5	10
Hours of Solar Radiation	7.25	5.5	6.75	4.75

greatest amount of direct solar radiation (7.25 hours from 09:00-16:15). Its mouth (connection with main channel) was wide and deep (>1 m) and its location and dimensions varied greatly with varying river stage. The foot (terminal end) of this site remains a backwater except under high discharges (510 m^3/s = 18,000 cfs) not seen during this study, which would inundate the site. This backwater contained a dense mat of aquatic macrophytes, including *Potamogeton* and *Anacharis* with *Equisetum* and *Typha* along its sides.

The backwater at 95.9 L was very small (13 m), narrow (2 m) and shallow (Table 1). Its mouth was also shallow and narrow and the size of this backwater did not vary greatly with river elevation. This site would be inundated by flows barely exceeding those seen during this study. Due to its location, partially under an overhanging ledge, and the fact that the river there flows north to south, this backwater received little direct solar radiation (5.5 hours; 11:00-15:30). The only aquatic vegetation in this backwater was *Cladophora* that had drifted in from the main channel.

The backwater at RK 97.8 L was long (34 m) and wide (8 m) with both deep and shallow sections (Table 1). The mouth was wide, but very shallow. However, a boulder along one shore provided a site for scouring under high flows which created a deep hole. This site would also require flows exceeding 510 m^3/s for inundation. It was also very exposed to solar radiation (6.75 hours; 08:45-15:30) and contained much aquatic vegetation, including *Potamogeton* and *Equisetum* in the shallow areas and *Cladophora* in the deeper areas.

The backwater at RK 102.5 R was short (18 m), wide (10 m) and shallow with two arms and its mouth was wide and deep (Table 1). It was located in a narrow section of the canyon with Tapeats limestone walls that blocked much sunlight, resulting in only 4.75 hours of direct solar radiation each day (09:15-14:00). This backwater contained no aquatic vegetation except *Cladophora* that had drifted in.

Temperature

Water temperatures in the main channel and backwaters displayed regular, diel fluctuations under fluctuating and steady flow regimes (Fig. 2). Maximum backwater temperatures occurred in midday (09:00-16:00, depending on the site) while the main channel was warmest around 18:00. Minimum backwater temperatures occurred near 06:00 for most sites, but around 00:00 for the backwater at 94.6L and in the main channel between 06:00-09:00.

In the main channel, mean temperature was 8.4° C under fluctuating flows but was significantly higher ($P<0.01$) at 8.92° C under steady flows (Table 2). Mean daily minimum temperature also significantly increased from 7.8° C to 8.1° C. Mean daily maximum and diel temperature range were not significantly different ($P \geq 0.08$) between flow regimes in the main channel.

In backwaters, daily mean, minimum and maximum temperatures and diel temperature range were significantly greater under steady than fluctuating flows ($P<0.01$; Table 2). Daily mean temperature under fluctuating flows was 11.9° C, increasing to 14.2° C under steady flows. Mean daily minimum temperature increased from 10.5°C under fluctuating flows to 11.5° C under steady flows. Mean

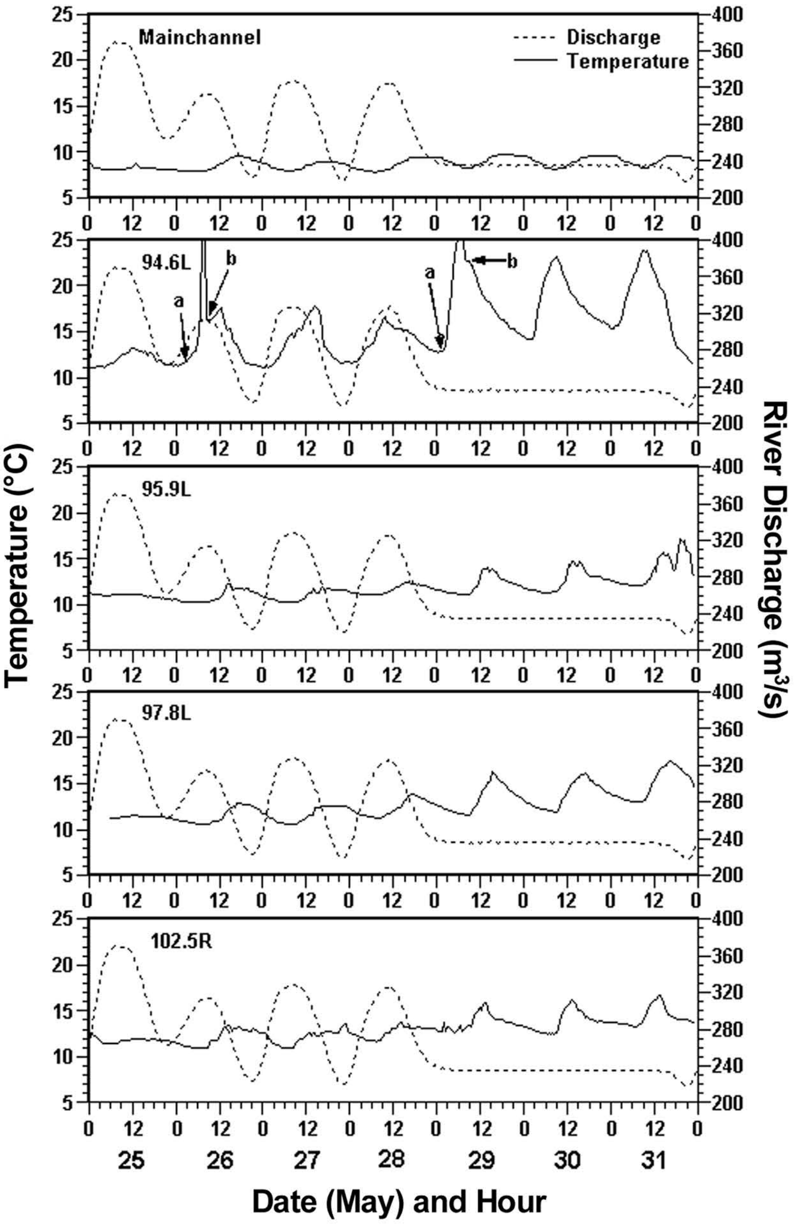

Figure 2. Temperature changes, in main channel (RK 98.2) and backwaters (RK 94.6L, 95.9L, 97.8L and 102.5R), and river discharge during fluctuating and steady flows in the Colorado River, Grand Canyon, 25-31 May 1994. Temperature gauge in backwater at 94.6L was dewatered (a) and resubmerged (b).

Table 2. Mean, minimum and maximum temperature in the sampled backwaters and main channel during fluctuating and steady flows in the Colorado River, Grand Canyon, 25-31 May 1994.

Habitat/	Fluctuating Flow				Steady Flow			
Location	Mean	Min	Max	Std Dev	Mean	Min	Max	Std Dev
Backwaters	11.9	10.1	17.7	1.2	14.2	10.9	23.8	2.2
94.6L	13.2	10.8	17.7	1.9	17.7	11.3	23.8	3.3
95.9L	11.0	10.1	12.5	0.6	12.7	10.9	17.0	1.4
97.8L	11.6	10.4	13.8	0.8	13.9	11.5	17.3	1.6
102.5R	12.0	10.8	13.7	0.7	13.9	12.3	16.6	1.0
Main Channel	8.4	7.6	9.4	0.5	8.9	8.0	9.6	0.5

daily maximum backwater temperature under steady flows was 18.7° C, but only 14.4° C under fluctuating flows. The mean diel temperature range was only 2.7° C under fluctuating flows, but increased to 5.6° C under steady flows.

In individual backwaters, daily mean and maximum water temperatures were significantly higher ($P<0.05$) under steady flows in each backwater (Table 2). Daily minimum water temperature significantly increased ($P<0.01$) at all sites, except RK 94.6L ($P>0.07$).

Turbidity

Mean turbidity decreased under steady flows, but not significantly ($P\geq 0.35$). Mean main channel turbidity decreased from 6.936 to 2.681 Nephelometric Turbidity Units (NTU) under fluctuating and steady flows, respectively (Table 3). During fluctuating flows mean backwater turbidity was 9.396 NTU and decreased to 5.875 NTU under steady flows.

Table 3. Mean, minimum and maximum turbidity in the sampled backwaters and main channel during fluctuating and steady flows in the Colorado River, Grand Canyon, 25-31 May 1994.

Habitat/	Fluctuating Flow				Steady Flow			
Location	Mean	Min	Max	Std Dev	Mean	Min	Max	Std Dev
Backwaters	9.4	1.6	31.3	5.3	5.9	1.2	11.4	2.1
94.6L	6.5	2.7	13.4	6.0	7.5	5.7	8.7	1.6
95.9L*	6.5	6.5	6.5	--	6.4	3.4	9.4	4.3
97.8L	6.1	1.6	10.0	4.2	2.1	1.2	3.0	0.9
102.5R	18.6	5.9	31.3	18.0	7.5	5.0	11.4	3.4
Main Channel	6.9	1.8	23.6	4.4	2.7	1.1	3.1	0.3

*Turbidity was measured only once during fluctuating flows at this site.

Dissolved Oxygen

Dissolved oxygen (DO) in the backwater at RK 98.7L fluctuated daily under both flow regimes (Fig. 3). Maximum DO levels occurred in late afternoon and the minimum occurred in early morning under both flow regimes. Mean DO level was significantly lower (*P*<0.01) under steady flows (10.0 mg/L) than fluctuating flows (10.8 mg/L). Mean minimum DO was 10.1 under fluctuating flows and decreased significantly (*P*<0.01) to 8.9 mg/L under steady flows. Mean maximum DO level

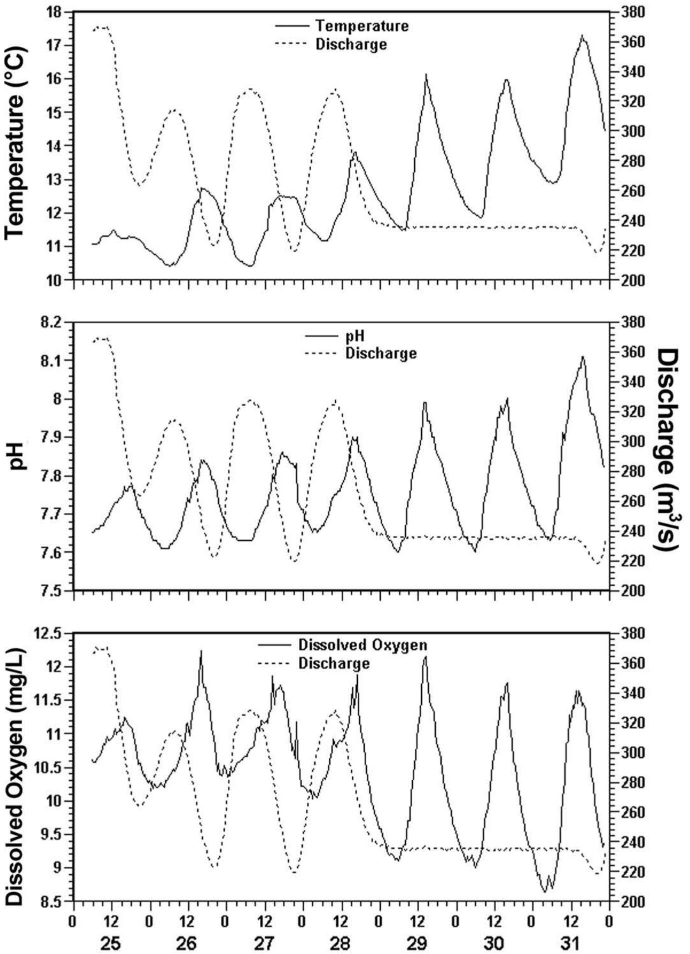

Figure 3. Changes in temperature, pH and dissolved oxygen in the backwater at RK 97.8L and river discharge during fluctuating and steady flows in the Colorado River, Grand Canyon, 25-31 May 1994.

decreased from 11.90 mg/L under fluctuating to 11.86 mg/L under steady flows, but was not significantly different ($P=0.92$). Diel DO range increased ($P<0.05$) to 2.97 mg/L under steady flows, from that seen under fluctuating flows (1.79 mg/L).

pH

pH levels showed regular diel variations in the backwater at RK 97.8L under fluctuating and steady flow regimes, with maximum pH occurring in the afternoon and minimum in early morning (Fig. 3). Mean, maximum, and diel range of pH were higher ($P<0.05$) under steady than fluctuating flows, while mean minimum pH did not significantly change ($P=0.15$). Mean pH increased from 7.72 to 7.80, while maximum pH increased from 7.9 under fluctuating flows, to 8.1 under steady flows. Diel range of pH also increased from 0.23 to 0.44. Minimum daily pH decreased from 7.63 to 7.61, but was not significantly different.

DISCUSSION

It is evident that a 64-hour (three periods of daylight) regimen of steady flows caused changes in water quality parameters in the Colorado River main channel and backwaters. Temperature and pH increased, while DO and turbidity decreased. These changes and the potential for greater biotic and abiotic changes, under longer term steady flows, have important implications for native fishes in the Colorado River in Grand Canyon.

I found that the 3-day steady flow caused an increase in water temperature in backwaters and the main channel of the Colorado River during late May 1994. The full potential for backwater warming was probably not reached during this short period, and these data are insufficient to estimate the limit of warming or other water quality changes. The water did warm in both the backwaters and the main channel. It is, however, safe to say that temperatures would not have reached those of pre-dam conditions.

The amount of warming in the backwaters monitored in this study varied and was likely influenced by ambient temperature, physical location (accessibility to direct solar radiation), main channel temperature, the amount of water exchange between the backwater and main channel and backwater morphometry (size of mouth and surface area and volume of the backwater). Under fluctuating flows, backwaters may warm, but daily flushing with main channel river water resets backwater temperatures to approximately that of the main channel. Under the steady flow regime, diel fluctuations in temperature were still influenced by solar radiation and diel changes in ambient temperature but were less influenced by the main channel. With minimum temperatures well above that of the main channel and no surge of main channel water under the steady flow regime, backwaters held heat better than under fluctuating flows, allowing them to warm further the next day. In all sites, except RK 94.6L, the highest daily mean and minimum temperatures occurred on the last day of steady flows, and at all sites the highest maximum temperature occurred on the last day, indicating an increase of temperature over time, which would probably continue if the steady flows were of longer duration.

The diel cycle of flow fluctuations near the LCR is such that temperature variation in backwaters are maximized. During fluctuating flows, peak discharges reached the LCR gauge between 06:00 and 09:00, leaving the remainder of the day under steady or decreasing discharges. This permits backwaters in this area to warm considerably throughout the day due to little input of new, cold water from the main channel. In most other areas of the Colorado River in Grand Canyon warming should occur to a lesser degree since the timing of high and low discharge occurs at different times of the day. If low discharge occurs in the early to mid-morning, warming of backwaters should be greatly diminished as they will be continuously filled with cold river water during daylight hours.

Backwater temperatures that I recorded under fluctuating flows were not those preferred by native Grand Canyon fishes. Humpback chub prefer water temperatures of 21 - 24.4° C (Bulkley et al. 1982) and other native Colorado River fishes probably have similar preferences (Valdez and Ryel 1995, Arizona Game and Fish Department 1996). These preferred temperatures are far from the 7.6 - 9.6° C temperature range recorded in the main channel during this study under fluctuating and steady flows. Even in the monitored backwaters, maximum recorded temperature was 17.6° C under fluctuating flows. However, under the steady flow regime mean diel temperature in one backwater (RK 94.6L) reached 18.1° C, nearing the preferred temperature range for native fishes, and mean maximum temperature reached 23.8° C, well within the preferred range. Also, temperature in most backwaters showed indications of increasing with each day of steady flows. Therefore, it appears that under a regime of steady flows, temperature in backwaters will approach and may even exceed the preferred temperature range of native fishes. This is most likely to occur during warmer months, in shallow areas of backwaters and in lower reaches of the Colorado River in Grand Canyon.

Through warming of the water and reduced mixing with the main channel, steady discharges also affect other water quality properties of backwaters, such as dissolved oxygen, pH and turbidity. The Colorado River was extremely clear during the entire study and turbidity decreased in both backwaters and the main channel, but not significantly. Decreased turbidity may result in increased predation on larval and juvenile fish and main channel turbidity is probably already sufficiently low to affect fish behavior. Colorado River fishes evolved in a turbid system (Minckley 1991) and likely prefer turbid water. Arizona Game and Fish Department (1996) reported increased catches of juvenile humpback chub, flannelmouth sucker, speckled dace and fathead minnow under turbid conditions (>30 NTU). Valdez and Ryel (1995) reported increased catches of sub-adult and adult humpback chub in trammel nets at night and during periods of high turbidity (also >30 NTU) in the Colorado River. Sabo et al. (1991) found that high quality nursery ponds along the Mississippi River contained higher turbidity, dissolved oxygen and conductivity than low quality nursery areas.

As seen with temperature, DO and pH also varied with regular diel fluctuations under both flow regimes. Daily mean, minimum and/or maximum levels of these parameters changed under the steady flow regime due to increased photosynthetic/

respiratory activity by algae and macrophytes (Wetzel 1983). Under steady flows, daily maximum DO did not significantly vary between flow regimes. Dissolved oxygen was highest during the late afternoon when algal and macrophytic photosynthesis was greatest. Daily mean and minimum DO significantly decreased under steady flows with increases in water temperature and as biological oxygen demand during the night used O_2 which was not replenished by the nightly influx of new water that occurs under fluctuating flows. However, DO levels recorded in these backwaters were never near 6 mg/L, below which fish growth and survival may be affected (Boyd 1979, Piper et al. 1982).

During the late afternoon, pH was also highest, probably due to the use of CO_2 by algal and macrophytic photosynthesis (Wetzel 1983). Although pH increased significantly, the changes were small and it is unlikely that pH is limiting fish in this system, since fish generally do well in waters with a pH of 6.5 - 9.0 (Boyd 1979, Piper et al. 1982).

Therefore, it appears that fluctuations in river discharge also moderated the diel changes in DO and pH in this backwater caused by daily cycles of photosynthesis and respiration. However, as with changes in temperature, the limits of these changes under an extended period of steady flow cannot be predicted from these data.

These results show that backwaters and the main channel (to a lesser extent) will warm under a steady flow regime. Several biotic changes may be expected to be caused by this warming and subsequent changes, which may include alterations in algal, invertebrate and fish communities and the possibility of an increase in the distribution and prevalence of diseases and parasites. These changes in habitat and the biotic community are complex and may be beneficial or detrimental for native fish populations.

Algal and invertebrate communities in backwaters may change under steady flow conditions. It is likely that steady flows will cause an increase in backwater invertebrate densities in response to warmer temperatures and a lack of flushing. Increases in aquatic invertebrates under the current interim flow regime (small fluctuations) as compared to a peaking power flow regime (large fluctuations) have already been observed (Cole and Kubly 1976, Haury 1986, 1988, Arizona Game and Fish Department 1996). Steady flows and increased invertebrate densities would further improve backwaters as feeding areas for juvenile fishes. Although not examined in this study, the short duration of these flows was probably not long enough for significant changes to occur in populations of even those invertebrates with the shortest life cycles. Leibfried and Blinn (1987) reported an increase in total benthic standing crop (based on drift) in the main channel Colorado River under five months of steady flows, as compared to fluctuating flows. Warmer water and increased food abundance should cause an increase in fish growth and survival in all native fish. Lupher and Clarkson (1994) reared humpback chub larvae in 10°C, 14°C and 20°C water and found that length increased 10%, 37% and 83% and weight increased 28% 195% and 951% over 30 days, in the respective groups. Similar, but less dramatic, results are expected in situ. However, it may be that increased use of backwaters by fish and subsequent changes in growth rates will not occur until invertebrate populations increase.

There are potential negative aspects to long periods of steady flows for native fishes. Main channel temperatures will increase, particularly in lower reaches of the river and may become hospitable to exotic warm and cool water predators and competitors already found in the Colorado River and/or the reservoirs immediately upstream (Lake Powell) and downstream (Lake Mead) from Grand Canyon, (Maddux et al. 1987, Valdez and Ryel 1995, Arizona Game and Fish Department 1996). These predators include striped bass, *Morone saxatilis*, walleye, *Stizostedion vitreum*, smallmouth bass, *Micropterus dolomieu,* and channel catfish, *Ictalurus punctatus.* Exotic competitors include fathead minnow, *Pimephales promelas*, which is already common, plains killifish, *Funduls zebrinus,* and red shiner, *Cyprinella lutrensis,* which are becoming increasingly common, and green sunfish, *Lepomis cyanellis,* presently found in low numbers within the system. Additionally, Blinn et al. (1989) found that epiphytic diatom communities from the Glen Canyon Dam tailwaters changed from large, upright forms to smaller, closely adnate forms with an increase in water temperature from 12°C to 18°C. Adnate forms of diatoms may be more difficult for grazing fish to consume.

It is possible that backwater temperatures may rise too high during the late afternoon, making these areas unsuitable for juvenile fishes, particularly in the lower reaches of the Grand Canyon. Maximum backwater temperatures recorded under the current discharge regime of modified fluctuations reached as high as 26.6° C in May (Arizona Game and Fish Department 1996). It is also possible that increased algae, phytoplankton and macrophyte growth may make backwaters anoxic during darkness, further reducing their suitability to fish. This has been observed in the backwater at RK 88.86 (Arizona Game and Fish Department 1996).

Increased temperature may also allow the invasion of new parasites and diseases. Fifteen species of parasites have been found in the lower LCR (Clarkson et al. 1997, Brouder and Hoffnagle 1997, Hoffnagle et al. 2000). Increased mainstem temperatures may allow these parasites to expand their distributions within Grand Canyon. *Bothriocephalus acheilognathi*, the Asian fish tapeworm, is a thermophilic parasite of planktivorous cyprinid and cyprinodontid fishes and has been known to cause high mortality rates in fish (Hoffman and Schubert 1984). Cold temperatures in the mainstem Colorado River presently appear to keep this parasite from being able to complete its life cycle in the Colorado River in Grand Canyon. In the LCR, it infects humpback chub, speckled dace, plains killifish, common carp, red shiner and fathead minnow (Clarkson et al. 1997, Hoffnagle et al. 2000). The maximum temperature recorded in this study was 23.8°C and maximum daily mean temperature was 18.07°C, very close to the 20°C needed by this parasite to complete its life cycle (Granath and Esch 1983). Brouder and Hoffnagle (1997) examined the distribution of *B. acheilognathi* in humpback chub, speckled dace, fathead minnow and plains killifish throughout the Grand Canyon in 1994 - 1995 and found infected fish to be most common in and near the LCR. However, an infected speckled dace was found in the main channel Colorado River as far as 214 km downstream and in the mouth of Kanab Creek (132 km downstream). Hoffnagle and Landye (1999) reported the captured of speckled dace infected by *B. acheilognathi* in Kanab Creek in 1998. Increasing Colorado River water temperatures to those preferred by humpback chub will likely increase the infection rate by *B. acheilognathi* in all susceptible fish. That, coupled with the continual displacement of fish downstream, will facilitate the invasion of *B. acheilognathi* into other tributaries and possibly the main channel. Increased infection of humpback chub by *B. acheilognathi* could threaten this endangered fish. Other parasites found in the LCR may be more dangerous to humpback chub, including some that may alter the behavior of their hosts (Hoffnagle et al. 2000).

My results clearly demonstrate that water temperature will increase under a regime of steady flows during periods of warm weather. Additionally, dissolved oxygen and pH will be affected by this flow regime and turbidity changes may also be expected under longer-term steady flows. The effects of steady flows and changing river and backwater conditions on plankton, aquatic invertebrates and fishes were not tested but could be considerable. Therefore, it is apparent that further study is needed to assess the potential changes of long-term steady flows on larval and juvenile native fishes, their food sources, parasites and habitat before such changes are made. These studies, both laboratory and in situ, should provide significant information on the utility of steady releases for management of native fish populations in the Colorado River, Grand Canyon.

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LITERATURE CITED

Arizona Game and Fish Department. 1996. Ecology of Grand Canyon backwaters. Final report prepared for the U.S. Bureau of Reclamation, Upper Colorado Region, Glen Canyon Environmental Studies, Flagstaff, Arizona. Cooperative Agreement No. 9-FC-40-07940. Arizona Game and Fish Department, Phoenix.

Blinn, D. W., R. Truitt and A. Pickart. 1989. Response of epiphytic diatom communities from the tailwaters of Glen Canyon Dam, Arizona, to elevated water temperature. Regulated Rivers: Research and Management 4: 91-96.

Boyd, C. E. 1979. Water quality in warmwater fish ponds. Agricultural Experiment Station, Auburn University, Auburn, Alabama.

Brouder, M. J. and T. L. Hoffnagle. 1997. Distribution and prevalence of the Asian fish tapeworm, *Bothriocephalus acheilognathi*, in the Colorado River and tributaries, Grand Canyon, Arizona, including two new host records. Journal of the Helminthological Society of Washington 64: 219-226.

Bulkley, R. V., C. R. Berry, R. Pimentel and T. Black. 1982. Tolerance and preferences of Colorado River endangered fishes to selected habitat parameters. Pages 185-241 *in* Colorado River Fishery Project, Final Report, Part 3. U. S. Fish and Wildlife Service, Bureau of Reclamation, Salt Lake City, Utah.

Carter, J. G., R. A. Valdez, R. J. Ryel and V. A. Lamarra. 1985. Fisheries habitat dynamics in the upper Colorado River. Journal of Freshwater Ecology 3: 249-264.

Clarkson, R. W., A. T. Robinson and T. L. Hoffnagle. 1997. Asian tapeworm, *Bothriocephalus acheilognathi*, in native fishes from the Little Colorado River, Grand Canyon, Arizona. Great Basin Naturalist 57: 66-69.

Cole, G.A. and D.M. Kubly. 1976. Limnologic studies on the Colorado River from Lee's Ferry to Diamond Creek, Colorado River Research Series Contribution No. 37, Grand Canyon National Park.

Granath, W. O. and G. W. Esch. 1983. Temperature and other factors that regulate the composition and infrapopulation densities of *Bothriocephalus acheilognathi* (Cestoda) in *Gambusia affinis* (Pisces). Journal of Parasitology 69: 116-1124.

Haury, L. R. 1986. Zooplankton of the Colorado River from Glen Canyon Dam to Diamond Creek. Glen Canyon Environmental Studies Technical Report. Bureau of Reclamation, Salt Lake City, Utah, GCES Rep. No. B-10.

Haury, L. R. 1988. Zooplankton of the Colorado River, Glen Canyon Dam to Diamond Creek. Pages 205-215 *in* Executive Summaries of Technical Reports. Glen Canyon Environmental Studies, U.S. Bureau of Reclamation, Flagstaff, Arizona.

Hoffman, G. L. and G. Schubert. 1984. Some parasites of exotic fishes. Pages 223-261 *in* W. R. Courtney, Jr. and J. R. Stauffer, Jr., (eds.) Distribution, biology and management of exotic fishes. Johns Hopkins University Press, Baltimore.

Hoffnagle, T. L. 1996. Changes in water quality parameters and fish usage of backwaters during fluctuating vs. short-term steady flows in the Colorado River, Grand Canyon. Final report submitted to Glen Canyon Environmental Studies, U.S. Bureau of Reclamation, Flagstaff, Arizona. Arizona Game and Fish Department.

Hoffnagle, T. L. and J. Landye. 1999. Summary of fish health and parasitology studies. Pages 27-30 *in* O. T. Gorman and R. G. Bramblett, (eds.) Monitoring and studies of native fishes of the Colorado River ecosystem in Grand Canyon, Arizona. 1998 interim report submitted to Grand Canyon Monitoring and Research Center, Flagstaff, Arizona. Grand Canyon Fisheries Resources Office, U.S. Fish and Wildlife Service, Flagstaff, Arizona.

Hoffnagle, T. L., R. A. Cole and A. Choudhury. 2000. Parasites of native and non-native fishes of the Lower Little Colorado River, Arizona. 2000 Annual report submitted to Navajo Fish and Wildlife Branch, Window Rock, Arizona, Grand Canyon National Park, U. S. Park Service, Grand Canyon, Arizona, and U.S. Fish and Wildlife Service, Albuquerque, New Mexico. Arizona Game and Fish Department, Phoenix, and National Wildlife Health Center, U.S.G.S. - B.R.D., Madison, Wisconsin.

Holden. P. B. 1978. A study of the habitat use and movement of the rare fishes in the

Green River, Utah. Transactions of the Bonneville Chapter of the American Fisheries Society 1978: 64-89.

Jourdonnais, J. H. and F. R. Hauer. 1993. Electrical frequency control and its effects on flow and river ecology in the lower Flathead River, Montana. Rivers 4: 132-145.

Kennedy, D. M. 1979. Ecological investigations of backwaters along the lower Colorado River. Doctoral dissertation. University of Arizona, Tucson.

Leibfried, W. C. and D. W. Blinn. 1987. The effects of steady versus fluctuating flows on aquatic macroinvertebrates in the Colorado River below Glen Canyon Dam, Arizona. Final Report, Contract No. 6400042, Arizona Game and Fish Department, Phoenix.

Lupher, M. L. and. R. W. Clarkson. 1994. Temperature tolerance of humpback chub (*Gila cypha*) and Colorado squawfish (*Ptychocheilus lucius*), with a description of culture methods for humpback chub. *In* Glen Canyon Environmental Studies Phase II 1993 Draft Annual Report. Prepared for the U.S. Bureau of Reclamation, Upper Colorado Region, Glen Canyon Environmental Studies, Flagstaff, AZ, Cooperative Agreement No. 9-FC-40-07940, Arizona Game and Fish Department, Phoenix.

Maddux, H. R., D. M. Kubly, J. C. deVos, Jr., W. R. Persons, R. Staedicke and R. L. Wright. 1987. Effects of varied flow regimes on aquatic resources of Glen and Grand Canyons. Final report Prepared for the U.S. Department of Interior, Bureau of Reclamation, Contract No. 4-AG-40-01810. Arizona Game and Fish Department, Phoenix.

Minckley, W. L. 1991. Native fishes of the Grand Canyon region: an obituary? Pages 124-177 *in* National Academy of Sciences, (eds.) Colorado River ecology and dam management, National Academy Press, Washington, D.C.

Piper, R. G., I. B. McElwain, L. E. Orme, J. P. McCraren, L. G. Fowler and J. R. Leonard. 1982. Fish Hatchery Management. U.S. Fish and Wildlife Service, Department of the Interior, Washington, D.C.

Rubin. D. M., J. C. Schmidt and J. N. Moore. 1990. Origin, structure, and evolution of a reattachment bar, Colorado River, Grand Canyon, Arizona. Journal of Sedimentary Petrology 60: 982-991.

Sabo, M. J., W. E. Kelso, C. F. Bryan and D. A. Rutherford. 1991. Physiochemical factors affecting larval fish densities in Mississippi River floodplain ponds, Louisiana (U.S.A.). Regulated Rivers: Research and Management 6: 109-116.

U.S. Fish and Wildlife Service. 1990. Humpback chub recovery plan. U.S. Fish and Wildlife Service, Denver.

U.S. Fish and Wildlife Service. 1994. Final biological opinion on operation of Glen Canyon Dam. Ecological Services, Arizona State Office, U. S. Fish and Wildlife Service, Phoenix, Arizona, Report Number 2-21-93-F-167.

Valdez, R. A. and G. H. Clemmer. 1982. Life history and prospects for recovery of the humpback and bonytail chub. Pages 109-119 *in* W. H. Miller and H. M. Tyus, (eds.) Fishes of the upper Colorado River system: present and future. Proceedings of the Western Division meeting, American Fisheries Society, Bethesda, Maryland.

Valdez, R. A. and R. J. Ryel. 1995. Life history and ecology of the humpback chub (*Gila cypha)* in the Colorado River, Grand Canyon, Arizona. Final Report to Glen Canyon Environmental Studies, U.S. Bureau of Reclamation, Flagstaff, Arizona. Contract No. 0-CS-40-09110, BIO/WEST Report No. TR-250-08.

Wetzel, R. G. 1983. Limnology, second edition. Saunders College Publishing, Forth Worth, Texas, USA.

Ponderosa Pine Tree Selection by Roosting Merriam's Turkeys in North-Central Arizona

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Abstract: We compared ponderosa pine (*Pinus ponderosa*) trees used for roosting by Merriam's turkeys (*Meleagris gallopavo merriami*) in north-central Arizona with randomly selected ponderosa pine trees ≥40 cm diameter breast height (dbh) to determine which factors best identified trees that Merriam's turkey select for roosting. Roost trees were older (P= 0.007), greater in diameter (P < 0.001), taller (P <0.001), had greater surrounding basal area (BA; P= 0.086), and had a greater height to first limb (P= 0.063) than did randomly-located, ≥40 cm diameter trees. A logistic regression model, developed using a forward-stepwise approach, correctly classified 92.3% of all trees. Our model can be used to identify potential turkey roost trees by using only tree dbh and immediately surrounding BA. Used in conjunction with existing models, this model now allows managers to more accurately rank and prioritize potential roosting habitat for land management planning.

Key words: *Meleagris gallopavo merriami*, Merriam's turkey, ponderosa pine, roost.

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INTRODUCTION

Merriam's turkeys consistently select clumps of the largest ponderosa pine trees for roosting (Hoffman 1968, Scott and Boeker 1977, Rumble 1992, Mollohan et al. 1995, Wakeling and Rogers 1996, 1998); therefore, habitat selected for roosting may be more characteristic and easily identified than other habitats that turkeys occupy. Most trees used for roosting exceed 40 cm diameter breast height (dbh) (Boeker and Scott 1969, Mackey 1984, Mollohan et al. 1995). In addition to large trees, high basal area (BA) (>20 m^2/ha), dense overstory canopy (>50% closure), and steep slopes (>30%) are other characteristics common to roosting habitat (Boeker and Scott 1969, Mackey 1984, Rumble 1992). Conversely, aspect and landform were selected less consistently by roosting turkeys, depending on season and area (Schemnitz et al. 1985, Rumble 1992, Mollohan et al. 1995, Wakeling and Rogers 1996, 1998). Mollohan et al. (1995) found that trees with characteristics selected by roosting turkeys were extremely rare when compared with availability of those characteristics throughout the forests of north-central Arizona.

Merriam's turkeys predominately limit diurnal activities to within 1.6 km of roosting sites (Wakeling 1997), and inadvertent removal or isolation of a roosting site, through management activities such as timber harvest, can be detrimental to Merriam's turkey populations (Scott and Boeker 1977). In recognition of this fact, protection of known roosting sites has been a practice of most land management agencies since the mid-1980s. But in many instances, documentation of roosting sites can be difficult and has not occurred. Numerous descriptions of roosting habitats have been developed (Boeker and Scott 1969, Phillips 1980, Rumble 1992), including qualitative (Mollohan et al. 1995) and mathematical models (Wakeling and Rogers 1996, 1998) that may be used to identify suitable roosting areas. Turkeys seem to select roosting sites in part by individual tree characteristics, yet no mathematical model is available to assist in the identification of suitable roost trees.

We studied the differences between known roost trees at Merriam's turkey roosting sites in northern Arizona and paired, randomly located ponderosa pine trees ≥40cm dbh. Our objective was to infer from this comparison if Merriam's turkeys differentiated among large trees when selecting roosts. A second objective was to develop a mathematical model that would assist resource managers to more easily identify suitable roosting trees in north-central Arizona.

STUDY AREA

We studied roost trees in ponderosa pine forests south of Flagstaff, Arizona, on the Coconino National Forest and south of Winslow, Arizona, on the Apache-Sitgreaves National Forests. All roosting sites occurred within mixed conifer or ponderosa pine habitat associations, at elevations of 1,850 to 2,450 m, within areas that had been previously studied by Mollohan et al. (1995) and Wakeling and Rogers (1998). Greater detail of habitat descriptions may be found in Wakeling and Rogers (1998).

METHODS

We measured characteristics associated with 13 ponderosa pine trees that had been used by roosting Merriam's turkeys and on 13 paired, randomly located ≥40 cm dbh ponderosa pine trees. We randomly selected 1-2 roost trees from eight roosting sites that had been located during previous Merriam's turkey research studies (Mollohan et al. 1995, Wakeling and Rogers 1996, 1998). The random roost trees were selected by identifying the closest known roost tree on a computer-generated random bearing from the geographic center of a roosting site. The eight roosting sites represented three winter roosts, three summer roosts, and two roosts from yearlong range. We sampled two trees from each winter and yearlong roosting site and one tree from each summer roosting site because winter and yearlong roosting sites contained 2-3 times as many trees as summer roosting sites.

We measured the following variables specific to each roost tree: dbh with a diameter tape; tree height and height to first limb by measuring a known distance perpendicular to the tree with a tape and using a clinometer to measure angles to the apex, first limb, and base of the tree; age of tree, by extracting a core sample from the tree with an increment bore (the sample was marked and tree rings enumerated later using a 10X magnification microscope in the laboratory); and presence or absence of horizontal branches >3 cm diameter within the upper third of the tree crown that approximated a level perching surface (i.e., < 10% slope).

In addition, we collected information pertaining to the site surrounding the roost tree. We measured slope (%) from 15 m above to 15 m below the roost tree using a clinometer. Stem density of trees >2.5 cm dbh was enumerated on a 0.05-ha circular plot (12.6-m radius). We calculated percent canopy closure according to Strickler (1959) by taking readings with a spherical densiometer at site center and at 12.6 m from site center on four bearings, each 90 degrees from the previous, with the first bearing randomly oriented. We used a 10-factor prism to estimate basal area (BA) surrounding the roost tree.

Immediately upon completing measurements on the roost tree, we randomly located a ponderosa pine tree >40 cm dbh for comparison. These random trees included trees within and outside the roosting site because we were unable to determine conclusively if all trees within a site had been used for roosting. To locate random trees, we walked a computer-generated random bearing for a distance of 40-500m. When we reached the random distance, we continued along the bearing until encountering the first ponderosa pine tree >40 cm dbh. We then recorded the same measurements taken at the roost tree.

We analyzed data using paired *t*-tests for continuous data (i.e., age, diameter, height, stem density, BA, slope, height to first limb, and canopy closure) and contingency tables for categorical data (i.e., horizontal branch presence). We then included all variables in a forward-stepwise logistic regression equation (Hosmer and Lemeshow 1989) to determine what variables best predicted roost tree identification.

RESULTS

We found that many characteristics differed between roost and random trees: roost trees averaged greater age ($P = 0.007$), dbh ($P < 0.001$), height ($P < 0.001$), height to first limb ($P = 0.063$), and basal area (BA) ($P = 0.086$) surrounding the tree (Table 1). Roost and random trees had the same number of horizontal branches (12 of 13) while slope and percent canopy closure did not differ between sites. The logistic regression model correctly classified 92.3% of roost vs. non-roost trees at all locations (Table 2). In this model, roost trees were associated with greater tree dbh and surrounding BA than were randomly located trees >40 cm dbh.

Table 1. Mean (SD) and paired *t*-test probabilities (*P*) for characteristics of random ponderosa pine trees and those selected for roosting by Merriam's turkeys, in north-central Arizona.

Characteristic	Roost tree (n = 13)	Random tree (n = 13)	*P*
Age of tree (years)	161.5 (48.8)	104.6 (49.5)	0.007
Diameter at breast height (cm)	71.4 (12.0)	48.1 (7.6)	<0.001
Height of tree (m)	27.1 (4.0)	19.1 (5.1)	<0.001
Stem density on 0.5-ha circular plot	21.0 (9.8)	19.9 (12.2)	0.792
Basal area surrounding roost tree (m^2/ha)	21.5 (8.3)	16.2 (6.7)	0.086
Slope at roost tree (%)	15.8 (11.2)	16.2 (15.4)	0.931
Height to first limb (m)	5.9 (2.5)	3.9 (2.7)	0.063
Canopy closure (%)	49.3 (15.9)	44.2 (21.8)	0.503

Table 2. Logistic regression model (logit scale) explaining ponderosa pine roost tree selection by Merriam's turkey in north-central Arizona.

n		χ^2	*P*	Model[a]	Percent correct		
Used	Random				Used	Random	Overall
13	13	26.5	<0.001	Y=-20.266+0.055BA+0.274DBH	92.3	92.3	92.3

[a] BA is the basal area (m^2/ha) surrounding the roost tree, and DBH is the diameter at breast height (cm) of the roost tree.

DISCUSSION

Although many studies have found that 40 cm dbh was the minimum size roost tree used by Merriam's turkeys, and large, overmature ponderosa pine trees are most suitable for roosting, we speculate that 40 cm dbh is not a functional minimal threshold for roost tree diameter. Rumble (1992) found Merriam's turkeys using ponderosa pine trees < 40 cm dbh in the Black Hills, South Dakota, but these were the largest trees available on his study site. Because turkeys strongly favored trees that were older, taller, and larger diameter than the average ≥40 cm dbh tree in our study, we suggest that there may not be a critical minimum above which tree diameter becomes irrelevant. Although Merriam's turkeys inhabit areas that lack larger trees, they seem to consistently prefer the largest available trees.

Basal area (BA) is apparently also influential in the selection of roost trees. Greater BA seems favorable to roosting site selection regardless of maximum available BA. Even in South Dakota second growth ponderosa pine, Rumble (1992) found Merriam's turkeys roosting in sites with >20 m^2/ha BA. Thus, selection of roosting sites by Merriam's turkeys consistently favors older, mature trees with high surrounding BA.

Our logistic regression model can be used to assist in prioritizing potential roosting sites and roost trees when planning land management activities such as timber harvest or other impact developments. This roost tree model can be used in conjunction with broader scale models provided for roosting site selection during winter (Wakeling and Rogers 1996) or summer (Wakeling and Rogers 1998; Table 3). Roosting site models could be used to identify potential roosting habitat, whereas the roost tree model could be used to assist with ranking priorities on trees within those potential sites. Sites with similar scores from roosting habitat models could be protected and managed for roosting habitat regardless of the score, if Merriam's turkeys are a featured management species. In accordance with Wakeling (1997), roosting sites should be managed at tree densities of ≥1.25/km^2.

Table 3. Logistic regression models (logit scale) describing Merriam's turkey roosting site selection during winter and summer in north-central Arizona.

Season	Model[a]	Citation
Winter	Y = -21.290 + 9.803CPY + 0.742PD +0.386SLOPE	Wakeling and Rogers (1996)
Summer	Y = -6.614 + 1.435CG + 0.160PBA + 0.101SLOPE	Wakeling and Rogers (1998)

[a] CPY is closed overhead canopy presence (absent = 0, present = 1), PD is the mean ponderosa pine diameter at breast height (cm), SLOPE is slope at site (%), CG is conifer ground cover <46 cm in height (%), and PBA is the basal area provided by ponderosa pine at the site (m^2/ha).

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LITERATURE CITED

Boeker, E. L., and V. E. Scott. 1969. Roost tree characteristics of Merriam's turkey. Journal of Wildlife Management 33: 121-124.

Hoffman, D. M. 1968. Roost sites and habits of Merriam's turkeys in Colorado. Journal of Wildlife Management 32: 859-866.

Hosmer, D. W., Jr., and S. Lemeshow. 1989. Applied logistic regression. John Wiley and Sons, Inc., New York. 307pp.

Mackey, D. L. 1984. Roosting habitat of Merriam's wild turkeys in south-central Washington. Journal of Wildlife Management 48: 1377-1382.

Mollohan, C. M., D. R. Patton, and B. F. Wakeling. 1995. Habitat selection and use by Merriam's turkey in northcentral Arizona. Arizona Game and Fish Department Technical Report 9, Phoenix. 46pp.

Phillips, F. 1980. A basic guide to roost site management for Merriam's turkeys. Arizona Game and Fish Department Wildlife Digest 12, Phoenix. 6pp.

Rumble, M. A. 1992. Roosting habitat of Merriam's turkeys in the Black Hills, South Dakota. Journal of Wildlife Management 56: 750-759.

Schemnitz, S. D., D. L. Goerndt, and K H. Jones. 1985. Habitat needs and management of Merriam's turkey in New Mexico. Proceedings of the National Wild Turkey Symposium 5: 199-231.

Scott, V. E., and E. L. Boeker. 1977. Responses of Merriam's turkey to pinyon-juniper control. Journal of Range Management 30: 220-223.

Strickler, G. S. 1959. Use of the densiometer to estimate density of forest canopy on permanent sample plots. USDA Forest Service Research Note PNW-180. 5pp.

Wakeling, B. F. 1997. Winter movement patterns of Merriam's turkeys in north-central Arizona. Proceedings of the Biennial Conference of Research on the Colorado Plateau 3: 93-100.

Wakeling, B. F., and T. D. Rogers. 1996. Winter diet and habitat selection by Merriam's turkeys in north-central Arizona. Proceedings of the National Wild Turkey Symposium 7: 175-184.

Wakeling, B. F., and T. D. Rogers. 1998. Summer resource selection and yearlong survival of male Merriam's turkeys in north-central Arizona, with associated implications from demographic modeling. Arizona Game and Fish Department Technical Report 28, Phoenix. 50pp.

The Suitability of Butterflies as Indicators of Ecosystem Condition: A Comparison of Butterfly Diversity Across Stand Treatments in Northern Arizona

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Abstract. Past human activities have resulted in a broad spectrum of ponderosa pine (*Pinus ponderosa*) stand conditions on the Colorado Plateau. A team of researchers at Northern Arizona University's School of Forestry is using common experimental plots to evaluate how highly-variable forest conditions influence potential ecological indicator species and guilds. Butterflies are one of several insect guilds that we are evaluating. During 1997 and 1998, we monitored populations of adult butterflies within replicated unmanaged, thinned, thinned and prescribed-burned, and wildfire-affected ponderosa pine sites. We did not detect a significant effect of stand treatment on butterfly abundance or similarity at the family level after two years, despite our large plot size (20-80 ha). Important treatment effects may be masked by butterfly movement between plots, heterogeneous forest stand structure, time since treatment, number of stands sampled, climate, and our sampling of adult butterflies. We suggest that sampling effort should be increased and data analyzed at the species level to quantify butterfly response to stand treatment.

Key words: Lepidoptera, *Pinus ponderosa*, indicator species, forest treatments, thinning, prescribed fire, wildfire

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INTRODUCTION

Past human activities (e.g, logging, grazing, fire suppression) have impacted stand conditions in ponderosa pine forests across the Colorado Plateau (Weaver 1951, Covington et al. 1997). The combination of past human activities has lead to structural and functional forest changes, often resulting in dense stands with low understory plant diversity (Harrington and Sackett 1992, White 1985, Covington and Moore 1994, Fulé et al. 1997). A team of researchers (STIFH, Stand Treatment Impacts on Forest Health) at Northern Arizona University's School of Forestry is evaluating the effects of past stand treatments on insects, fungi, understory plants, forest structure, and eventually ecosystem function. Butterflies (Lepidoptera) are one of several guilds that we are evaluating as a potential ecological indicator of forest condition in northern Arizona. Our goal is to find a group of species that is easy to evaluate, in addition to exhibiting changes in abundance and richness in response to differences in stand treatments.

Indicator species are thought to either signal the presence/abundance of other species, or to signal chemical/physical changes in the environment through changes in their own presence or abundance (Landres et al. 1988, Simberloff 1998). The second of these types of indicators is referred to as an ecological indicator (McGeoch 1998). One of the key goals in using an indicator is to simplify measurements of a complex system without losing important information (Ferris and Humphrey 1999). A number of authors have proposed criteria for selecting indicator species (e.g., Landres et al. 1988, Rodriguez et al. 1998, Ferris and Humphrey 1999). Recently, Hilty and Merenlender (2000) organized and compiled these criteria into a comprehensive list. They suggest that no indicator can meet all the suggested criteria, but should meet a majority of the standards.

In many regions of the world, Lepidoptera are widely accepted as ecological indicators of ecosystem health (Rosenberg et al. 1986, New et al. 1995, Beccaloni and Gaston 1995, Oostermeijer and van Swaay 1998), and meet a number of the criteria set forth by Hilty and Merenlender (2000). Butterflies have a fairly clear taxonomy, and their life history and biology are well defined (Nelson and Anderson 1994, Wood and Gillman 1998). Many of their physiological tolerances, such as light, temperature, and habitat requirements, have been quantified (Warren 1985, Thomas and Harrison 1992, Greatorex-Davies et al. 1993, Sparks et al. 1996, Oostermeijer and Swaay 1998, Pollard et al. 1998), and correlations with changes in ecosystem conditions have been demonstrated (Bowman et al. 1990, Thomas and Harrison 1992, Hill et al. 1995, Pullin 1996, Sparks et al. 1996, Spitzer et al. 1997, Pollard et al. 1998, Schultz 1998, Swengel 1998). In addition, butterflies are small, have high reproductive rates, and are at a low trophic level that allow them to quickly respond to environmental stress. Many butterflies specialize on a specific plant species for oviposition or feeding (Ehrlich 1984, Oostermeijer and van Swaay 1998). Butterflies tend to be easy to find and measure. Also, they are charismatic, and the public tends to show interest in them.

There are drawbacks to using butterflies as ecological indicators: (1) they are fairly mobile and may be able to tolerate some levels of disturbance because of their ability to move and find resources; (2) their ability to respond to change can be a hindrance in areas with high climatic variability, as changes detected in their abundance may be in response to a climatic condition instead of ecosystem structure (Pollard and Yates 1993).

We evaluated how the abundance and diversity of butterflies varied among four replicated forest treatments in northern Arizona. We hypothesized that butterfly abundance and diversity should be lower in unmanaged areas than in treated stands, and that high intensity fire (represented by stand-replacing wildfire) should correlate with high butterfly abundance and diversity. Another study, using our same stands and other stands from the STIFH project, found the abundance of nectar-bearing plants highest in stands that experienced wildfire, and lowest in stands that did not have applied silvicultural treatments (Griffis et al. 2001). We attempt, by showing correlations between butterfly abundance and diversity, to assess the suitability of using butterflies as environmental indicators in northern Arizona ponderosa pine forests.

METHODS

Study Site

The study area, located on the Coconino Plateau in northern Arizona (Fig. 1), is approximately 2,000 to 2,450 m elevation in a ponderosa pine/Arizona fescue (*Pinus ponderosa* Dougl. ex Laws /*Festuca arizonica* Vasey) association (USDA Forest Service 1997). The dominant overstory species was *Pinus ponderosa* (ponderosa pine) with a small component of *Quercus gambelii* (gambel oak). The understory is characterized by the most common native species; *Festuca arizonica*, *Elymus elymoides* (Raf.) Swezey,

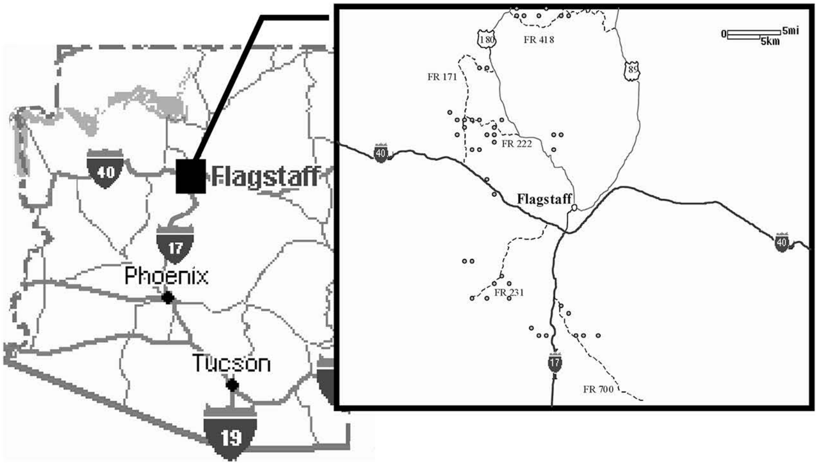

Figure 1. Location of STIFH research plots in ponderosa pine forests near Flagstaff, Arizona. Circles on inset illustrate individual plots. From Bailey et al. (this volume).

Cirsium wheeleri (Gray) Petrak., *Carex* spp., *Muhlenbergia montana* (Nutt.) A.S. Hitchc., *Lupinus argenteus* Pursh, and *Achillea millefolium* L.; and the most common exotic species; *Salsola kali* var. *tenuifolia* Tausch., *Verbascum thapsus* L., *Poa pratensis* L., *Chenopodium graveolens* Willd., *Bromus tectorum* L., and *Descurainia obtusa* (Greene) O.E. Schulz (Griffis et al. 2001). During the first year of the study (1997), three stand treatments were examined: unmanaged, thinned and burned, and wildfire. In the second year, 1998, thinned stands were sampled in addition to the 1997 treatments. Three stands per treatment were sampled in 1997; four stands per treatment were sampled in 1998. Stands ranged in size from 20-80 ha (50-200 acres).

Stands were selected randomly from a larger pool of stands used in the STIFH project (Fig. 1). Our stands were composed of mature, even-aged blackjack (younger than approximately 125 years) ponderosa pine, with larger, yellow pine (older than approximately 125 years and larger than 64 cm dbh) not exceeding 10 trees/ha. Thinned stands had greater than 30% of their basal area removed between 1987 and 1993, with at least 50% of this coming from diameter classes greater than 30 cm (pulpwood size). Thinned and prescribed burned stands additionally received a broadcast burn treatment within 3 to 4 years of thinning. Three of these stands were burned in 1991 and one in 1995. Overstory survival following the broadcast burn was greater than 90%. Unmanaged stands have not received a density altering treatment within the last 30 years, such that the stands have greater than 60% of maximum stand density index (and thus are actively self-thinning). Wildfire areas are stands in which greater than 90% of the basal area was killed and/or consumed by wildfire since 1994 (Bailey et al. 2001).

Butterfly Sampling in 1997

All butterfly specimens captured in 1997 were included in the establishment of a permanent reference collection used for identification in later studies. Two person hours of sampling were conducted at each site every three weeks for five visits from May to August 1997. Butterflies were collected using a time-constrained area search during peak flight periods (0900 to 1500 hours), using standard 18” insect collecting nets. The same people collected data throughout the year to minimize variation in collection methods. We searched the pre-delineated stand, collecting as many butterflies as possible. All specimens were handled and mounted using conventional procedures, with butterflies identified using Pyle (1981) and Tilden and Smith (1986). When further taxonomic identification was necessary, wing venation was examined, as described by Borror et al. (1976). External experts confirmed most species identification.

Butterfly Sampling in 1998

We conducted a time-constrained area search and counted all Lepidoptera observed and captured, using the same techniques and time constraints for capture as in the previous year (1997). All stands were visited once during the summer during peak butterfly activity (based on information from 1997 surveys). We only used one sampling visit based on when the largest numbers of lepidopterans were active during 1997. Butterfly populations fluctuate throughout the year based on species life history. Our goal was to assess using butterflies as a very rapid and simple indicator of the amount of disturbance in a stand; therefore, we made our sampling as simple as possible. At the end of the sampling period, we recorded the number and family of all butterflies observed and caught, and released all insects. Data were summarized at the family level because of identification ease in the field, and because others have shown responses of insects to changes in the environment at higher taxonomic and guild levels (Greenburg and McGrane 1996, Kevan 1999).

Data Analysis

We used data from 1997 to calculate Jaccard's similarity index to compare the similarity of butterfly species across treatments. Data from 1997 and 1998 were analyzed separately due to differences in sampling procedures. The butterfly numbers in 1997, by family, were averaged across repeated sampling over time to calculate one number per family per plot. We used Kruskal-Wallis rank tests to assess variation in number of individuals per family, by treatment type for both years.

RESULTS

The numbers of individuals caught in each treatment for each butterfly family in the analyses are listed in Table 1. A list of butterfly species caught during 1997 and verified to species is listed in Table 2. The total number of butterflies did not vary among treatment types for either 1997 ($\chi^2 = 0.622$, df = 2, p = 0.733) or 1998 ($\chi^2 = 0.969$, df = 3, p = 0.809). Neither species similarity nor abundance of butterflies by families was significantly different across the four experimental treatments. Butterfly similarity from Jaccard's similarity index, were statistically equal in 1997 across the experimental treatments (Table 3). These analyses were not repeated in 1998. Likewise, total abundance of butterflies distributed by treatment type was not statistically significant in either 1997 or 1998 (Table 4).

Table 1. The numbers of individuals within families of Lepidoptera captured (1997) and captured and observed (1998) in ponderosa pine cover type under four experimental stand conditions (unmanaged, thinned, thinned and burned, and wildfire) on the Coconino National Forest.

Family	**Unmanaged**		**Thinned**		**Thinned and Burned**		**Wildfire**	
	97'	**98'**	**97'**	**98'**	**97'**	**98'**	**97'**	**98'**
Lycanidae	6	81	-	59	3	79	1	43
Peridae	26	9	-	4	26	20	12	27
Nymphalidae	1	18	-	16	1	2	13	26
Hesperidae	0	3	-	3	0	2	1	5
Papilionidae	0	0	-	0	0	0	0	1

Table 2. Species of butterflies collected and verified in 1997 and 1998 in ponderosa pine cover type under four experimental stand conditions (unmanaged, thinned, thinned and burned, and wildfire) on the Coconino National Forest.

Family	Scientific Name	Common Name
PIERIDAE:	*Neophasia menapia*	Pine White
	Pontia protodice	Checkered White
	Colias eurytheme	Orange Sulphur
	Nathalis iole	Dainty Sulphur
LYCAENIDAE:	*Callophrys eryphou*	Western Pine Elfin
	Strymon melinus	Gray Hairstreak
	Hemiargus isola	Reakirt's Hairstreak
	Celastrina ladon	Spring Azure
	Lycaeides melissa	Melissa Blue
	Icaricia icariodes	Boisduval's Blue
	Icaricia lupini	Lupine Blue
NYMPHALIDAE:	*Euptoieta claudia*	Variegated Fritillary
	Poladryas minuta	Dotted Checkerspot
	Vanessa cardui	Painted Lady
	Vanessa virginiensis	American Lady
	Phyciodes pratensis	Field Crescent
HESPERIDAE:	*Pyrgus communis*	Common Checkered-Skipper

The butterfly community in this ponderosa pine system is dominated by three families: Lycaenidae, Pieridae, and Nymphalidae. The abundance of individuals within these families varied between years (Fig. 2). There appeared to be a trend of decreased abundance of lycanid butterflies across the treatment gradient in both years. There was an increase in perid butterflies across the same gradient in 1998, but a decrease in 1997. There may also be an increase in nymphalid species for both years across the disturbance gradient (Fig. 2).

DISCUSSION

We did not detect differences in butterfly abundance or diversity among forest treatments, but a similar study focused on forest restoration, including thinning and

Table 3. Jaccard's similarity index calculated based on butterfly species similarity for 1997 sampling on the Coconino National Forest.

Comparison	Jaccard's Similarity Index
Thinned and Prescribed Burned vs. Control	0.575
Thinned and Burned vs. Wildfire	0.650
Wildfire vs Control	0.575

Table 4. Results from Kruskal-Wallis rank tests on the distribution of butterfly families among treatments (unmanaged, thinned, thinned and prescribed burned, stand replacing wildfire) for 1997 and 1998 on the Coconino National Forest, northern Arizona.

Family		χ^2	df	P-value
1997	Lycaenidae	2.249	2	0.325
	Pieridae	1.689	2	0.430
	Nymphalidae	3.684	2	0.159
	Hesperidae	2.889	2	0.236
1998	Lycaenidae	1.994	3	0.574
	Pieridae	2.051	3	0.562
	Nymphalidae	6.357	3	0.095
	Hesperidae	0.489	3	0.921
	Papilionidae	3.000	3	0.392

burning treatments in northern Arizona, demonstrated increased species richness and abundance in treated areas of the ponderosa pine forest (Waltz and Covington 1999). Their study concluded that there was an increase in butterfly abundance, correlated with an increase in flowering plants, in response to restoration treatments. However, their study compared a single transect in a thinned and burned stand with a single control-stand transect. Their lack of replication can decrease variance and artificially increase the chances of detecting significant relationships between treatments and butterflies.

Other studies have detected changes in abundances of various insect taxa, including butterflies, in response to silvicultural treatments (Greenburg and McGrane 1996, Swengel 1998, Wood and Gillman 1998). Furthermore, some have suggested that sampling at the genus or family level of insects may give enough detailed information to permit evaluation of the health or sustainability of the system in question (Paoletti 1999). However, when the butterflies are lumped by family, it is likely that individual species effects are masked (Weaver 1995). Species within a family vary in their life histories and, hence, may vary in their responses to environmental perturbation. It is often at the individual or population level that organisms respond to changes in the environment (Maltby 1999). Future work should include a focus on individual species, as well as the family, and in particular species and families that are relatively abundant but specific in their ecological requirements (Thomas and Mallorie 1985).

We also want to point out that butterfly numbers varied greatly between years. This variation could be an artifact of our small sample size. In addition, at high elevations climatic conditions (e.g., temperature, precipitation, wind) can vary erratically and cyclically between years (Gass and Lertzman 1980, Griffis 1999). Butterflies

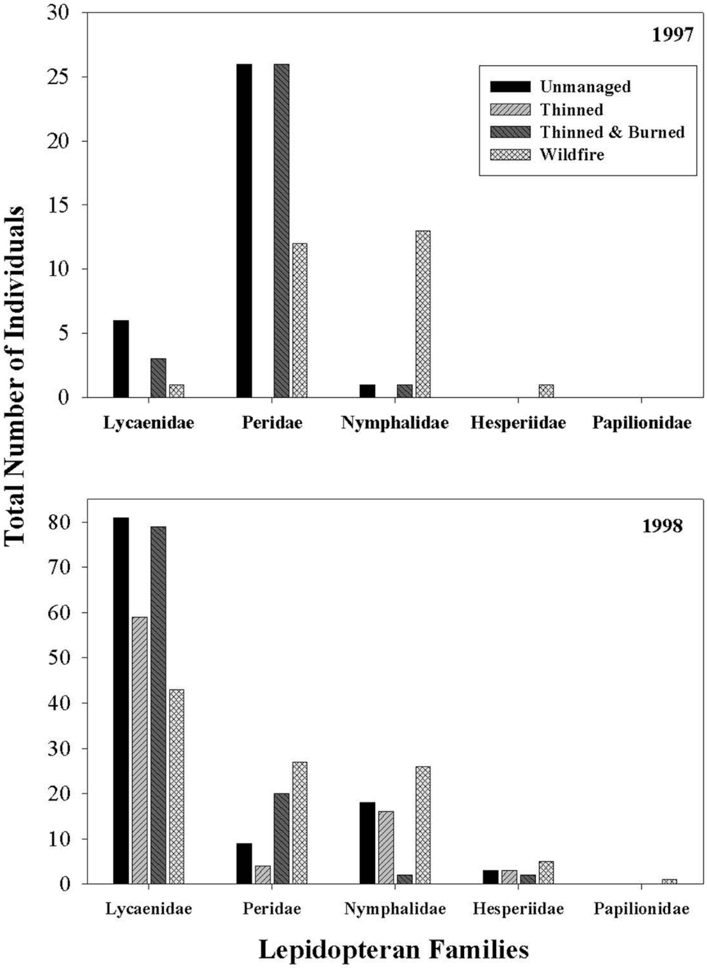

Figure 2. Total numbers of butterflies observed and captured; grouped by family during 1997 and 1998 in relation to forest stand treatments on the Coconino National Forest. Notice the difference in scales between graphs.

may respond more directly to climatic conditions than to stand conditions (Pollard and Yates 1993). This alone would make them very difficult to utilize as an indicator of stand condition. In addition, when surveying, we recorded adult butterfly diurnal behavior and did not measure butterfly fitness (i.e., survival or reproductive success) in relation to habitat patch. If butterflies disperse from a source population into marginal habitat, we may just be measuring density dependent population responses or dispersal events, and not responses to stand condition.

Finally, the methods that we used in this study may be better used for assessing presence or absence of a species/family (e.g., Thomas and Harrison 1992). We suggest using transect counts, which can give quantitative estimates of abundance based on area, and may be better used to quantify butterfly abundance in heterogeneous forest stands (Pollard et al. 1975, Thomas 1983).

We suggest that at the family level, butterflies may not be an indicator of ecosystem health that is both simply and rapidly measured. It is possible, with a sampling design based on achieving quantitative estimates of abundance and species identification, butterflies could be used as ecosystem indicators. However, in an arid environment such as northern Arizona, achieving a sample size large enough to account for climatic variation may be difficult. Also, the length of response time from treatment may influence butterfly presence.

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LITERATURE CITED

Bailey, J.D., M.R. Wagner, and J. Smith. 2001. Stand Treatment Impacts on Forest Health (STIFH): Structural Responses Associated with Silvicultural Treatments. Pages 137-145 *in* C. van Riper III, K.A. Thomas, and M.A. Stuart, (eds.). Proceedings of the Fifth Biennial Conference of Research on the Colorado Plateau. October 25-27, 1999. Flagstaff, AZ.

Beccaloni, G.W., and K.J. Gaston. 1995. Predicting the species richness of Neotropical forest butterflies: Ithominae (Lepidoptera: Nymphalidae) as indicators. Biological Conservation 71: 77-86.

Borror, D.J., D.M. Delong, and C.A. Triplehorn. 1976. An Introduction to the Study of Insects, Fourth Edition. Holt, Rhinehart and Winston. New York. 852 pp.

Bowman, D.M, J.C. Woinarski, D.P. Sands, A. Wells, and V.J. McSHane. 1990. Slash-and-burn agriculture in the wet coastal lowlands of Papua New Guinea: response of birds, butterflies and reptiles. Journal of Biogeography. 17: 227-239.

Covington, W.W., and M.M. Moore. 1994. Southwestern ponderosa pine forest structure and resource conditions: changes since Euro-American settlement. Journal of Forestry 92: 39-47.

Covington, W.W., P.Z. Fulé, M.M. Moore, S.C. Hart, T.E. Kolb. J.N. Mast, S.S. Sackett, and M.R. Wagner. 1997. Restoring ecosystem health in ponderosa pine forests of the Southwest. Journal of Forestry 95: 23-29.

Ehrlich, P.R. 1984. The structure and dynamics of butterfly populations. Pages 25-40 *in* R. I. Vane-Wright and P. R. Ackery, (eds.). The Biology of Butterflies. Academic Press, London.

Ferris, R., and J.W. Humphrey. 1999. A review of potential biodiversity indicators for application in British forests. Forestry 72: 313-328.

Fulé, P.Z., W.W. Covington, and M.M. Moore. 1997. Determining reference conditions for ecosystem management of southwestern ponderosa pine forests. Ecological Applications 7: 895-908.

Gass, C.L., and K.P. Lertzman. 1980. Capricious mountain weather: a driving variable in hummingbird territorial dynamics. Canadian Journal of Zoology 58: 1964-1968.

Greatorex-Davies, J.N., T.H. Sparks, M.L. Hall, and R.H. Marrs. 1993. The influence of shade on butterflies in rides of coniferised lowland woods in southern England and implications for conservation management. Biological Conservation 63: 31-41.

Greenberg, C.H., and A. McGrane. 1996. A comparison of relative abundance and biomass of ground-dwelling arthropods under different forest management practices. Forest Ecology and Management 89: 31-41.

Griffis, K.G. 1999. Bird use of small aspen stands in northern Arizona. MS Thesis, Northern Arizona University.

Griffis, K.G., J.A. Crawford, M.R. Wagner, and W.H. Moir. 2001. Understory response to management treatments in northern Arizona ponderosa pine forests. Forest Ecology and Management 146: 239-245.

Harrington, M.G., and S.S. Sackett. 1992. Past and present fire influences on southwestern ponderosa pine old-growth. Pages 44-50 *in* M.R. Kaufmann, W.H. Moir, and R.L. Bassett, technical coordinators. Old-growth forests in the Southwest and Rocky Mountain regions, Portal Arizona; March 3-19, 1992. U.S. Department of Agriculture, Forest Service General Technical Report RM-213. Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.

Hill, J.K., K.C. Hamer, L.A. Lace, and W.M.T. Banham. 1995. Effects of selective logging on tropical forest butterflies on Buru, Indonesia. Journal of Applied Ecology 32: 754-760.

Hilty, J., and A. Merenlender. 2000. Faunal indicator taxa selection for monitoring ecosystem health. Biological Conservation 92: 185-197.

Kevan, P.G. 1999. Pollinators as bioindicators of the state of the environment: species, activity and diversity. Agriculture Ecosystems and the Environment 74: 373-393.

Landres, P B., J. Verner, and J.W. Thomas. 1988. Ecological uses of vertebrate indicator species: a critique. Conservation Biology 2: 316-328.

Maltby, L. 1999. Studying stress: the importance of organism level responses. Ecological Applications 9: 431-440.

McGeoch, M.A. 1998. The selection, testing and application of terrestrial insects as bioindicators. Biological Review 73: 181-201.

Nelson, S.M., and D.C. Anderson. 1994. An assessment of riparian environmental quality by using butterflies and disturbance susceptibility scores. The Southwestern Naturalist 39: 137-142.

New, T.R., R.M. Pyle, J.A. Thomas, C.D. Thomas, and P.C. Hammond. 1995. Butterfly conservation management. Annual Review of Entomology 40: 57-83.

Oostermeijer, J.G.B., and C.A.M. van Swaay. 1998. The relationship between butterflies and environmental indicator values: a tool for conservation in a changing landscape. Biological Conservation 86: 271-280.

Paoletti, M.G. 1999. Using bioindicators based on biodiversity to assess landscape sustainability. Agriculture, Ecosystems and Environment 74: 1-18.

Pollard, E., D.O. Elias, M.J. Skelton, and J.A. Thomas. 1975. A method of assessing the abundance of butterflies in Monks Wood National Nature Reserve in 1973. Entomologist's Gazette 26: 79-88.

Pollard, E., and T.J. Yates. 1993. Monitoring Butterflies for Ecology and Conservation: The British Butterfly Monitoring Scheme. Chapman and Hill, London.

Pollard, E., I.P. Woiwod, J.N. Greatorex-Davies, T.J. Yates, and R.C. Welch. 1998. The spread of coarse grasses and changes in numbers of Lepidoptera in a woodland nature reserve. Biological Conservation 84: 17-24.

Pullin, A.S. 1996. Restoration of butterfly populations in Britain. Restoration Ecology 4: 71-81.

Pyle R.M. 1981. National Audubon Society Field Guide of North American Butterflies. Chanticleer Press, Inc. New York. 924 pp.

Rodriguez, J.P., D.L. Pearson, and R. Barrera. 1998. A test for the adequacy of bioindicator taxa: are tiger beetles (Coleoptera: Cicindelidae) appropriate indicators for monitoring the degradation of tropical forests in Venezuela? Biological Conservation 83: 69-76.

Rosenberg, D.M., H.V. Danks, and D.M. Lehmkuhl. 1986. Importance of insects in environmental impact assessment. Environmental Management 10: 773-783.

Schultz, C.B. 1998. Dispersal behavior and its implications for reserve design in a rare Oregon butterfly. Conservation Biology 12: 248-292.

Simberloff, D. 1998. Flagships, umbrellas, and keystones: is single-species management passe in the landscape era? Biological Conservation 83: 247-257.

Sparks, T.H., J.N. Greatorex-Davies, J.O. Mountford, M.L. Hall, and R.H. Marrs. 1996. The effects of shade on the plant communities of rides in plantation woodland and implications for butterfly conservation. Forest Ecology and Management. 80: 197-207.

Spitzer, K., J. Jaros, J. Havelka, and J. Leps. 1997. Effects of small-scale disturbance on butterfly communities of an Indochinese montane rainforest. Biological Conservation 80: 9-15.

Swengel, A.B. 1998. Effects of management on butterfly abundance in tallgrass prairie and pine barrens. Biological Conservation 83: 77-89.

Thomas C.D., and S. Harrison. 1992. Spatial dynamics of a patchily distributed butterfly species. Journal of Animal Ecology 61: 437-446.

Thomas, C.D., and H.C. Mallorie. 1985. Rarity, species richness and conservation: butterflies of the Atlas Mountains in Morocco. Biological Conservation 33: 95-117.

Thomas, J.A. 1983. A quick method for estimating butterfly numbers during surveys. Biological Conservation 27: 195-211.

Tilden J.W., and A.C. Smith. 1986. The Peterson Field Guide to Western Butterflies. Houghton Mifflin Company. New York.

USDA Forest Service. 1997. Plant Associations of Arizona and New Mexico, Edition 3 Habitat Typing Guide. Volume 1: Forests. USDA Forest Service Southwestern Region. Albuquerque, NM. 291 pp.

Waltz, A.E.M., and W.W. Covington. 1999. Butterfly richness and abundance increase in restored ponderosa pine ecosystem (Arizona). Ecological Restoration 17: 244-246.

Warren, M.S. 1985. The influence of shade on butterfly numbers in woodland rides with special reference to the wood white *Leptidea sinapis*, Biological Conservation 33: 147-164.

Weaver, H. 1951. Fire as an ecological factor in southwestern ponderosa pine. Journal of Forestry 49: 93-98.

Weaver, J.C. 1995. Indicator species and scale of observation. Conservation Biology 4: 939-942.

White, A.S. 1985. Presettlement regeneration patterns in a southwestern ponderosa pine stand. Ecology 66: 589-594.

Wood, B., and P. Gillman. 1998. The effects of disturbance on forest butterflies using two methods of sampling in Trinidad. Biodiversity and Conservation 7: 597-616.

Stand Treatment Impacts on Forest Health (STIFH): Structural Responses Associated with Silvicultural Treatments

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Abstract: A major gap currently exists in our understanding of how landscape-level operational silviculture affects ponderosa pine (*Pinus ponderosa*) forest ecosystem health in northern Arizona. More than 70% of our forested landscape is in relatively young, even-aged stands resulting from a history of grazing, fire exclusion, atypical climatic events, and large ('yellow') pine removal. This multi-year, multiple-investigator project specifically examined stands that have been thinned to improve forest ecosystem health, or similarly thinned and then treated with prescribed underburning. These two treatments were not different from one another with respect to any aboveground structural characteristic. However, every measure of living overstory density (trees and saplings) was lower in thinned treatments than in untreated stands, and mean tree size (stem and crown) was consistently greater in thinned treatments. Areas burned by stand-replacing wildfire in 1996, now without an overstory, had zero seedlings and saplings as well as greater densities of standing dead trees than treated and untreated stands. The STIFH project as a whole is examining a range of species-specific and ecosystem responses to this spectrum of stand conditions, including fungi, insect, and understory plant composition.

Key words: ponderosa pine, forest ecosystem health, silviculture, thinning, prescribed fire.

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INTRODUCTION

A major research gap currently exists in our understanding of how landscape-level operational stand treatments, like thinning and prescribed fire, affect forest development and health in northern Arizona. In 1998, Northern Arizona University's School of Forestry began to fill that gap with a multi-year, multiple-investigator research project in the ponderosa pine (*Pinus ponderosa* var. *scopulorum*) forests of the Coconino and Mogollon Plateaus. We identified treatment specifics and stands that could potentially be used for a broad forest ecosystem health study that examines aboveground forest structure, soils, and insect and fungal populations (Harvey 1994).

As many in northern Arizona are aware, a large percentage of our forested land is in relatively young, dense even-aged stands. This atypical condition has resulted from a management history that includes over-grazing, fire exclusion, uncommon climatic events, and major removal of large overstory pine (Pearson 1949, Swetnam and Betancourt 1990, Covington et al. 1994, Sampson and Adams 1994). The Stand Treatment Impacts on Forest Health (STIFH) project was designed specifically to examine stands that have been treated in the last decade with either thinning (TH) or thinning with prescribed burning (TB) to reduce fuel accumulations and stimulate tree vigor, thus improving overall stand health (Sampson and Adams 1994). In addition, we examined untreated control stands (UN), with neither thinning nor fire in the last 20-30 years, and areas burned by stand-replacing wildfire in 1996 (WF). These four broad "treatments", defined below in detail, paint a wide spectrum of stand conditions available for management (Smith et al. 1996) and a broad range of disturbances both with and without fire (Fig. 1). In the future, other stand types/treatments (e.g., pine/oak mixes and large-scale ecological restoration treatments) will be available to include in the design to broaden its scope.

STIFH was designed to examine large (> 40 ha), mechanically-thinned stands with and without prescribed low-intensity surface fire. These are typical silvicultural approaches used by land managers to improve forest health, reduce the risk of wildfire, and improve aesthetics (Smith et al. 1996). Such treatments will remain as likely objectives for much of the western landscape, particularly for reducing the risk

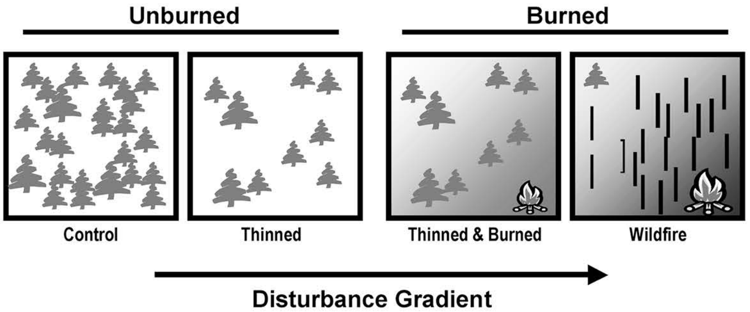


Figure 1. Conceptual representation of the four study 'treatments' arranged along a disturbance gradient, both with/without fire and with/without mechanical treatment.

of fire in the urban-wildland interface. Future treatment refinements likely will be spawned from these traditional silvicultural practices as well as new ecosystem-based management ideas and practices (including many aspects of ecological restoration). The initial four STIFH treatments represent our best first guess at two reasonable silvicultural options and two polar alternatives currently available for comparison; they are the only treatments available in large pieces across this landscape. Large land areas are necessary for evaluation of many forest ecosystem health parameters (e.g., most wildlife habitat, plant dispersion, and watershed process issues).

METHODS

Stand Selection

The first step in this project was to identify candidate stands of greater than 40 ha on the Coconino or Mogollon Plateau (within two hours of Flagstaff) in each of the four "treatments" using the following selection criteria:

Unmanaged (UN) – stands dominated by even-aged, smaller (< 40 cm diameter at breast height (DBH)) 'blackjack' ponderosa pine trees (a common name based on bark characteristics), with only a scattering of larger (> 60 cm DBH) 'yellow' ponderosa pine, Gambel oak (*Quercus gambelii*), or other tree species. Specifically, the average density of yellow pine in this treatment does not exceed 10 trees/ha, with no stand exceeding 37 trees/ha, and oak/juniper stems comprising less than 10% of tree density. These stands had not received a density-altering treatment within the last 30 years, based on USDA Forest Service records and field observations, such that the stands have a Stand Density Index (Rieneke 1933) in excess of 270 and, thus, the trees are crowded and actively self-thinning (Smith et al. 1996). These stands serve as a control treatment for examining disturbance.

Thinned stands (TH) – stands of mature, even-aged 'blackjack' ponderosa pine, similar to the unmanaged stands (i.e., a low density of 'yellow' pine, oak and/or other species), but which have had greater than 30% of their basal area removed between 1988 and 1995. At least half of the volume removal came from diameter classes < 30 cm ('pulpwood' size). Potential stands were identified from management records available from the USDA Forest Service.

Thinned and prescribed burned stands (TB) – stands like the thinned stands that also received at least one prescribed broadcast surface burn treatment within three to four years of thinning (1989 to 1997). Overstory survival, following the broadcast burn, has been greater than 90%, indicating minimal fire disturbance to overstory trees.

Wildfire areas (WF) – stands typically like the unmanaged stands prior to a stand-replacing wildfire during the summer of 1996, in which greater than 90% of the ponderosa pine basal area (blackjack and yellow pine) was killed and/or consumed by the fire. This treatment serves as the maximum disturbance.

Ten to twenty stands were identified in each of the first three treatments, from which ten stands were selected randomly for this study (Fig. 2). Due to the limited availability of wildfire stands on comparable terrain and soil, only seven wildfire areas were identified and included in the study.

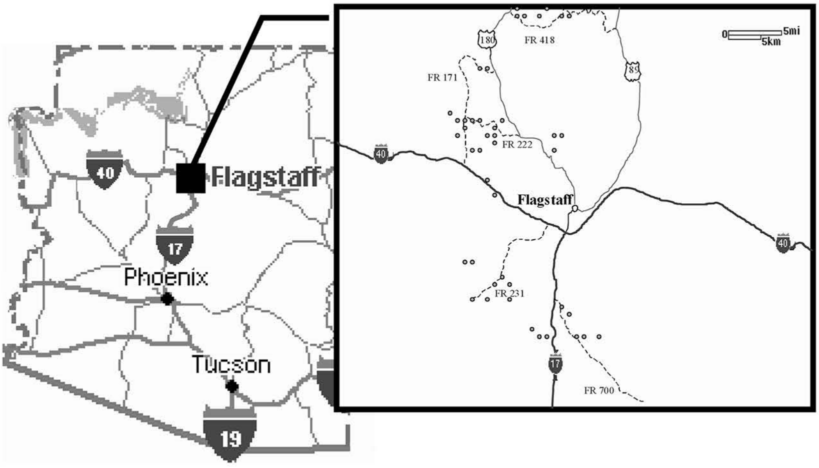


Figure 2. Location of STIFH research plots in ponderoda pine forests of northern Arizona. Circles on inset denote individual plots.

Data Collection and Analysis

Ten randomly-located (systematic following a random start), 20 m by 20 m square plots were established in each stand for sampling overstory trees, saplings (small trees between 0.1 and 7.4 cm DBH) and seedlings (Table 1) using standard forest mensurational techniques (Avery and Burkhart 1994). The intent was to augment and update existing data available for each stand, to establish permanent plot locations that can be re-measured over time, and to provide identifiable locations for sampling of other taxa (plant and animal) which may be related to tree vegetation and forest ecosystem health. Permanent plot centers were established with labeled iron pins inside painted PVC sleeves; neighboring trees were tagged with similar labels. Corners were pin-flagged for delimiting the plot and corner fuel transects.

A systematic, random sample of ten plots within stands (along a grid with a random start) allowed calculation of stand means and variances for comparisons among stands, and will allow the exploration of correlations among different taxa within stands. Comparisons among treatments were based on the 7 or 10 randomly-selected stands within each treatment. Live overstory and seedling density and structure were compared among the UN, TH, and TB treatments only; the WF treatment had no live trees. We used analysis of variance (ANOVA) to test for differences in structural characteristics among the treatments. Tukey's Honestly Significant Difference (Tukey's HSD) was used as a multiple comparison test for means that had significant ($P \leq 0.05$) ANOVA results (Zar 1996).

RESULTS AND DISCUSSION

Unmanaged (UN) stands had significantly higher total tree density (trees/ha) and Stand Density Index (SDI) (Rieneke 1933) than their thinned (TH) and thinned/

Table 1. Aboveground stand structure variables collected at each plot in each stand on STIFH, near Flagstaff, Arizona

Trees greater than 7.6 cm (3 in) in 20 m by 20 m square plot - tagged:

- tree number: 1 - x,
- 1-letter species code: P = pipo, Y = yellow pipo, Q = quga, J = jude or jusc,
- DBH: with d-tape just above the nail,
- total height and height to live crown: with clinometer,
- crown radius in longest dimension and clockwise perpendicular to that radius: with distance tape,
- crown position (i.e., D = dominant, C = codominant, I = intermediate, or S = suppressed),
- Hawksworth dwarf mistletoe rating (0-6),
- bark beetle rating (0-2, see below), and
- Keen's crown classification.

Saplings less than 7.6 cm (3 in) within 20 m by 20 m square plot:

- direction and distance from point: with hand compass and distance tape, or laser,
- 1-letter species code (as above),
- DBH: with d-tape at 1.4 m (4.5 ft),
- total height and height to live crown (as above),
- crown radius in longest dimension and perpendicular to that radius (as above),
- Hawksworth dwarf mistletoe rating (as above), and
- bark beetle rating (as above).

Seedlings (saplings less than 1.4 m (4.5 ft) height) within 20 m by 20 m square plot:

- direction and distance from point (as above),
- 1-letter species code (as above),
- total height with tape, and
- severity of browse — number of past clippings/forks.

Stumps within 20 m by 20 m square plot:

- 1-letter species code, and
- inside bark diameter: with tape.

Snags, oak, and yellow pines within 50 m (164 ft) radius:

- landscape density rating (0-3, see below).

Bark Beetle Rating system (from USDA, FS Forest Insect and Diseases Field Guide):

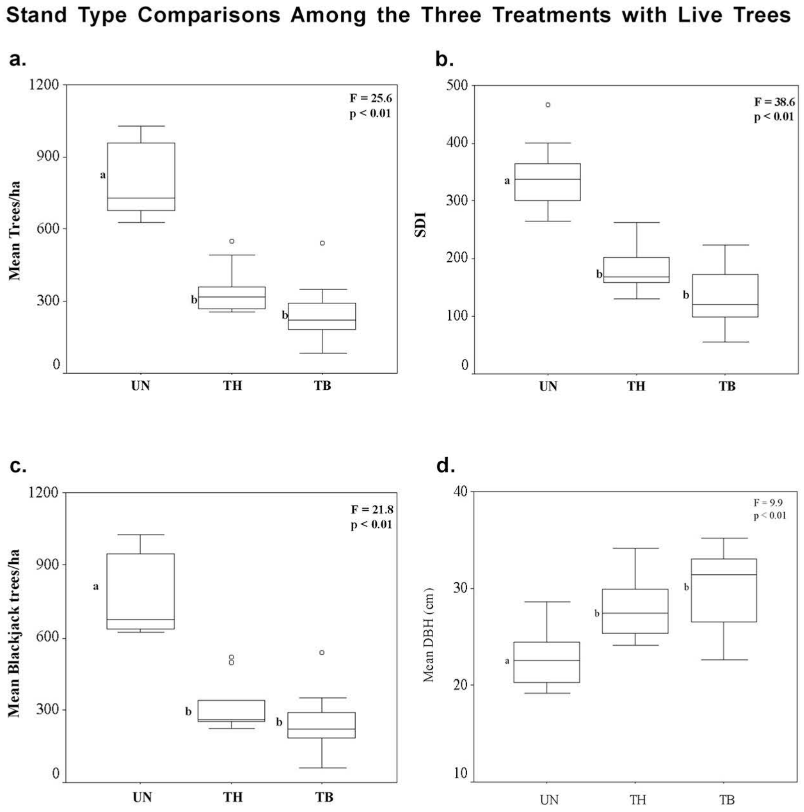
0 - no attack
1 - old attacks; pitch tubes on tree bole hard and pink to reddish. Needle color from green to yellowish-green or reddish to rusty brown.
2 - fresh attack; green needles, but with soft pinkish-white pitch tubes on the bole. Dry reddish-brown boring dust in bark crevices and at the tree base.

Snag, Oak, and Yellow Pine Landscape Density Rating system:

0 - none visible within 50 m (164 ft)
1 - low density; not in plot but less than 10 individuals within 50 m
2 - medium density; 11-20 within 50 m with perhaps some in the plot
3 - high density; greater than 20 individuals with 50 m with some in the plot.

burned (TB) counterparts (Figs. 3a and 3b). This is logical given past management that removed overstory trees, and simply confirms that thinning treatments were effective. These data also show that the TB treatment, which includes prescribed surface fire, was not significantly different from the unburned, TH treatment in terms of overstory density and, as shown below, individual tree characteristics.

Differences in density across the three treatments were traceable to a higher density of small-diameter, blackjack pine trees in UN stands (Fig. 3c), which leads to notable differences in average tree stem and crown characteristics. Unmanaged stands had lower average stem diameters at breast height (DBH), which together with shading suppression and lower average live crown ratios (LCR), led to lower average



Stand Type Comparisons Among the Three Treatments with Live Trees

Figure 3 a-d. a. Mean overstory tree density (trees/ha); b. mean Stand Density Index; c. mean density of small-diameter 'blackjack' pine trees (stems/ha); d. mean DBH (cm). ANOVA F-statistic and observed significance (p) values are shown in the upper right corner of each graph. Significant differences among individual treatment means are denoted with letters to the left of each box plot. Each whisker represents range of values. Boxes represent interquartile range. Means are lines within boxes. Outliers (circles) represent values greater than 1.5 box lengths.

crown diameters (Figs. 3d-3f). Such differences in tree characteristics are predictable given differences in overstory stand density (Smith et al. 1996). Unmanaged stands had a higher density of saplings (Fig. 3g). These saplings, however, were predominantly suppressed individuals from the same cohort as the overstory trees, rather than younger, vigorously-growing saplings that can contribute to future stand structure (Smith et al. 1996). There were no significant differences in seedling density among treatments (Fig. 3h).

Comparisons were made across all four treatments with regard to the standing dead component. Wildfire stands had significantly higher densities of standing dead trees as a result of these stand-replacing events – an efficient way to kill trees (Fig. 4).

Stand Type Comparisons Among the Three Treatments with Live Trees

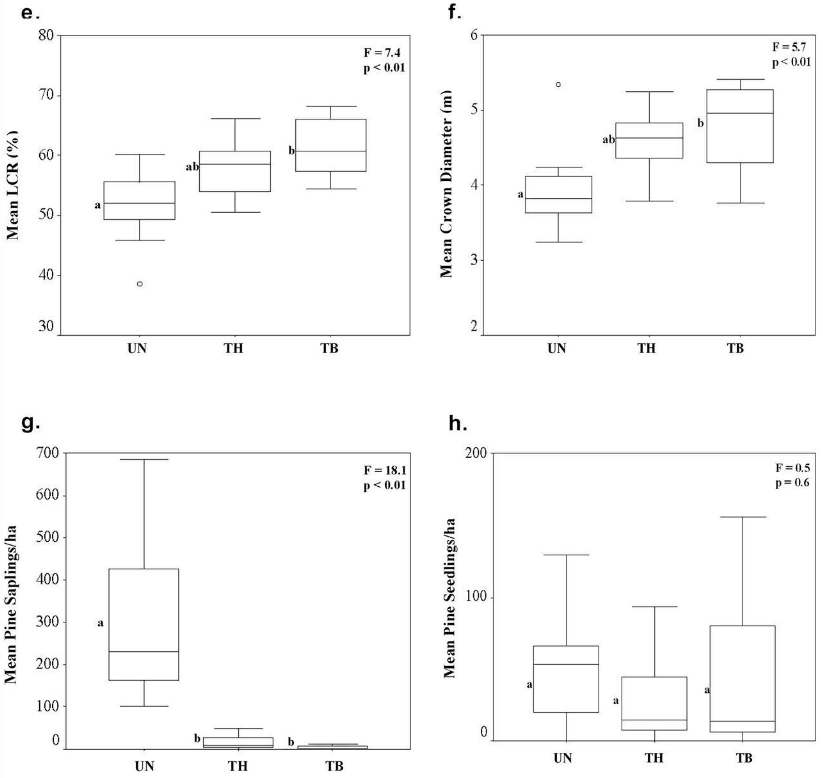


Figure 3 e-h. e. Average live crown ratio (percent); f. mean crown diameter (m); g. mean density of living saplings (stems/ha); h. mean density of living seedlings (stems/ha). ANOVA F-statistic and observed significance (p) values are shown in the upper right corner of each graph. Significant differences among individual treatment means are denoted with letters to the left of each box plot. Each whisker represents range of values. Boxes represent interquartile range. Means are lines within boxes. Outliers (circles) represent values greater than 1.5 box lengths.

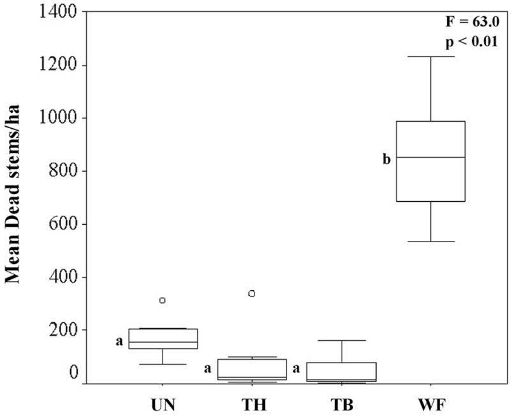


Figure 4. Mean density of standing dead trees (stems/ha). ANOVA F-statistic and observed significance (p) values are shown in the upper right corner of each graph. Significant differences among individual treatment means are denoted with letters to the left of each box plot. Each whisker represents range of values. Boxes represent interquartile range. Means are lines within boxes. Outliers (circles) represent values greater than 1.5 box lengths.

Understory prescribed burning resulted in no tree mortality, which is consistent with the fire-adapted nature of ponderosa pine (Pearson 1949, Covington et al. 1994).

MANAGEMENT IMPLICATIONS

Knowledge of aboveground structural conditions in these four treatments will develop with additional data collection and analysis to support ongoing research on various taxa associated with assessing forest ecosystem health. These first results establish that the only difference between TH and TB treatments is the prescribed underburning, which should not affect aboveground tree structure. A possible exception to this could be the impact of prescribed fire on seedling density (Bailey and Covington, in press), though these results do not show a difference in seedling density between TH and TB treatments. Analysis of fuels transect data were not available to truly characterize the TB treatment.

Unmanaged stands were high-density stands with an over-abundance of smaller diameter, suppressed ponderosa pine and associated ecosystem conditions identified by Covington et al. (1994). These stands represent a condition ripe for stand-replacing wildfire during some impending drought year similar to 1996. Indeed, one of the UN treatments became a WF treatment during the 2000 fire season. We hope to have more results from the STIFH project that can provide conclusions about the overall ecosystem health implications of having a large percentage of our forested landscape in an unmanaged condition, heading for a wildfire condition.

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LITERATURE CITED

Avery, T.E. and H.E. Burkhart. 1994. Forest Measurements, 4th Edition. McGraw-Hill, Inc. New York, NY.

Bailey, J.D. and W.W. Covington. 2001. Evaluating ponderosa pine regeneration rates following ecological restoration treatments in northern Arizona, U.S.A. Forest Ecology and Management. In press.

Covington, W. W., R. L. Everett, R. W. Steele, L. I. Irwin, T. A. Daer, and A. N. D. AuClair. 1994. Historical and anticipated changes in forest ecosystems of the Inland West of the United States. Journal of Sustainable Forestry 2:13-63.

Harvey, A.E. 1994. Integrated roles for insects, diseases and decomposers in fire dominated forests of the inland western United States: Past, present and future forest health. Pages 211-220 *in* Samson and Adams, (eds.). Assessing Forest Ecosystem Health in the Inland West. The Haworth Press, Inc. Binghamton, NY.

Pearson, G.A. 1949. Management of Ponderosa Pine in the Southwest. U.S Department of Agriculture. Monograph No. 6, USDA Forest Service, Washington, DC. 218 pp.

Reineke, L.H. 1933. Perfecting a stand-density index for even-aged forests. Journal of Agriculture Res. 46: 627-638.

Sampson, R.N. and D.L. Adams. 1994. Assessing Forest Ecosystem Health in the Inland West. Haworth Press, New York, NY.

Smith, D.M., B.C. Larson, M.J. Kelty, and P.M.S. Ashton. 1996. The Practice of Silviculture: Applied Forest Ecology. 9th Edition. John Wiley & Sons, New York, NY.

Swetnam, T. W. and J. L. Betancourt. 1990. Fire – Southern oscillation relations in the southwestern United States. Science 249: 1017-1020.

Zar, J.H. 1996. Biostatistical Analysis, 3rd Ed. Prentice-Hall, Inc. New Jersey.

Post-fire Treatment of Noxious Weeds in Mesa Verde National Park, Colorado

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Abstract. Re-introduction of fire as a management strategy can be detrimental to conservation of native ecosystems by promoting "noxious weeds" within invasion-susceptible plant communities. This idea was central to treatments following fire in the piñon-juniper (*Pinus edulis, Juniperus osteosperma*) woodlands and mountain shrublands *(Amelanchier utahensis, Quercus gambelii, Fendlera rupicola*) of Mesa Verde National Park, southwestern Colorado.

Fire is an integral ecological process in piñon- juniper woodlands and adjacent petran chaparral shrublands. However, wildfires in 1989 and 1996 created opportunities for the proliferation of noxious weeds, especially *Carduus nutans*, *Cirsium arvense*, and to a lesser extent, *Bromus tectorum.* Old-growth piñon-juniper woodlands were especially susceptible to non-native invasion and required aggressive management actions. In this study, we evaluated the effectiveness of three treatment strategies (mechanical, herbicide, and native grass seeding) in these high risk habitats. Introducing native perennial grasses, within three years of the fire, proved the most effective treatment in reducing non-native plant proliferation

Key words: noxious weeds, aerial seeding, Mesa Verde, species of concern

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INTRODUCTION

In contrast to the early twentieth century, disturbed habitats today are increasingly targeted by non-native species (Heywood 1989, Mooney and Drake 1989, Soule 1990, Westman 1990, Floyd-Hanna and Romme 1993, Burke and Grime 1996). Fire has been an important natural disturbance agent on the Colorado Plateau, but fire frequencies have increased in the past century (Covington et al. 1997, Grissino-Mayer and Swetnam 1997,Turner et al. 1998), thus changing fire-related ecological patterns. Native seed reserves and declines in native forb diversity are two such changes (Crawley 1987, Hobbs and Huenneke 1992). Possibly as a result of these changes, post fire succession commonly includes non-native plant species. In Mesa Verde National Park (MVNP) in southwestern Colorado, large wildfires that occurred earlier in the twentieth century (1934, 1959, 1972) were not associated with weed invasion. However, following extensive fires in 1989 and 1996, recovery was characterized by significant non-native plant invasion. Based on this information, a series of mitigative treatments were tailored specifically for each burned community considered at risk for noxious weeds after the 1996 Chapin 5 fire in Mesa Verde National Park.

Vegetation recovery and treatment of noxious weeds were funded under the Burned Area Emergency Rehabilitation (BAER) program, 1996-1999. Mitigation treatments outlined in this paper involved mechanical and chemical controls and seeding treatments. Biological controls were also introduced as part of the BAER program and will be discussed elsewhere (Kendall, pers. comm.). In this paper, we focus specifically on the effectiveness of weed treatment strategies on high weed-risk areas following the 1996 fire.

STUDY AREA

Mesa Verde National Park (MVNP) is located in the extreme southwestern corner of Colorado (Fig. 1). The Park encompasses over one-half of a prominent cuesta, the top of which gently slopes from 2050 m in the south to approximately 2485 m in the north. The southern end of the cuesta drops into the canyons of the Mancos River, while the northern end terminates in a steep, highly eroded escarpment. The cuesta is composed of Cretaceous sandstone and shale substrates: Mancos Shale, Point Lookout Sandstone, Menefee Shale, and Cliffhouse Sandstone (Griffits 1990). The top of the cuesta consists of numerous north-south trending, relatively flat ridges or "mesas," separated by rugged canyons.

Annual precipitation at MVNP averaged 45.8 cm between 1923 and 1994. Most precipitation falls in winter months as snow, or during the summer monsoons as thundershowers. July (avg. 4.52 cm) and August (avg. 5.2 cm) are the highest precipitation months. Lightning from mid-July through mid-August is the cause of 94% of the fires at MVNP.

Mesa Verde exhibits an elevation gradient in pre-fire vegetation communities. In the northern portions are several types of mountain shrublands, collectively called Petran chaparral (Fig. 1, light gray). These shrublands are of variable composition, often dominated by *Quercus gambelii* (gambel oak), *Amelanchier utahensis* (Utah serviceberry), *Cercocarpus montanus* (mountain-mahogany), *Fendlera rupicola* (fendlerbush)

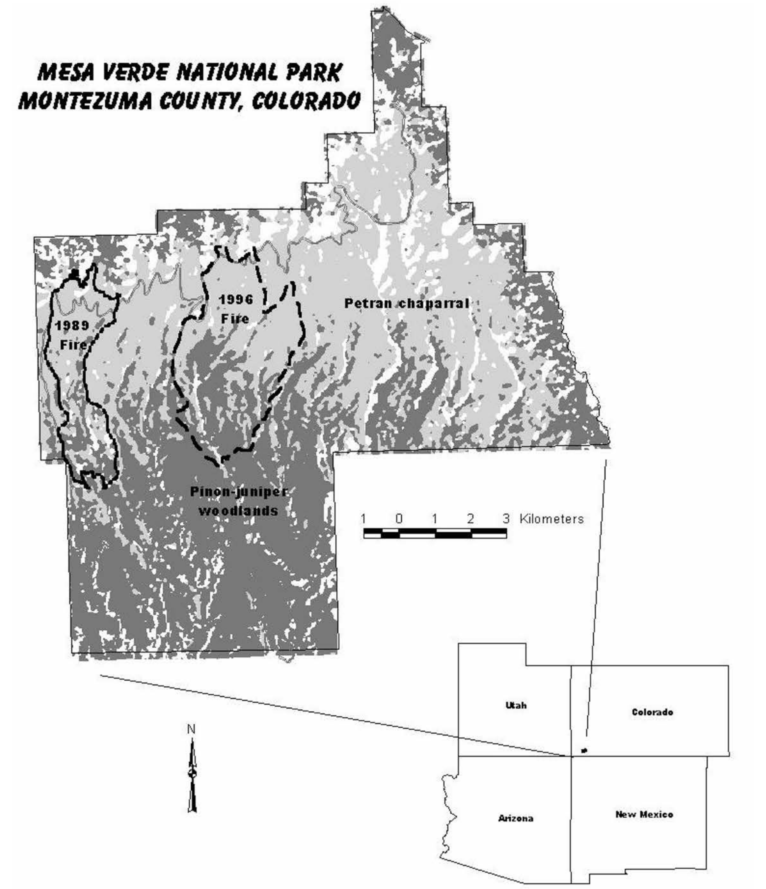

Figure 1. Locations of Long Mesa (1989) and Chapin 5 (1996), Mesa Verde National Park, Colorado.

and other perennial shrubs (Spence et al. 1995). Piñon-juniper woodlands (Fig. 1, dark gray) commonly interdigitate with these chaparral communities that share many of the same species, but have distinctly different structure. The woodlands are dominated by *Pinus edulis* (Colorado piñon pine) and *Juniperus osteosperma* (Utah juniper), and may have shrub understory dominated by gambel oak or *Purshia tridentata* (bitterbrush).

Disturbance History

Small, lightning-caused fires are frequent in MVNP; the annual average for fire starts between 1926-1969 was 5 per year, and between 1970-1997 was 18 per year. Most fires started in the piñon-juniper woodlands and burned less than 1 hectare. Large fires occurred in 1934, 1959, 1972, 1989, and 1996. The southern half of Mesa Verde is covered with dense, old-growth piñon-juniper woodlands that had not burned for several centuries. However, the 20th century has seen several spectacular wildfires that burned extensive portions of the pinon-juniper woodlands. The Chapin 5 fire began with a lightning strike in the dense piñon-juniper/bitterbrush woodland on the archeologically-rich Chapin Mesa, and burned through Soda Canyon, Little Soda Canyon, and large portions of the research area Park Mesa, before it stopped at the Visitors Center and hotel complex in dense oak and serviceberry shrublands. The fire covered 1934 ha, including seven pre-fire vegetation communities (Fig. 1).

Fire is the major disturbance factor in MVNP, but numerous smaller gaps also occur throughout the woodland canopy. Small gaps are often caused by pathogens, such as the Black stain root rot, *Ophiostoma wagnerii* Goheen and Cobb (= *Verticicladiella wagnerii=Ceratocycsis wagnerii*) which kills patches of up to 50 piñon trees, and has been present in southwestern Colorado since the 1930's (Harrington and Cobb 1998). Also, roads and park facilities provide continual disturbances. The woodlands are also disturbed in narrow belts, surrounding housing and park buildings, by annual fuel reduction activities. Thus, small patches of noxious weeds have been present in MVNP in the last 3 decades (M. Colyer, pers. comm.).

Weed Species of Special Concern in MVNP

Following the last two large fires, *Cirsium arvense* (Canada thistle) and *Carduus nutans* (musk thistle) aggressively invaded bare mineral soils. Musk thistle has an extensive native range from North Africa, Europe, Siberia, to Asia Minor. It has spread to New Zealand, Australia, and North America, where it is still expanding its range (Shea and Kelly 1998). In 1976, populations of musk thistle were located in eastern Colorado (Dunn 1976), and since that time, it has spread at an alarming rate through the state. Musk thistle is usually a biennial, but it can also be annual or perennial, reproducing exclusively from seed. Treatments of herbicide (Colorado State University Extension Service), biocontrol agents, and limitations on grazing (Rees 1982, Shea and Kelly 1998) are used to control its local distribution.

Canada thistle is more difficult to control because of horizontal adventitious roots that may extend 2 m deep (Hodgson 1968, Rees 1990), from which it rapidly resprouts after fires. Canada thistle is an aggressive weed which can reproduce from seed or vegetative buds, expands 2-4 m in one year, and significantly reduces forage in pastures throughout the western United States. The expansion of Canada thistle is controlled locally by herbicides, mowing, and biological controls (Colorado State University Extension Service). *Urophora cardui* and *Ceutrohynus litura* are commonly used biological control agents in Colorado (McCarty and Lamp 1982).

Other invasive species, which have become persistent in disturbed sites within MVNP and the surrounding region, include *Cirsium vulgare* (Bull thistle), *Salsola iberica* (Russian thistle), *Centaurea dehisa* (knapweed), *Centaurea repens* (knapweed), *Lactuca serriola* (wild lettuce), *Ranunculus testiculatus, Tamarix ramosissima (T. pentandra)* (tamarix), *Alyssum minor*, *Linaria vulgare* (butter and eggs), *Lepidium latifolia* (pepperweed), and the grasses *Festuca pratense, Agropyron intermedium* (intermediate wheatgrass), *Bromus tectorum* (cheatgrass), and *Bromus inermis* (smooth brome).

METHODS

Rehabilitation Treatments

Aerial Seeding Treatments

Although seeding treatments typically occur in a narrow window of opportunity within months of a fire, our treatments involved aerial seeding with assemblages of native grass seeds during three time periods: (1) immediately after the Chapin 5 fire, (2) on bare soils that remained one year after the fire, and (3) on bare soils two years after the fire. Perennial grass mixes simulated, as much as possible, the native grass community for the elevation, substrate, and pre-fire vegetation of each area (Appendix A). Seeds were primarily obtained from the Park itself or from local vendors who grow local seed varieties. In 1996, the extent of severely burned areas in the Chapin 5 burn exceeded the availability of native grass seeds (the demand for seeds was high because of numerous fires in the western United States). Therefore, we aerially seeded only 278 acres of the high-risk portion of the burn (Fig. 2).

In 1997, additional areas of the fire were seeded. Again, seeds were obtained locally with every attempt made to ensure that local seed sources were used. The selected areas either encompassed a very high density of archeological sites, were particularly susceptible to erosion, or had very little regrowth and were, therefore, at high risk of weed invasion (Fig. 2).

The 1996 and 1997 seeding treatments were quite successful in reducing weed invasion (see below). However, in the southern portion of the burn, up to 50 % of the soils remained exposed in some areas that had not been treated. These soils could be targets for the incoming noxious weeds, native forb and grass species, or seeded grasses, if introduced. In 1998, we took the bold step of applying additional seeding treatments to six small areas that were deemed particularly vulnerable to weed invasion.

During each year, seeds were applied with mechanical seeders from a Bell Jet Ranger helicopter (Mark Santee, pilot and Bob Greeno, seeder engineer). Seeding treatments took place in early October.

Success of seeding was measured in a series of 80 m^2 circular plots, placed at approximately 500 m intervals within treated areas (20 plots), and adjacent burned controls (20 plots), in the spring following each seeding treatment. In addition, a series of 20 plots were established within unburned portions of Park Mesa. Since the seeded species were bunch grasses, it was possible to identify individuals in the early stages of growth; therefore, the density, rather than the cover, of each species was recorded. The density of each weed species was also recorded.

Herbicide Treatments

Twenty-three Canada thistle patches were located (with GPS), photographed, and sprayed in June and again in August, 1998, with back-pack sprayer application of Curtail (3,6-dichloro-2-pyridinecarboxylic acid, monothanolamine salt 7.5 %, 2,4-dichlorophenoxy acetic acid, tris-propanolmaine salt 38.4 %), mixed with Improved JLB oil plus and IFA- S-90 Surfactant. Each stand was revisited within two months of spraying treatment, post-application photographs taken, and the percent mortality was estimated visually.

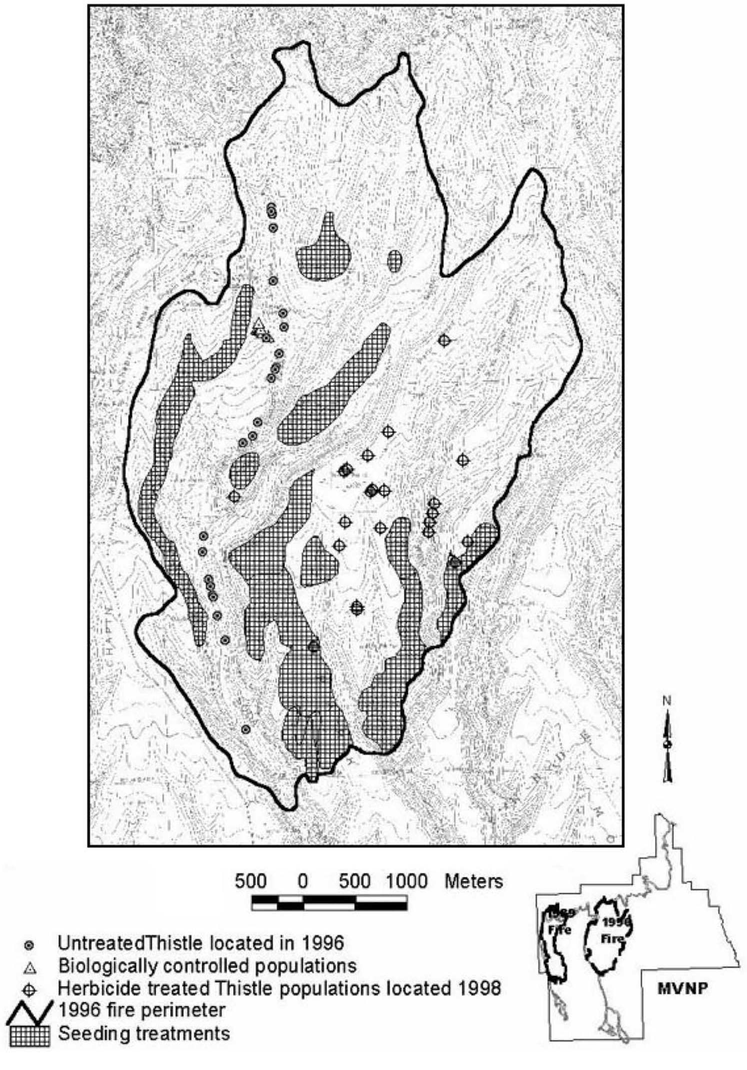

Figure 2. Weed treatments at Chapin 5 Fire site, Mesa Verde National Park.

In 1999, each stand was revisited, and if the noxious weeds were still alive, an additional application of Curtail was used. Photographs were taken of each plot, and an ordinal variable was created whose values approximated the percent of Canada thistle mortality.

Mechanical Treatments

Particularly dense stands of musk thistle were removed by digging up the rosettes (hand-grubbing) in June-August 1977 and June 1998. Treatment areas included canyon bottomlands, where native grasses were likely to resprout, and rocky canyon walls and mesa tops, where residual vegetation was lacking. A year after treatment, the number of musk thistle was counted in belt transects, each 33 m long and 4 m (132 m^2) wide, in each mechanical treatment stand. Fifteen transects were established in treatment areas, paired with an adjacent, non-treated "control" stand, and the density of musk thistle was statistically compared with a paired T-test.

Data were analyzed using one-way analysis of variance or T-tests to compare means of each dependent variable across treatments (seeded or control). All data were analyzed with SPSS, Statistical Package for the Social Sciences, version 10.

RESULTS

Aerial Seeding Treatments

One year after seeding treatment, grass density was significantly higher in the seeded areas than in nearby control plots (Table 1). This trend was also apparent in nearby plots the following two years (Floyd et al. unpub.). All species flowered and produced seeds in 1997 and 1998. *Agropyron trachycaulum* (slender wheatgrass), *Sitanion hystrix* (squirreltail grass), and *Oryzopsis hymenoides* (Indian ricegrass) were especially conspicuous.

The potential effect of the seeding treatment on the expansion of noxious weeds was analyzed in 1998 and 1999. We monitored the density of all non-native species; however, during the first 2 years, only musk thistle and Canada thistle had spread appreciably. Scattered patches of cheatgrass arrived later (in 1999). In the 1996 treatments, there was a 7.5-times reduction in musk thistle in the seeded areas, compared with the control; there was a 4-times reduction in weed density following the 1997 seeding (Table 2). Weed invasion was absent from all unburned control plots; therefore, unburned controls were not shown in Table 2. During summer, 1999, we monitored the germination of grass seed applied in fall, 1998. Germination was successful, resulting in significantly greater grass density than in control areas; however, the effect of the 1998 seeding on reduction of musk thistle cannot be evaluated until next year.

In related studies (Floyd-Hanna et al. 1999) recovery by native species was tracked for over three years following the fire. Abundant native forbs included *Polygonum sawachensis* (knotweed), *Lupinus caudatus* (lupine), *Lupinus ammophila* (lupine), and *Penstemon linearoides* (low penstemon). There has been no evidence to date that native forb diversity has declined due to seeding treatments compared with adjacent burned control plots.

Herbicide Treatments

Upland patches of Canada thistle were treated with herbicide applications. It should be noted that herbicide was not used in drainage systems near water. Herbicide treatments with Curtail varied in their effectiveness. In 75% of the herbicide applications, Curtail was locally effective, killing between 70-100% of the ramets of Canada thistle within two months of spraying, and maintaining an average of 80% kill the next year. In 25 % of the application, live plants persisted on the periphery of

Table 1. The density of native perennial grasses one year after aerial treatment, Chapin 5 fire, Mesa Verde National Park. Each value is mean ± standard deviation. Sample sizes were n=20 per treatment. T-tests indicate significant differences between seeded and control (not seeded) burned treatments. (*denotes P<0.05).

Grass Species	Control Density	Seeded Density	Significance
Poa fendleriana	1.0 ±2.1	12.0 ±17.4	T= 2.2*
Sitanion hystrix	0.0	5.9 ±6.0	T= 3.5*
Oryzopsis hymenoides	1.0 ±2.3	0.6 ±.9	T= 0.6
Agropyron trachycaulum	0	5.6 ±6.3	T= 3.2*

the patch. In Soda Canyon, Canada thistle had been well-established before the fire, and re-sprouting was visible within a few weeks. These areas are strictly treated with biological controls, reported elsewhere (Kendall, pers. comm.).

Mechanical Treatments

Only extremely dense patches of musk thistle were chosen for mechanical treatments. Results varied considerably among the mechanically treated (hand-grubbed) areas. No significant difference in musk thistle density was detected one year after treatment in areas where grasses were lacking (pre-treatment average 32,400/ha, post-treatment average 37,600/ha). However, there was a three-fold (pre-treatment average 28,400, post-treatment 9,300/ha) and five-fold (pre-treatment average 33,900, post-treatment average 6650 ha) decrease in density in two treated areas where mechanical treatment was followed by "natural" grass invasion. While it appeared that mechanical reduction was an effective local treatment if followed by natural or artificial grass seeding, further long-term evaluation is needed.

Table 2. The density of musk thistle, *Carduus nutans*, in seeded and control (not seeded) treatments, one year after treatment, Chapin 5 fire, Mesa Verde National Park. Each value is the mean ± standard deviation. Sample sizes were n=20 per treatment. Analysis of variance tests indicate significant differences between seeded and control (not seeded) treatments in 1996 treatments (F=10.9, P<0.05) and 1997 treatments (F=8.1, P<0.05).

Treatment	Density of musk thistle (#/80m^2)
1996	
Mesa top seeding	10.4 ±8.3
Control, unseeded mesa top	83.1 ±66.6
1997	
Canyon site seeding	28.0 ±53.4
Control, unseeded canyon	96.5 ±47.2

DISCUSSION

In the three years following the 1996 Chapin 5 wildfire in Mesa Verde National Park, burned old-growth piñon-juniper woodlands supported the greatest diversity and density of non-native plant species relative to the six other vegetation types burned. In many of the other vegetation communities, residual vegetation, in the form of resprouting perennial shrubs and grasses, allowed rapid recovery and prevented noxious weed invasions (Floyd-Hanna et al. 1999). Post-fire mitigation activities conducted under the Burned Area Emergency Rehabilitation (BAER) program, were designed to prevent noxious weed invasion and severe erosion, and to encourage native plant species. These were carried out most intensively in the old-growth piñon-juniper community.

In all three treatments, we documented a significant reduction in weed densities. Of the treatments applied, seeding with native grass species has shown the most pronounced effects in reducing weed density. Furthermore, there has been no evidence that the diversity of native forbs has declined by introducing native perennial grasses. Herbicide and mechanical treatments were effective in the short-term, but whether they reduce population expansion, decreasing subsequent seedling germination and establishment, is not yet known. Mechanical treatment was only effective if followed by native grass invasion. Both mechanical and herbicide treatments can only be applied, realistically, in small patches; aerial seeding of native grasses can be applied over large areas. The effect of biological controls will not be evident for at least several more years (Kendall, pers. comm.).

While it cannot be known to what extent the noxious weeds would have spread had we not performed the treatments, it is reasonable to assume that the spatial extent has been reduced by at least the areas treated. BAER funding is available only to treat emergencies; therefore, we could only apply treatments to the most severely burned or threatened habitats (primarily old-growth piñon-juniper communities). Over one-half of untreated piñon-juniper communities were invaded by musk thistle within three years of the fire, as detected by helicopter survey (Floyd-Hanna et al. 1999). Musk thistle is now the dominant species in these areas. Thus, we recommend that future fires be seeded with native species extensively in burned communities that lack residual vegetation, such as dense, old-growth piñon-juniper woodlands. Such treatments promote native, perennial grass growth and reduce the proliferation of non-native species.

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LITERATURE CITED

Burke, M.J. and J.P. Grime. 1996. An experimental study of plant community invasibility. Ecology 77: 776-789.

Covington, W.W., P.Z Fule, M.M. Moore, S.C. Hart, T.E. Kolb, J.N. Mast, S.S. Sackett and M.R. Wagner. 1997. Restoring ecosystem health in ponderosa pine forests of the southwest. Journal of Forestry 95: 23-29.

Crawley, M.J. 1987. What makes a community invasible? Pages 429-454 *in* M. J. Crawley, P.J. Edwards and A.J. Gray (eds.). Colonisation, succession and stability. Blackwell Scientific, Oxford.

Dunn, P.H. 1976. Distribution of *Carduus nutans, C. acanthoides, C. pycnocephalus* and *C. crispus* in the United States. Weed Science 24: 518-524.

Floyd-Hanna, L. and W.H. Romme. 1993. Biological invasions after fire, Mesa Verde National Park. Park Science 29: 12-14.

Floyd-Hanna, L., D. D. Hanna and W.H. Romme. 1999. Post-fire vegetation studies, BAER Final Report: Chapin 5 Fire.

Griffits, M. O. 1990. Guide to the geology of Mesa Verde National Park. Mesa Verde Museum Association, Lorraine Press, Utah.

Grissino-Mayer, H.D. and T.W. Swetnam. 1997. Multi-century history of wildland fire in the ponderosa pine forests of El Malpais National Monument. New Mexico Bureau of Mines and Mineral Resources Bulletin 156: 163-171.

Harrington, T.C. and F.W. Cobb. 1988. Leptographium Root Diseases on conifers. APS Press, the American Phytopathological Society, St. Paul, Minnesota.

Heywood, V.H. 1989. Patterns, extents and modes of invasions by terrestrial plants. Pages 31-55 *in* J.A. Drake, H.A. Mooney, F. diCastri, R.H. Groves, F.J. Kruger, M. Rejmanek, and M. Williamson, (eds.). Biological invasions: a global perspective. SCOPE, Wiley & Sons.

Hobbs, R.J., and L.F. Huenneke. 1992. Disturbance, diversity, and invasion: implications for conservation. Conservation Biology 6: 324-337.

Hodgson, J.M 1968. The nature, ecology, and control of Canada thistle. USDA Technical Bulletin 1386.

McCarty, M.K. and W.O. Lamp. 1982. Effect of a weevil, *Rhinocyllus conicus* on musk thistle seed production. Weed Science 30: 136-140.

Mooney, H.A., and J.A. Drake. 1989. Biological invasions: a SCOPE program overview. Pages 491-510 *in* J.A. Drake, H.A. Mooney, F. diCastri, R.H. Groves, F.J. Kruger, M. Rejmanek, and M. Williamson, (eds.). Biological invasions: a global perspective. SCOPE, Wiley & Sons.

Rees, N.E. 1982. Collecting, handling and releasing *Rhinocyllus conicus,* a biological control agent of musk thistle. USDA Agricultural Handbook No. 579.

Rees, N.E. 1990. Establishment, dispersal, and influence of *Ceuthorhynchus litura* on Canada thistle in the Gallatin Valley of Montana. Weed Science 38: 198-200.

Shea, K. and D. Kelly. 1998. Estimating biocontrol agent impact with matirx models: *Carduus nutans* in New Zealand. Ecological Applications 8: 824-832.

Spence, J.R., W.H. Romme, L. Floyd-Hanna, and P.G. Rowlands. 1995. A preliminary vegetation classification for the Colorado Plateau. Pages 193-213. *in* C. van Riper III, (ed.). Proceedings of the Second Biennial Conference on Research in Colorado Plateau National Parks. 25-28 October 1993. National Park Service Transactions and Proceedings Series NPS/NRNAU/NRTP-95/11.

Soule, M.E. 1990. The onslaught of exotic species, and other challenges in the coming decades. Conservation Biology 4: 233-239.

Turner, M.G., W.L. Baker, C.J. Peterson, and R.K. Peet. 1998. Factors influencing succession: lessons from large, infrequent disturbances. Ecosystems 1: 511-523.

Westman, W.E. 1990. Park management and exotic plant species: problems and issues. Conservation Biology 4: 251-260.

Appendix A. Community-specific native grass seed mixes used for rehabilitation of the Chapin 5 fire, Mesa Verde National Park. Locations of seeded areas are shown in Figure 2; approximate acreage which were seeded are shown in parentheses.

- Seeding Area A: (77 acres)
  - *Kohleria cristata,* June Grass, 2 lb/acre
  - *Oryzopsis hymenoides*, Indian Rice Grass, 6 lb/acre
  - *Agropyron trachycaulum* , Slender Wheat Grass, 5 lb/acre
  - *Sitanion hystrix,* Squirrel-tail Grass, 6 lb/acre
- Seeding Area B: (201 acres)
  - *Poa fendleriana*, Mutton Grass, 2 lb/acre
  - *Oryzopsis hymenoides*, Indian Rice Grass, 6 lb/acre
  - *Agropyron trachycaulum* , Slender Wheat Grass, 5 lb/acre
  - *Sitanion hystrix,* Squirrel-tail Grass, 6 lb/acre
- Seeding Area C.: (250 acres)
  - *Agropyron smithii,* Western Wheat grass, 8lbs/acre
  - *Poa fendleriana*, Mutton Grass, 1.5 lb/acre
  - *Oryzopsis hymenoides*, Indian Rice Grass, 6 lb/acre
  - *Agropyron trachycaulum* , Slender Wheat Grass, 5.5 lb/acre
- Seeding Area D: (110 acres):
  - *Kohleria cristata,* June Grass, 1.0 lb/acre
  - *Sitanion hystrix*, Squirrel-tail Grass, 2.4lb/acre
  - *Agropyron trachycaulum* , Slender Wheat Grass, 5.5 lb/acre
  - *Stipa comata*, Needle and thread grass, 3.5 lb/acre
- Seeding Area E: (125 acres)
  - *Oryzopsis hymenoides*, Indian Rice Grass, 6 lb/acre
  - *Agropyron trachycaulum* , Slender Wheat Grass, 5.5 lb/acre
  - *Sitanion hystrix*, Squirrel-tail Grass, 2.4lb/acre
  - *Poa fendleriana*, Mutton Grass, 1.5 lb/acre
- Seeding Area F: (50 acres)
  - *Kohleria cristata,* June Grass, 2 lb/acre,
  - *Oryzopsis hymenoides*, Indian Rice Grass, 5 lb/acre
  - *Agropyron trachycaulum* , Slender Wheat Grass, 5 lb/acre
  - *Sitanion hystrix*, Squirrel-tail Grass, 2.5 lb/acre
- Seeding Area G: (125 acres)
  - *Poa fendleriana*, Mutton Grass, 2 lb/acre
  - *Oryzopsis hymenoides*, Indian Rice Grass, 6 lb/acre
  - *Agropyron trachycaulum* , Slender Wheat Grass, 5 lb/acre
  - *Sitanion hystrix*, Squirrel-tail Grass, 6 lb/acre
  - *Agropyron smithii,* Western Wheat Grass, 5 lb/acre
- Seeding Area H: (35 acres)
  - *Poa fendleriana*, Mutton Grass, 2 lb/acre
  - *Oryzopsis hymenoides*, Indian Rice Grass, 6 lb/acre
  - *Agropyron trachycaulum* , Slender Wheat Grass, 5 lb/acre
  - *Sitanion hystrix*, Squirrel-tail Grass, 6 lb/acre
- Seeding Area I: (60 acres)
  - *Kohleria cristata,* June Grass, 2 lb/acre,
  - *Oryzopsis hymenoides*, Indian Rice Grass, 6 lb/acre
  - *Agropyron trachycaulum* , Slender Wheat Grass, 5 lb/acre
  - *Stanion hystrix*, Squirrel-tail Grass, 6 lb/acre
  - *Agropyron smithii,* Western Wheat Grass, 5 lb/acre
  - *Stipa comata*, Needle and thread grass, 2 lb/acre

Mapping Land Cover and Animal Species Distributions for Conservation Planning: An Overview of the Southwest Regional Gap Analysis Program in Arizona

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Abstract. The Southwest Regional Gap Analysis Program will build upon previous gap analysis programs conducted in Arizona, Colorado, Nevada, New Mexico, and Utah to provide products that are consistent among areas of this large geographic region. The program will develop new land cover, vertebrate species distributions, and land stewardship data layers using a cooperative approach and similar methods across the five states. The three data layers will be seamless across the five state region, and detailed in resolution and content. The data layers will be used in a gap analysis to evaluate the conservation status of natural habitats and vertebrate species within and among all five states, and point out biotic elements needing further protection or management attention. The program will also provide region-wide digital map and database products that allow land managers, planners, scientists, and policy makers to make better informed land use decisions.

Key words: gap analysis, biodiversity, Southwest, Arizona, remote sensing, vegetation, land cover, wildlife habitat relationship models, GIS.

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BACKGROUND

Loss of biological diversity is a serious ecological problem, with a major cause being human action in the form of altering land use (Freedman 1989). Human-caused changes have accelerated extinction (Wilcove et al. 1998), which threatens biodiversity. With foresight, people can minimize further biodiversity loss due to human activity. One important tool is biodiversity gap analysis, which has been developed by geographers and biologists to map distributions of vertebrate species and vegetation communities and identify gaps in their protection (McKendry and Machlis 1991, Scott et al. 1993). This coarse filter approach can be used for conservation planning at the ecosystem level (Noss 1987).

Kepler and Scott (1985) found a gap in endangered Hawaiian honeycreeper protection on the island of Hawaii. They modeled the distribution of three honeycreeper species and compared maps of their distributions to determine areas of honeycreeper richness. Maps of existing nature reserves were then compared with the honeycreeper richness map to determine if reserves coincided with species-rich areas. As a result of their findings, the Hakalau Forest National Wildlife Refuge was established in one of the areas of highest honeycreeper richness, addressing the gap in protection revealed by their analysis (Scott et al. 1993). This study became the founding research for the National Gap Analysis Program.

The National Gap Analysis Program (GAP), initially housed within the U.S. Fish and Wildlife Service and now managed by the U.S. Geological Survey, has guided the subsequent development and application of biodiversity gap analysis throughout the nation and internationally. The Gap Analysis Program maps distributions of land cover (vegetation communities) and vertebrate species. These maps are overlaid in a geographic information system with maps of land stewardship (showing levels of biodiversity management) to identify biotic elements at potential risk of endangerment because of "gaps" in conservation management. A gap in conservation management is identified where a biotic element (vegetation community or animal species) is not present, or only occurs marginally in areas protected and managed primarily for biodiversity. One of the major goals of GAP is to provide consistent, periodic, regional assessments of the gaps in conservation management; in other words, to determine the conservation status of native vertebrate species and natural land cover types, and facilitate the application of this information to land acquisition, protection, and other management activities.

In this paper, we describe the second generation gap analysis in the Southwest, which builds upon the successes and shortcomings of previous work on gap analysis in the region. This effort, the Southwest Regional Gap Analysis Program (SW ReGAP), is being conducted as a multi-state effort between Arizona, Colorado, Nevada, New Mexico, and Utah. This five state region covers almost 140 million hectares with 21% of that, or almost 30 million hectares, within the state of Arizona. The project is developing the operational model for the next phase of biodiversity gap analysis projects in the west (Prior-Magee, SW ReGAP Coordinator, pers. comm.). In addition to much-improved resolution and accuracy of map products, important refinements within the regional effort are consistent land cover classification throughout the area, and seamless coverage of maps across political and agency management boundaries.

First Generation GAP – The State Model

Gap analysis has traditionally been conducted on a state-by-state basis, with first generation biodiversity GAP completed in 10 states. In the Southwest, first generation gap analysis programs were initiated in the early 1990s. A complete gap analysis and accompanying map products were published in Utah (Edwards et al. 1995) and New Mexico (Thompson et al. 1996). Partial map products were produced in Arizona (USGS WERC 2001) and Nevada. Colorado is currently finishing the first generation GAP products for their state (Schrupp et al. 2000).

The first generation Arizona project began in 1991. This effort, initially directed by Lee Graham of University of Arizona, Tucson, produced land cover, vertebrate distribution, and land stewardship maps in 1994. The USGS Sonoran Desert Field Station in Tucson, revised the initial Graham maps and plans on completing analysis for this first generation project. When published, their report will represent the first-ever detailed maps on a state-wide level of biotic elements and their conservation status.

State boundaries rarely coincide with ecological units. The island ecosystem of Hawaii was convenient for mapping and conducting gap analysis because of the island's boundaries. However, a continental ecosystem such as the Colorado Plateau has fuzzy boundaries and may span several states, making mapping and conducting a gap analysis more difficult on a state-by-state basis. Gap analyses confined to a state's boundary tend to give incomplete or biased results when taken in the context of an extensive ecosystem. For example, a species may be rare in a state only because it is at the edge of its range. To recommend protection for this species in one state, when it is common in adjacent states, is not accounting for the regional nature of the distribution. For this reason, strategies to manage for the long-term maintenance of biodiversity are better focused on the characteristic biota of larger regions (Noss 1983).

Individual state GAP maps have proven difficult to merge into regional representations. State data layers typically have different classification systems, such that similar vegetation types are given different names in each state. This necessitates a cumbersome process to merge the types among the different classifications, followed by a cross-walk to the least detailed classification.

In addition to classification problems, another edge-matching issue arises when the resolution of the data layer differs between states. The use of different primary data sources and methods to derive polygons can create maps that have different spatial properties across state lines. An ecoregional land cover map was created for the Mojave Desert using portions of the first generation Arizona, California, Nevada, and Utah GAP maps. The resulting ecoregional land cover map shows striking differences in map unit delineation across state lines (Fig. 1). The map unit inconsistencies could be due to source imagery resolution differing between the states because the Arizona, Nevada, and Utah projects used Thematic Mapper imagery with 30 meter pixel resolution, while the California project used Multispectral Scanner imag-

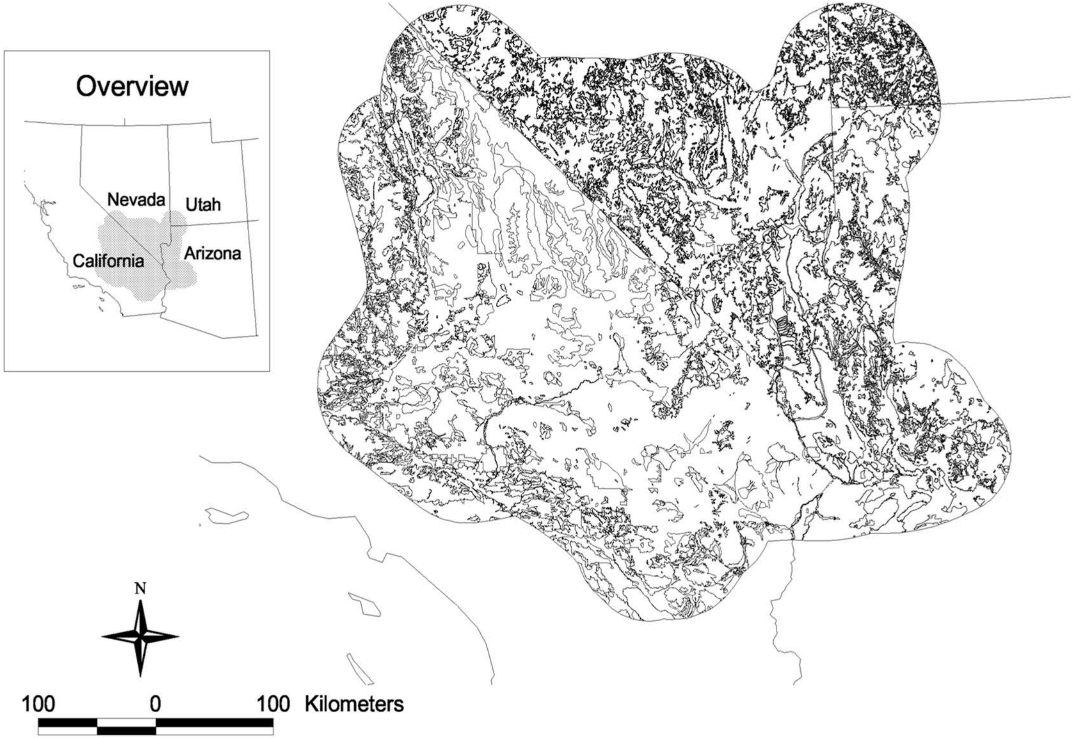

Figure 1. Mojave Desert Ecoregion Project land cover map (MDEP 1998) showing map unit inconsistencies across state boundaries.

ery with 80 meter pixel resolution. The different resolutions of the base imagery layer and available technology produced land cover maps with different resolutions (100 ha in California vs. 40 ha in Arizona).

Differences in spatial properties of land cover map units can introduce error in predictions of vertebrate species distributions, where distributions are modeled using the land cover map. Uneven map units can result in errors of omission or commission in predicted species' occurrence.

Another motivation for second generation GAP studies is that gap analysis was designed to be repeated at approximately 10-year intervals, in order to provide periodic reassessment of the distribution of biota and their conservation management. Changes in distribution of land cover and vertebrate species may occur due to naturally occurring disturbances (e.g., fire or flood), direct human disturbance (e.g., land clearing), or from the indirect effects of human activities (e.g., global warming).

This second generation gap analysis in the Southwest will provide an updated view of current conditions, and is specifically designed to utilize a regional model. This will correct some of the problems that arose from the state model, such as the poor match across state boundaries of vegetation classification, map unit spatial discontinuity, and lack of a regional gap analysis.

Second Generation GAP – The Regional Model

The Southwest Regional Gap Analysis Program is multi-year, and will create land cover, vertebrate species distributions, and land stewardship data layers. This effort will conduct a gap analysis conservation assessment for each state and for the entire five-state region. Some remote sensing and animal modeling activities will be conducted by regional teams for the benefit of all participating states. State projects will collect distribution data, create models and map labels for their state, and coordinate with regional teams. A regional project coordinator will facilitate activities among regional teams, state projects, and federal agency offices.

The project in Arizona will produce data layers that support a well-documented gap analysis conservation assessment throughout the state. These data and analyses will be readily available to land and resource managers, whether private, tribal, state, or federal. The project in Arizona is being coordinated by the USGS Forest and Rangeland Ecosystem Science Center, Colorado Plateau Field Station, in Flagstaff.

While Arizona, Colorado, Nevada, New Mexico, and Utah have previously conducted a gap analysis, vast improvements in technology and cooperative efforts will make this project more fruitful than first generation projects. The project will address the inconsistencies of methodology, information, classification, resolution, and expertise to produce seamless data layers across state boundaries for the Southwest.

METHODS

Mapping Land Cover

A consistent approach to mapping land cover is essential for success of a regional gap analysis. A seamless land cover map for the region will contribute to vertebrate species distributions and gap analyses that encourage an ecoregional approach to land management.

National Vegetation Classification

In previous GAP projects, each state had its own accepted standard of vegetation classification, which often did not correspond with neighboring states. The regional project will use a standardized classification system, the National Vegetation Classification (NVC; Grossman et al. 1998), to ensure classification consistency across the region and to retain an acceptable level of detail. In 1997, the Federal Geographic Data Committee recommended the that NVC become the standard for all federally funded vegetation mapping projects (FGDC 1997). Since that time, National GAP has sponsored the development of vegetation type (alliance) descriptions so as to provide a consistent, repeatable classification system across state and administrative boundaries.

The NVC is regarded as a major step toward enhancing our ability to understand, protect, and manage the natural resources of the United States. It provides a hierarchical framework for describing vegetation, and a convention for identifying and naming additional vegetation types. The first five levels of the hierarchy are based on physiognomic characteristics of the vegetation, and the last two levels are floristic (Table 1). A set of 105 preliminary alliance descriptions have been developed for Arizona, but it is expected that the project will expand and further identify and define alliances for Arizona. As an example, 15 preliminary alliances have been de-

Table 1. Hierarchy of the National Vegetation Classification.

Level	Primary Basis for Classification	Example
Class	Growth form and structure of vegetation	Woodland
Subclass	Growth form characteristics, e.g., leaf phenology	Evergreen woodland
Group	Leaf types, corresponding to climate	Temperate or subpolar needle-leaved evergreen woodland
Subgroup	Relative human impact (Natural/semi-natural, or cultural)	Natural/semi-natural
Formation	Additional physiognomic and environmental factors, including hydrology	Rounded-crowned temperate or subpolar needle-leaved evergreen woodland
Alliance	Dominant/diagnostic species of uppermost or dominant stratum	*Pinus ponderosa* woodland alliance
Association	Additional dominant/diagnostic species from any strata	*Pinus ponderosa/ Quercus gambelii* woodland

scribed for the relatively small region of Sunset Crater National Monument and environs (7,600 ha) in northern Arizona (Table 2).

The target of SW ReGAP is to map land cover to the alliance level, at 5-hectare spatial resolution. This is a fine resolution and level of floristic detail that has not yet been accomplished in a land cover mapping project of this size. Where distinction between alliances is not possible, due to the ecological complexity or difficulty in remotely sensing or modeling the vegetation type, groups of alliances, known as ecological complexes or compositional groups, may be used for map labels. The Association of Biodiversity Information, responsible for creation and maintenance of the NVC for the United States, will coordinate application of the NVC across the five states to promote the consistent development and application of map labels.

Table 2. Preliminary NVC alliances for Sunset Crater National Monument and environs, Arizona (Thomas et al. in prep).

Class	Alliance
Forest	*Pinus edulis* Forest Alliance
Forest	*Pseudotsuga menziesii* Forest Alliance
Woodland	*Pinus edulis* - (*Juniperus* spp.) Woodland Alliance
Woodland	*Pinus flexilis* Woodland Alliance
Woodland	*Pinus ponderosa* Woodland Alliance
Woodland	*Populus tremuloides* Woodland Alliance
Shrubland	*Ericameria nauseosa* Shrubland Alliance
Herbaceous	*Andropogon hallii* Herbaceous Alliance
Herbaceous	*Bouteloua gracilis* Herbaceous Alliance
Herbaceous	*Muhlenbergia montana* Herbaceous Alliance
Herbaceous	*Pascopyrum smithii* Herbaceous Alliance
Herbaceous	*Pinus ponderosa* Wooded Herbaceous Alliance
Sparse	*Eriogonum corymbosum* Sparsely Vegetated Alliance
Sparse	*Fallugia paradoxa* Sparsely Vegetated Alliance
Sparse	Lava Bed Sparsely Vegetated Alliance

Processing of Satellite Imagery

Most GAP projects used Landsat Thematic Mapper satellite as the base imagery layer. Also, previous GAP projects have used only one date of imagery per scene to keep costs low. However, this limited the ability to distinguish between land cover types, resulting in more generalized land cover classes. Methods for delineating land cover classes from satellite imagery have included photo interpretive techniques, supervised and unsupervised clustering, and modeling using ancillary data sets (Eve and Merchant 1998). However, the application of various techniques inconsistently across the landscape has produced different map unit boundaries, and caused edge-matching problems across state boundaries.

This project will use three dates of imagery in 1999, 2000, or 2001 from the latest earth-observing satellite, Landsat 7 Enhanced Thematic Mapper Plus. This imagery will be preprocessed (i.e., georectified and cleaned) and clustered by a regional remote sensing team. Preliminary cover types, using plot data supplied by each state and previous land cover maps, will then be assigned to the cluster map. Preliminary clusters will be given NVC vegetation type labels at the state level. The project in Arizona will use predictive modeling with ancillary data sources (e.g., elevation, slope aspect, precipitation, and soils) and focused field verification (i.e., labeling of individual polygons) for final cluster map labeling. The regional remote sensing team will then create a single land cover data layer for the entire Southwest region from individual state data layers.

Mapping Zones

Previous projects have mapped land cover on a satellite scene-by-scene basis (Eve and Merchant 1998). These scenes may contain a wide variety of ecological conditions and can cause confusion in delineating land cover types, leading to a land cover map that does not provide detailed floristic information. In this project, we will use vegetation-based mapping zones to maximize information extraction by separating imagery into more homogeneous areas prior to classification (Fig. 2). This will allow our classification to focus on a smaller set of land cover types, which will reduce variation and improve classification results (Homer et al. 1997). Our proposed mapping zones have been delineated primarily based on elevation, latitude, and longitude, which are important factors in the regional zonation of vegetation throughout the Southwest.

Each of the five states will be responsible for mapping zones that fall completely or partially within that state. Where a zone overlaps state boundaries, one state will take primary responsibility for mapping that zone, with the other state(s) providing logistical support and information. Each state project will collect existing and new field data for mapping zones, model specific vegetation/environmental parameters, work with the regional remote sensing team in developing cluster images, and provide final labeling of the land cover types in their assigned mapping zones.

The Arizona project has primary responsibility for classifying 11 of 73 regional mapping zones, an area of about 26 million hectares (19% of the region), and will contribute to land cover mapping in five shared zones. For each shared mapping zone, Arizona will coordinate with the adjoining state project(s) to map the overlapping areas. When land management crosses state and mapping zone boundaries, such as the Navajo Nation in the Four-Corners area, one state project will take the lead to coordinate with involved land manager.

The ecological labeling rules for vegetation types will be consistent within mapping zones. However, they may vary across mapping zones because of real differences in cover type distribution characteristics. For example, the elevation range of the "Pinyon Woodland Alliance" (Reid et al. 1999) will be higher in the Hualapai mapping zone in Arizona than in a mapping zone in Utah due to latitudinal changes. Farther north, the pinyon cover type occurs at lower elevations. We are ensuring consistency in applying map labels through periodic meetings with the state projects,

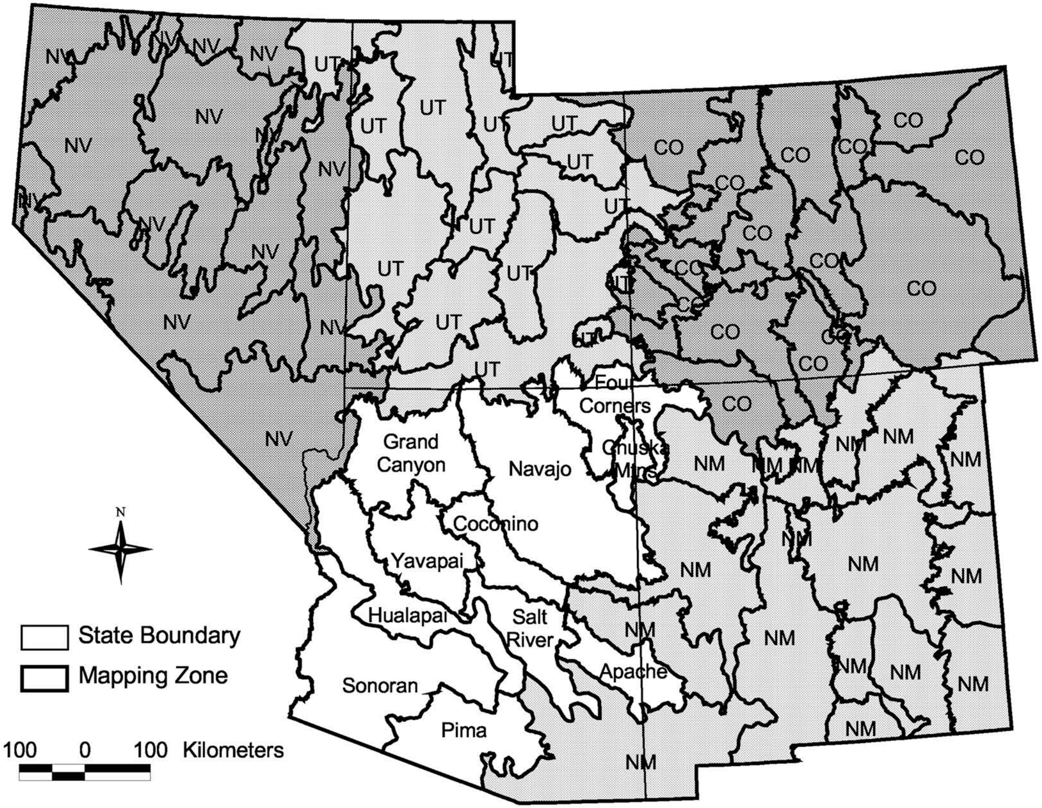

Figure 2. Mapping zones for SW ReGAP. Zones are labeled with a descriptive name in Arizona. Elsewhere, they are labeled with the state responsible for mapping the zone.

and by overview of map label application by the Association of Biodiversity Information and regional remote sensing team.

Vertebrate Species Distribution Maps

The regional project will model predicted distributions of each vertebrate taxon that resides, breeds, or uses habitat in the five-state Southwest region for a substantial part of its life history, including winter range and important migration stopovers. In addition to native species, the project will model subspecies of particular interest and widespread non-native species. There are approximately 960 vertebrate taxa within the region, and the Arizona project will model the distribution of approximately 570 taxa. A regional animal modeling team will be responsible for resolving differences in models of taxa that cross state boundaries.

Previous GAP projects developed vertebrate distribution models based on literature sources (USGS GAP 2000). Similarly, our project will construct wildlife habitat relationship models (WHRMs) from the best available literature on the distribution and habitat associations for each species, maintaining consistency with the traditional GAP approach to vertebrate distribution modeling. In addition, our project will use field information in a data-driven approach of distribution modeling for select groups of taxa. This process will be used for passerine birds and possibly other groups, depending on the availability of sufficient field inventory data. Primary data sources for birds will be breeding bird survey data (Sauer et al. 1999) and breeding bird atlas data currently being gathered for the state of Arizona (McCarthey et al. 1995). This data-driven approach will use correlation of georeferenced taxa location data (e.g., from census plots) with maps of habitat features (e.g., elevation and land cover type) to extract the WHRM.

The WHRMs will be applied to maps of habitat features to produce distribution maps indicating known, probable, and possible presence of each vertebrate taxon within its geographic range. Models produced from the data-driven approach will be compared with the traditional GAP approach to evaluate and then resolve any apparent differences.

Land Stewardship Map

Land ownership often does not cross state boundaries. However, in certain cases, such as tribal and federal lands, land ownership does cross state boundaries and will be mapped as such. In addition, the five states will cooperate to apply a consistent definition of land stewardship across the region.

Land stewardship of public and private land has traditionally been categorized by a four-level rating (Table 3). For the Arizona project, the first generation GAP land stewardship map will be used as a starting point; however, changes in land ownership and management are expected, and the land stewardship data layer will require an extensive update. Digital parcel boundaries will be obtained from each county within Arizona in order to refine the stewardship map resolution. Each tract will be attributed for land ownership, managing institution, and management status. A

Table 3. Biodiversity management status categories used in the land stewardship map (USGS 2000).

Status	Description
1	An area having permanent protection from conversion of natural land cover and a mandated management plan in operation to maintain a natural state within which disturbance events (of natural type, frequency, intensity, and legacy) are allowed to proceed without interference or are mimicked through management
2	An area having permanent protection from conversion of natural land cover and a mandated management plan in operation to maintain a primarily natural state, but which may receive uses or management practices that degrade the quality of existing natural communities, including suppression of natural disturbance
3	An area having permanent protection from conversion of natural land cover for the majority of the area, but subject to extractive uses of either a broad, low-intensity type (e.g., logging) or localized intense type (e.g., mining). It also confers protection to federally listed endangered and threatened species throughout the area
4	There are no known public or private institutional mandates or legally recognized easements or deed restrictions held by the managing entity to prevent conversion of natural habitat types to anthropogenic habitat types. The area generally allows conversion to unnatural land cover throughout

substantial effort will be made to identify and contact all known conservation land owners and/or managers holding tracts at least as large as the minimum resolution size (16 ha) in order to verify stewardship status of that land tract.

State and Regional Gap Analyses

The conservation gap analysis consists of intersecting land cover and vertebrate distribution maps with the stewardship map, and calculating the amount of each vegetation type and vertebrate species distribution in each land stewardship category. This analysis will identify important gaps that have potential for mitigation by land stewards (USGS 2000). The analysis will consist of two steps: individual state analyses and a regional analysis. This will allow land stewards to better assess their role and responsibility for biota occurring on their lands, and in the greater context of the Southwest.

ANTICIPATED RESULTS

The Southwest Regional Gap Analysis Program will provide detailed, spatially explicit information on the distribution and management status of each mapped vertebrate species and vegetation community within the greater Southwest region.

Map products and conservation analysis results will be released in the beginning of 2005 (Table 4). Preliminary products are expected to be available in 2004 for examination and comment.

Table 4. Products from Southwest Regional Gap Analysis Program in Arizona.

Product	Format	Outlet
Land Cover Map	ArcGIS layer	CD and website
Terrestrial Vertebrate Species Distribution Maps	ArcGIS layers	CD and website
Land Stewardship Map	ArcGIS layer	CD and website
Wildlife Habitat Relationship Models	Microsoft Access database and metadata	CD and website
Final Report for Arizona	Report	Technical Report
Final Report for the Southwest Region	Report	Technical Report

Important advances with this regional project for the Southwest include much finer resolution (5 ha) land cover mapping, use of a consistent vegetation classification system (NVC) at a fine level of detail, and coordinated mapping to eliminate edge-matching problems across state boundaries. Vertebrate distribution models will be developed based on comprehensive syntheses of information on habitat and distribution, and recent inventory data. Development of vertebrate distribution models will make specific use of detailed accuracy assessment of earlier GAP distribution models.

With the regional information base resulting from this project, decisions about human activities that affect biodiversity can be made with specific reference to scientific data on distribution of biota over entire landscapes and ecoregions. The application of a regional model will allow data users interested in locally-occurring plant communities or vertebrate species to evaluate species status in the context of a watershed, ecoregion, national range, or ultimately continental and global range (Crist and Jennings 1997). Cooperative planning among neighboring land managers (e.g., Bureau of Land Management, National Park Service, U.S. Forest Service, state lands, and private land owners) will benefit from the consistency afforded by the regional land cover and vertebrate distribution maps. In this way, products of this project will provide an important tool for management and conservation planning in the varied ecosystems of the Southwest.

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LITERATURE CITED

Crist, P. and M. Jennings. 1997. Regionalizing state-level data. Pages 15-16 *in* E. Brackney and M. Jennings, (eds.). Gap Analysis Bulletin, no. 6. USGS/BRD/GAP, Moscow, ID.

Edwards, T. C., Jr., C. H. Homer, S. D. Bassett, A. Falconer, R. D. Ramsey, and D. W. Wight. 1995. Utah Gap Analysis: An environmental information system. Final Project Report 95-1, Utah Cooperative Fish and Wildlife Research Unit, Utah State University, Logan, UT.

Eve, M. and J. Merchant. 1998. A national survey of land cover mapping protocols used in the gap analysis program. Final Report. Internet WWW page, at URL: http://www.calmit.unl.edu/gapmap/report.html.

FGDC (Federal Geographic Data Committee). 1997. Vegetation classification standard, FGDC-STD-005. Internet WWW page, at URL: http://www.fgdc.gov/Standards/Documents/Standards/Vegetation.

Freedman, B. 1989. Environmental ecology: The impacts of pollution and other stresses on ecosystem structure and function. Academic Press, San Diego, CA.

Homer, C. G., R. D. Ramsey, T. C. Edwards, Jr., and A. Falconer. 1997. Landscape cover-type modeling using a multi-scene thematic mapper mosaic. Photogrammetric Engineering & Remote Sensing 63: 59-67.

Grossman, D. H., D. Faber-Langendoen, A. S. Weakley, M. Anderson, P. Bourgeron, R. Crawford, K. Goodin, S. Landaal, K. Metzler, K. D. Patterson, M. Pyne, M. Reid, and L. Sneddon. 1998. International classification of ecological communities: terrestrial vegetation of the United States. Volume I. The National Vegetation Classification System: Development, status, and applications. The Nature Conservancy, Arlington, VA.

Kepler, C. B., and J. M. Scott. 1985. Conservation of island ecosystems. Pages 255-271 *in* P. O. Moors, (ed.). Conservation of Island Birds. International Council of Bird Preservation, Technical Publication 3.

McCarthey, T. D., T. E. Corman, and M. J. Latta. 1995. Arizona breeding bird atlas project: 1995 progress report. Arizona Game and Fish Department, Phoenix, AZ.

McKendry, J. E. and G. E. Machlis. 1991. The role of geography in extending biodiversity gap analysis. Applied Geography 11: 135-152.

MDEP (Mojave Desert Ecosystem Program). 1998. Mojave Desert Ecosystem Project CD-ROM. UBS4M 12/98 Department of Defense Legacy Program in cooperation with the Department of Interior.

Noss, R. F. 1987. From plant communities to landscapes in conservation inventories: A look at The Nature Conservancy (USA). Biological Conservation 41: 1-37.

Noss, R. F. 1983. A regional landscape approach to maintain diversity. BioScience 33: 700-706.

Reid, M. S., K. A. Schulz, P. J. Comer, M. H. Schindel, D. R. Culver, D. A. Sarr, and M. C. Damm. 1999. An alliance level classification of vegetation of the coterminous western United States. Unpublished final report to the University of Idaho Cooperative Fish and Wildlife Research Unit and National Gap Analysis Program, in fulfillment of Cooperative Agreement 1434-HQ-97-AG-01779. The Nature Conservancy, Western Conservation Science Department, Boulder, CO.

Sauer, J. R., J. E. Hines, I. Thomas, J. Fallon, and G. Gough. 1999. The North American Breeding Bird Survey, Results and Analysis 1966 - 1998. Version 98.1, USGS Patuxent Wildlife Research Center, Laurel, MD.

Schrupp, D., L. O'Brien, and S. Russo. 2000. Colorado Gap Analysis Project. Pages 29-30 *in* E. Brackney, R. Brannon, P. Crist, and K. Gergely, (eds.). Gap Analysis Bulletin, no. 9. USGS/BRD/GAP, Moscow, ID.

Scott, J. M., F. Davis, B. Csuti, R. Noss, B. Butterfield, C. Groves, H. Anderson, S. Caicco, F. D'Erchia, T. Edwards, Jr., J. Ulliman, and R. Wright. 1993. Gap analysis: A geographic approach to protection of biological diversity. Wildlife Monographs 123: 1-41.

Thompson, B. C., P. J. Crist, J. S. Prior-Magee, R. A. Deitner, D. L. Garber, and M. A. Hughes. 1996. Gap analysis of biological diversity conservation in New Mexico using Geographic Information Systems. Research Completion Report, New Mexico Cooperative Fish and Wildlife Research Unit, Las Cruces, NM. 968 pp.

USGS GAP (Gap Analysis Program). 2000. A handbook for conducting Gap Analysis. Internet WWW page, at URL: http://www.gap.uidaho.edu/handbook (version current at 24 February 2000).

USGS WERC (Western Ecological Research Center), Sonoran Desert Field Station. 2001. Arizona Gap Analysis Project. Final Draft 4/10/01. USGS WERC Sonoran Desert Field Station, Tucson, AZ.

Wilcove, D., D. Rothstein, and E. Losos. 1998. Quantifying threats to imperiled species in the United States. BioScience 48: 607-612.

Modeling Wildlife Habitat Corridors in the Greater Grand Staircase-Escalante Ecosystem

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Abstract. The Grand Staircase-Escalante National Monument was established, in part, to protect landscape connectors, a resource about which very little is known. In this paper we present a methodology that may be applied to identify potential wildlife movement corridors, in the absence of direct, scientific observation, but where something is known about habitat quality. Our analysis of the Monument landscape suggests that there are a number of places that deserve further scrutiny as potential movement corridors, including the heart of the Kaiparowits Plateau, the East Fork of the Virgin River east of Zion National Park, and the Dixie National Forest northeast of Bryce Canyon National Park. While we do not imply that these are movement corridors, we believe that our analysis provides new insights into potential habitat connectivity.

Key words: movement corridors, GIS modeling, least-cost path analysis, landscape ecology, roads, national monuments, Bureau of Land Management, Gap Analysis Program, Utah.

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INTRODUCTION

For as long as principles of island biogeography have been applied to conservation, habitat connectivity has been understood to play an important role in the viability of species populations (Diamond 1975, Wilson and Willis 1975, Meffe and Carroll 1997). Habitat connectivity increases the likelihood of interaction among individuals within a population, which, in turn: (1) increases effective population size; (2) maintains gene flow; and (3) facilitates regular migration and dispersal. Each of these processes helps insure the viability and long-term persistence of a population (Primack 1993, Hunter 1996, Meffe and Carroll 1997).

The role of "corridors" in providing habitat connectivity is less well understood. Corridors, which are generally defined as strips of natural vegetation between protected blocks of habitat (Bentley and Catterall 1997, Beier and Noss 1998), have been proposed by some as crucial to the maintenance of healthy wildlife populations in otherwise degraded landscapes. Proponents of corridor protection note that wildlife seem to have preferred pathways through the land, as borne out by historical evidence, such as records of vehicle-wildlife collisions and the familiar "wildlife crossing" sign (Beier 1993). Protection of relatively good habitat strips cannot help but facilitate movement among patches (Noss 1987, Hobbs 1992, Noss and Cooperrider 1994).

Skeptics, on the other hand, argue that while wildlife certainly do not use all space uniformly, there is very little evidence that natural vegetation strips left on an otherwise developed landscape will be used as migration routes (Mann and Plummer 1995). They point to controlled experiments in which model species move more or less randomly about the landscape despite the provision of corridors (Ezzard 1992). Elsewhere, especially in sparsely vegetated desert settings, "corridors" may follow geological features not typically associated with habitat quality. Others have suggested that corridors might actually harm populations by facilitating the spread of disease or by concentrating prey species, making them easy targets for ambush predators (Simberloff and Cox 1987, Simberloff et al. 1992, Hess 1994). Some skeptics have argued that scarce conservation resources ought to be spent increasing the size of reserves rather than protecting movement corridors (Simberloff et al. 1992).

In the midst of this debate, in September 1996, President Clinton designated the Grand Staircase-Escalante National Monument in southern Utah. In addition to saluting the remoteness and natural beauty of the area, the President recognized the important role that the monument plays as a landscape connector, specifically mentioning riparian corridors as an object of conservation under the Antiquities Act (Clinton 1996). Belnap (1997) noted, "The Monument contains several perennial streams that connect the high plateaus to the low desert, thus preserving these migration corridors and increasing the Monument's ability to conserve genetic and population diversity of plants and animals." Belnap's report states further that "the connection the Monument provides between Glen Canyon, Canyonlands, Grand Canyon, Capitol Reef, and Bryce Canyon National Park units increases the value of all these areas for protection of viability of plant and animal populations."

This notion of a greater Grand Staircase-Escalante ecosystem, in which the

Monument helps sustain the health of a larger landscape, was explored by The Wilderness Society (1999) in "Crown of the Canyons: An atlas of the ecology, economy and future of the greater Grand Staircase-Escalante National Monument ecosystem." Despite the attention brought to the larger ecosystem by the President, scientists, and the conservation community, the management plan for the Monument (USDI Bureau of Land Management 2000) is virtually silent on the role of the Monument as a landscape connector. Locations and sizes of key connectors remain unresolved, leaving managers unable to address one of the purposes for which the Monument was established.

In this paper, we present a methodology for developing information about habitat connectivity in the absence of direct wildlife movement observations. To illustrate these methods, we modeled potential wildlife corridors between four established protected areas in the vicinity of the Grand Staircase-Escalante National Monument. While, there is much more work that needs to be done before we can rely on corridors to achieve conservation, we believe connectivity across landscapes should be maintained. We present herein one type of analysis that may help natural resource managers and researchers understand where to concentrate their future efforts.

METHODS

We employed methods derived from Walker and Craighead (1997, 1998) who modeled potential habitat corridors for grizzly bears, mountain lion, and elk in Montana. Walker and Craighead acknowledged the uncertainty surrounding the corridor issue, and rather than assert that they could identify transportation routes that animals would surely use, they suggest that it may be possible to identify habitat connectors that would likely increase the probability of animal survival. Thus, movement would be facilitated by these routes, whether animals actively followed them or not. Their approach was based on a set of four reasonable assumptions:

1) **Good corridors are primarily composed of good habitat.** That is, good habitat makes a better connector than bad habitat. The question of what constitutes "good habitat" continues to occupy wildlife biologists. This evaluation assumes that habitat quality can be determined.

2) **Humans pose problems for successful wildlife transit.** Specifically, roads and human developments create barriers to successful movement. Like habitat quality, the actual effect of roads on wildlife is a topic of intense scientific interest. This modeling approach assumes that habitat quality is diminished near roads.

3) **Current human developments are permanent.** Walker and Craighead's model does not evaluate the possibility of removing barriers to facilitate movement.

4) **"Least-cost paths" constitute the best routes of transit.** This key assumption allows that animals will follow an optimum route between two points that minimizes their exposure to low quality habitat. In reality, animals cannot know what lies beyond their sensory range and, so, cannot choose a truly optimum

path. Instead, they select resources at a finer scale, which may not be "least-cost" across a broader landscape. Assuming a least cost path "balances habitat suitability, minimum Euclidean distance, and degree of 'connectivity' between the two endpoints" (Walker and Craighead 1997). Again, this is an assumption of the modeling process. The sensory range of wildlife varies with species, and some migrant wildlife species may respond to coarser-grained landscape cues (e.g., topographic gradients, riparian corridors) than are represented by our habitat grid. Actual behavior may vary with species, season, or time of day.

The process that we used is illustrated graphically in Figure 1. Geographic Information Systems (GIS) software from Environmental Systems Research Institute (ESRI) was used to model the spatial relationship between roads and species habitat to derive potential travel corridors for a number of species. The species, whose conservation was recognized in the President's proclamation as a reason for establishment of the Monument, included black bear, mountain lion, desert bighorn sheep, bald eagle, and peregrine falcon. We obtained species habitat suitability data in a 90-meter resolution grid from the Utah Gap Analysis Project (GAP) of the United States Geological Survey (USGS). The Utah GAP vegetation cover-type mod-

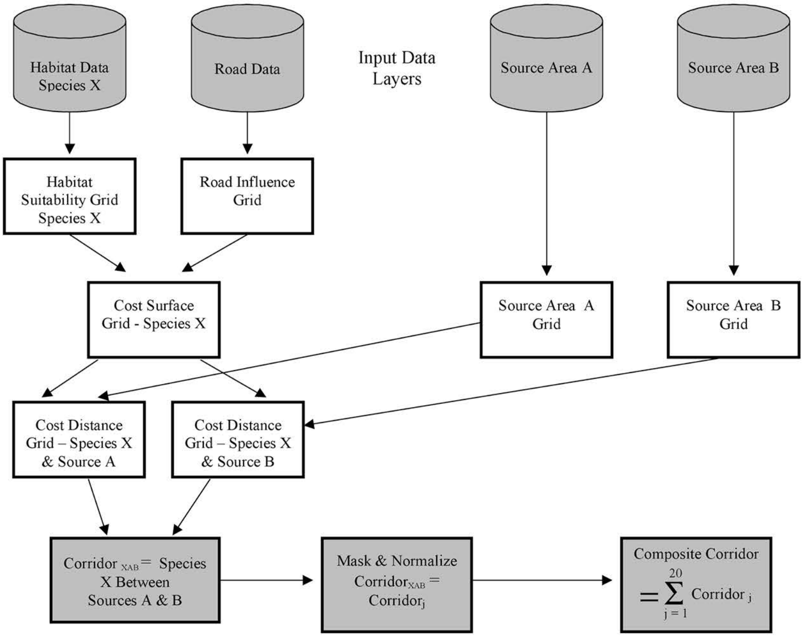

Figure 1. Flowchart describing the modeling process used in this study (see text for more specifics).

eling consisted of two phases: (1) correlation of cover-type associations with spectral values from 30-meter TM imagery; and, (2) ecological modeling based on ancillary information, which included 3 arc-second digital elevation data, slope, aspect, and region-specific vegetation cover-type polygons.

Classified pixel data were then aggregated to polygons (the GIS vector model) using a minimum mapping unit (MMU) of 100 ha. Riparian and wetlands polygons were derived with a 40 ha MMU. Species distribution was then predicted for each of the polygons based on the mapped cover-types, elevation, and existing species ranges. A distance-to-water buffer was also added to the species distribution models to correct distributions of species closely linked with water. These habitat suitability models are fixed in time and do not reflect seasonal variation in habitat quality, nor have they been empirically tested. Road data were obtained from the USGS as 1:100,000 digital line graphs (DLGs).

The GRID module of ESRI's ARC/INFO software provided the modeling tools that we used to develop our corridor identification methodology. The GRID module provides a built-in "corridor" function, which identifies the least cost path between two source areas. In this study, sources are defined as federally protected areas in the vicinity of the Monument, including Zion National Park to the west, Bryce Canyon and Capitol Reef National Parks to the north, and Glen Canyon National Recreation Area to the southeast (other potential source areas exist in Arizona, including the Vermilion Cliffs National Monument and Grand Canyon National Park, but these were not evaluated in this modeling effort). Movement between any two of these sources occurs across a "cost surface" that is a representation of species-specific habitat. Cost surfaces are based on the notion that low value habitat "costs more" (in terms of exposure to mortality risks, energy balance, etc.) to cross than does high-quality habitat.

A cost surface grid was derived for each species in the study based on GAP habitat suitability data. The GAP data identified habitat by five nominal classes (critical, high value, significant value, low value, and no habitat value), so we had to assign numerical values to these habitat classes in order to generate a cost surface. After conducting a sensitivity analysis in which we explored model behavior under a variety of scoring systems, we determined that a simple rating of 1 to 5 yielded the most acceptable model behavior. The sensitivity analysis involved varying the scores assigned to each nominal class (using constant, linear, and exponential increases) and the effect of roads as barriers. The model is extremely flexible and can be forced into a wide range of behaviors. Our sensitivity analysis led us to select parameter values that produced a reasonable wildlife movement behavior model.

Once developed, each cost surface was then modified to increase costs (i.e., degrade habitat value) according to the influence of roads. The USGS road data were divided into major (high volume) and minor (low volume) road classes. We subjectively determined that major roads have a zone of influence that extends 1600 meters, while minor roads have an influence to 400 meters. We recognize that our buffers are mostly arbitrary because different species respond differently to roads. As more is learned about the response of individual species to roads, the road effect may be tailored to fit particular species and road classes. For major roads, a road impact coefficient of 100 was applied at the surface of the road, with impact declining exponentially to a coefficient of one at 1600 meters. We assumed minor roads have 1/3 the maximum impact of major roads and, therefore, have a coefficient of 33 at the road, with influence decreasing exponentially to a coefficient of one at 400 meters. The final cost surface for each species was derived by multiplying the cell values from the respective habitat grids by the cell values from the road influence grid. The final cost grids represent the cost to move through a single grid cell.

To account for the accumulated cost of dispersing away from a source area, we next developed "cost distance" grids in pairs for reciprocal source areas. For example, to ultimately identify a corridor between Bryce Canyon NP and Capitol Reef NP, two cost surface grids are required — one that represents the accumulated costs of a species dispersing from Bryce Canyon NP and a reciprocal grid that represents the same species as it disperses from Capitol Reef NP. For each species, cost distance grids were derived for four pairs of source areas (Zion to Bryce, Bryce to Capitol Reef, Bryce to Glen Canyon, and Zion to Glen Canyon).

The pairs of cost distance grids were then combined using the GRID module's "corridor" function, resulting in a single grid that represented a continuum of values across the entire study area. Within this continuum, the corridor is represented by the lowest cell values, the "least-cost path." To isolate the corridor, a mask was applied to eliminate all but the lowest 1% of cell values. A total of 20 corridors were derived, one for each species between four pairs of sources (Fig. 2). To enable comparison, the cell values in each corridor were normalized to a scale of 1 to 50. A final, composite corridor (Fig. 3) was created by adding the normalized cell values from all 20 corridors and rescaling the resulting range of values from 1 to 255 to facilitate final map shading.

RESULTS AND DISCUSSION

The variability among species in corridors identified by our model shows clearly that model results are affected by the distribution of habitat quality for each species (Fig. 2). Though corridors do tend to avoid roads, roads do not drive the model. High quality black bear habitat on the Aquarius Plateau to the north of the Monument would allow bears to travel from Bryce to Capitol Reef through the forested uplands. Conversely, the absence of good habitat on the Aquarius Plateau for desert bighorn sheep forces sheep to travel from Bryce to Capitol Reef across the Kaiparowits Plateau. Our results seem to make biological sense, suggesting that this model may have utility in predicting where species are likely to move across the southern Utah landscape.

Despite these promising results, it is important to keep in mind that our model is speculative and represents only numerical manipulations. For example, while it may make sense for desert bighorn sheep traveling between Bryce and Capitol Reef to traverse the Kaiparowits Plateau, it may make no sense at all for bighorn sheep to even be found at Bryce Canyon. Desert bighorn sheep prefer open desert scrub, not

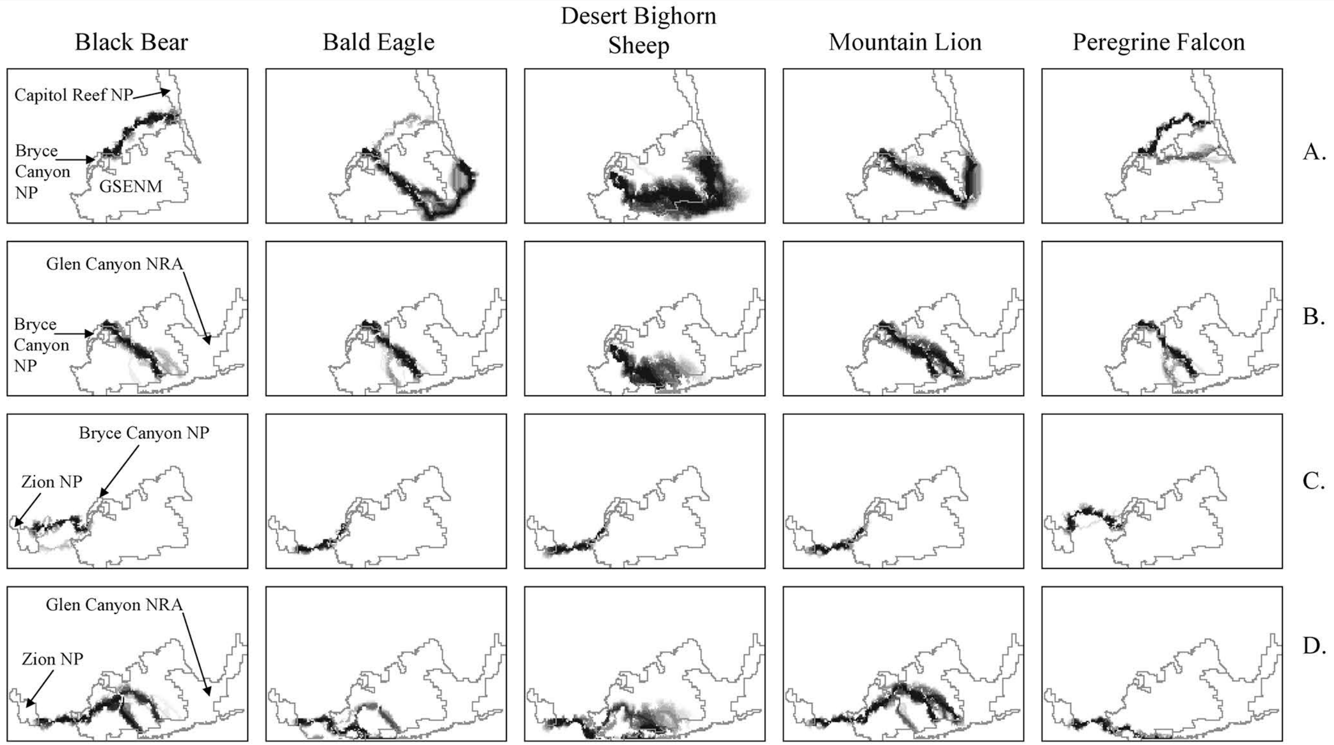

Figure 2. Potential wildlife habitat corridors for the five species between four pairs of protected areas in the greater Grand Staircase-Escalante ecosystem: A. Bryce Canyon National Park to Capitol Reef National Park; B. Bryce Canyon National Park to Glen Canyon National Recreation Area; C. Zion National Park to Bryce Canyon National Park; and D. Zion National Park to Glen Canyon National Recreation Area.

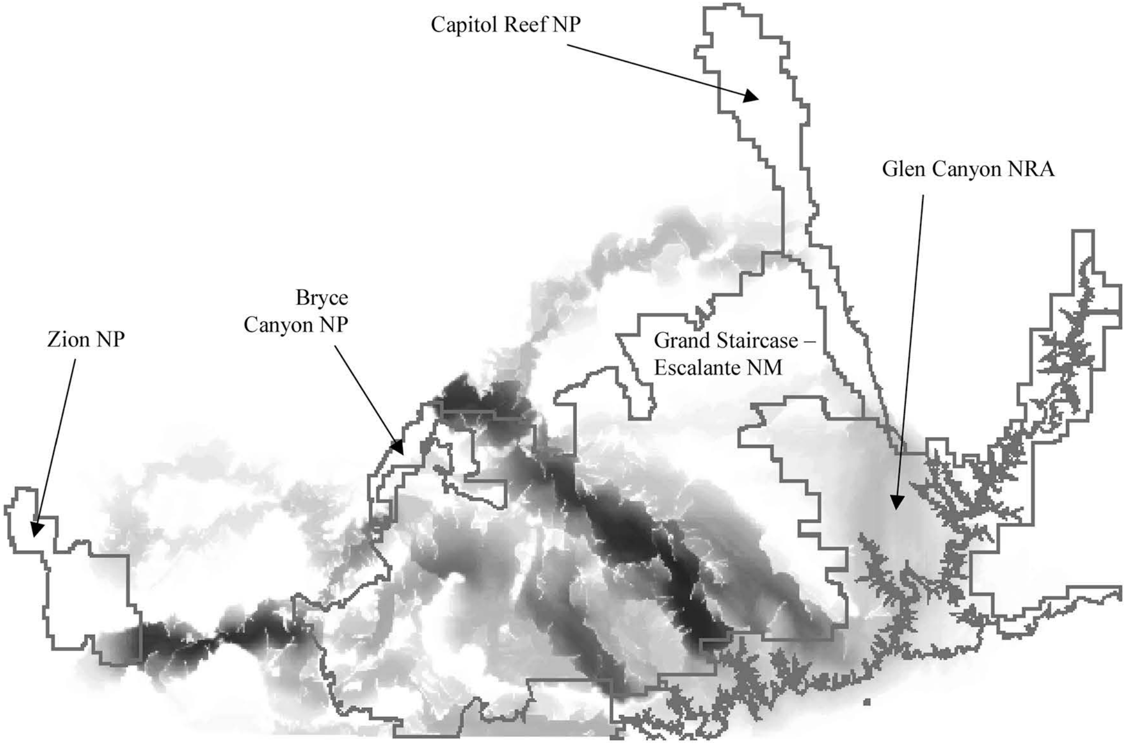

Figure 3. Composite wildlife habitat corridor map created by combining the 20 corridors in Figure 1. The darkest parts of the image indicate potential wildlife movement corridors.

the subalpine forests of the Paunsaugunt Plateau. We believe the best use of these results is to direct the attention of scientists and land managers to particular places on the landscape that are worthy of further investigation as wildlife habitat connectors. Nevertheless, in the absence of ground-based observations or scientific research, models such as this can provide new insights to land managers and scientists.

The compiled corridor map obscures information about individual species, but it does highlight some places that appear to be particularly important to landscape connectivity (Fig. 3). For example, the Kaiparowits Plateau in the center of the Monument is an obvious "hot spot." This is not surprising, given the area's legendary remoteness and unspoiled natural character.

Less predictable is the apparently very important connector east from Zion to the Monument along the East Fork of the Virgin River. This mostly BLM land was left out of the Grand Staircase-Escalante National Monument but has been recommended for inclusion in the National Wilderness Preservation System by the Utah Wilderness Coalition because of its outstanding natural character. In addition to the importance of the corridor, our image indicates a crucial constriction at Mt. Carmel Junction, where roads and development threaten to cut off connection. Similarly, the national forest land east of Bryce Canyon National Park in the vicinity of Powell Point appears to be an important connector between Bryce Canyon and the Aquarius and Kaiparowits Plateaus.

Managers of the Grand Staircase-Escalante National Monument will be making decisions implementing their management plan over the next several years. Among their decisions will be determinations of where to place developments and which roads to close and/or rehabilitate. Clearly, in the absence of scientific research to the contrary, our model suggests that they should maintain the corridor integrity between the Aquarius Plateau and Glen Canyon National Recreation Area. Similarly, managers of the Dixie National Forest should seek to protect habitat connectivity between Bryce Canyon and Powell Point, and the BLM, Forest Service, and local authorities should be concerned about development in the vicinity of Mt. Carmel Junction.

In presenting our model, we do not wish to assert that the corridors we have identified are the most important pathways for wildlife movement in the landscape. We are only suggesting that these may be productive places to focus further study. It is important to keep in mind that, ultimately, this work is only a mathematical model. However, in the absence of any other information on wildlife distribution and movement patterns, this represents the best available information, and management should take this information into account in conservation planning. Ultimately, we would prefer to see additional work done to examine the degree to which these *apparently* important corridors actually contribute to wildlife population viability. We hope that by presenting one feasible approach, we spur further work aimed at protecting wildlife habitat connectivity in this landscape and throughout the Colorado Plateau.

LITERATURE CITED

Beier, P. 1993. Determining minimum habitat areas and habitat corridors for cougars. Conservation Biology 7: 94-108.

Beier, P., and R.F. Noss. 1998. Do habitat corridors provide connectivity? Conservation Biology 12: 1241-1252.

Belnap, J. 1997. Ecological resources of the Grand Staircase-Escalante National Monument. Pages 17-25 *in* L.M. Hill, (ed.) Learning from the land: Grand Staircase-Escalante National Monument Science Symposium proceedings. USDI Bureau of Land Management, Salt Lake City, UT.

Bentley, J.M., and C.P. Catterall. 1997. The use of bushland, corridors, and linear remnants by birds in southeastern Queensland, Australia. Conservation Biology 11: 1173-1189.

Clinton, W.J. 1996. Establishment of the Grand Staircase-Escalante National Monument by the President of the United States of America, September 18, 1996: A proclamation.

Diamond, J.M. 1975. The island dilemma: lessons of modern biogeographic studies for the design of natural preserves. Biological Conservation 7: 129-146.

Ezzard. C. 1992. Wilderness corridors may not benefit all. Science News 8/29/92: 135.

Hess, G. 1994. Conservation corridors and contagious disease: a cautionary note. Conservation Biology 8: 256-262

Hobbs, R.J. 1992. The role of corridors in conservation: solution or bandwagon? Trends in Ecology and Evolution 7: 389-392

Hunter, M.L. 1996. Fundamentals of conservation biology. Blackwell Science, Cambridge, MA.

Mann, C.C., and M.L. Plummer. 1995. Are wildlife corridors the right path? Science 270: 1428-1430.

Meffe, G.K., and C.R. Carroll. 1997. Principles of conservation biology, 2nd edition. Sinauer Associates, Sunderland, MA.

Noss, R.F. 1987. Corridors in real landscapes: a reply to Simberloff and Cox. Conservation Biology 1: 159-164.

Noss, R.F., and A. Cooperrider. 1994. Saving nature's legacy: protecting and restoring biodiversity. Defenders of Wildlife and Island Press, Washington, D.C.

Primack, R.B. 1993. Introduction to conservation biology. Sinauer Associates, Sunderland, MA.

Simberloff, D., and J. Cox. 1987. Consequences and costs of conservation corridors. Conservation Biology 1: 63-71.

Simberloff, D., J.A. Farr, J. Cox and D. Mehlman. 1992. Movement corridors: conservation bargains or poor investments? Conservation Biology 6: 493-504.

The Wilderness Society. 1999. Crown of the Canyons: an atlas of the ecology, economy, and future of the greater Grand Staircase-Escalante National Monument ecosystem. The Wilderness Society, Denver, CO.

USDI Bureau of Land Management. 2000. Grand Staircase-Escalante National Monument Approved Management Plan and Record of Decision. USDI-BLM, Cedar City, UT.

Walker, R., and L. Craighead. 1997. Analyzing wildlife movement corridors in Montana using GIS. Presented at the 1997 ESRI Users Conference and published in the Proceedings on CD-ROM. Also available at http://www.grizzlybear.org/col/lcpcor.html.

Walker, R., and L. Craighead. 1998. Corridors: key to wildlife from Yellowstone to Yukon. Pages 113-121 *in* L. Willcox, B. Robinson and A. Harvey, (eds.) A sense of place: An atlas of issues, attitudes and resources in the Yellowstone to Yukon ecoregion. Yellowstone to Yukon Conservation Initiative, Canmore, Alberta.

Wilson, E.O., and E.O. Willis. 1975. Applied biogeography. Pages 522-534 *in* M.L. Cody and J.M. Diamond, (eds.) Ecology and evolution of communities. Belknap Press, Cambridge, MA.

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Climate of the Central Colorado Plateau, Utah and Arizona: Characterization and Recent Trends

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Abstract. The climate of the central portion of the Colorado Plateau is characterized using data from 27 climate stations. Mean annual temperature ranges from 16.9 °C at Lee's Ferry (978 m) to 4.4 °C at Bryce Canyon National Park (2412 m). Precipitation varies from 138-405 millimeters, and is weakly bimodal, with a strong late summer-early fall peak and a weaker late winter-early spring peak. Annual Thornthwaite potential evapotranspiration rates vary from 993 to 474 mm, and at all stations, rates exceed annual precipitation. Temperature, precipitation and evapotranspiration are all strongly controlled by elevation. Latitude and longitude have some additional effects on some variables. A strong southeast to northwest decline in temperature occurs across the study region. An analysis of trends among nine stations with good records reveals that annual minimum temperatures have increased significantly in most areas since the 1960's. Those stations that fail to show this trend do show significant increases in winter minimum temperatures. Maximum temperatures have not responded in the same manner, and some high elevation stations document declines in maximum temperatures. Longer-term records at Escalante and Lee's Ferry confirm the warming trend back to 1925 and 1944, respectively. Precipitation amounts have changed relatively little, although there is a weak trend towards increasing winter season precipitation. There is no evidence in the data for a strengthening of the summer monsoon, which is a prediction of some global warming models. Potential impacts of global warming scenarios and changes in extent and timing of precipitation on the vegetation and rare species of the Colorado Plateau are discussed.

Key words: central Colorado Plateau, climate, global warming, potential evapotranspiration, temperature, precipitation.

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INTRODUCTION

The Colorado Plateau consists of a series of plateaus formed from sedimentary rocks, with scattered laccolithic ranges such as the Henry Mountains, San Francisco Peaks, and Navajo Mountain. Elevation of the Plateau averages between 1500-1800 m, with several mountains exceeding 3300 m. The Colorado River has cut through the Plateau from northeast to southwest, and has carved a series of deep canyons ranging from 1400 m on the east edge in Colorado to 370 m on the west edge along the Grand Wash Cliffs in Arizona. Relatively little is known about the climate of the Plateau, particularly in the central region where population is sparse.

The central portion of the Colorado Plateau (Fig. 1) includes some of the lowest elevations on the Plateau. Along the Colorado River elevations range from 1219 m at Moab to 978 m at Lee's Ferry, a drop of only 241 m in 450 km. Along the river corridor, extensive mesas range in elevation from 1400-1800 m. The high Wastach and Kaibab Plateaus to the north, west and southwest produce an extensive rain shadow effect on this portion of the Plateau. Average annual rainfall throughout much of the region is < 200 mm, and to the north and east of the Henry Mountains, in the San Rafael and Green River deserts, is < 150 mm.

In this study, the climate of the central Colorado Plateau is characterized, using temperature, precipitation, and potential evapotranspiration, and their relationships with elevation. Because of the interest and speculation regarding the possible effects of global warming in the region, trends in temperature and precipitation are examined in detail for selected stations. The main objectives of this study are to (1) characterize the climate of the central Colorado Plateau, (2) provide regression equations for relationships between climate variables and elevation, and (3) document recent trends in climate.

BACKGROUND AND SETTING

The climate of the study area can be classified as temperate-arid (Walter 1985), with hot summers, extensive periods of frost in the winter, and low and variable precipitation. The average freeze-free season varies from > 200 days along the Colorado River to < 20 at the summit of the highest mountains (Ashcroft et al. 1992). Most of the study area experiences 120 or more frost-free days a year. During winter, the polar jet stream lies to the north of the study area, preventing most winter storms from reaching the Colorado Plateau (Mitchell 1976, Petersen 1994). Occasionally, the winter high-pressure ridge over the western U.S. moves westward into the Pacific Ocean. This allows the development of a low-pressure trough between the Sierra-Cascade Mountains and Rocky Mountains, bringing winter storms into the region. As the region warms in the spring, the polar jet stream moves northward, replaced by high pressure. When this high pressure begins to move north in late June or July, warm, wet air from the Gulf of Mexico moves northwest into the region, bringing the late summer monsoons. The average position of the northern edge of these monsoons bisects the Colorado Plateau from northeast to southwest (Petersen 1994; Fig. 1). This position varies from year to year, producing highly-variable summer and early fall precipitation in the study area. In some years, late summer tropical hurricanes off Baja, California bring extensive rain into the region from the southwest up the Colorado River Valley (Petersen 1994).

The study area comprises roughly the west-central portion of the Plateau, ranging from 36-38° latitude and 110-112° longitude (Fig. 1). The study area lies along the eastern edge of the Wastach Plateau, and is bounded on the north by the Book Cliffs, the east by the high plateaus of Canyonlands and the La Sal Mountains, the southeast by the Abajo and Chuska Mountains, and the south by the high rim of Black Mesa. Southeastern Utah, including towns like Moab, Monticello, and Blanding, are not included because preliminary inspection of climate data revealed a significant increase in summer moisture in that area; this may be an orographic effect produced by the high mountain masses of the La Sal, Abajo, and southern Rocky Mountains, or a closer proximity to the Gulf of Mexico.

The vegetation of the study area consists primarily of a variety of arid and semiarid plant communities. Extensive areas below ca. 1500 m are dominated by either *Coleogyne ramosissima* (blackbrush) shrubland on shallow soils, or mosaics of shrubland and grassland types in sandy soils. Clay barrens are common and generally vegetated by ephemeral annual forbs or dwarf shrubland that is dominated by species of *Atriplex*. Above ca. 1500 m, extensive areas are dominated by stands of *Pinus edulis* (two-needled pinyon) and *Juniperus osteosperma* (Utah juniper). *Pinus ponderosa* (Ponderosa pine) woodlands occur at elevations above 2300 m on the higher mountains. Above ca. 2700 m, a mixed conifer forest can be found, dominated by *Pseudotsuga menziesii* (douglas fir), *Abies concolor* (white fir), and *Populus tremuloides* (aspen). Patches of *Abies bifolia* (Rocky Mountain subalpine fir) -- *Picea engelmannii* (Engelmann spruce) forest, subalpine meadows, and alpine tundra occur on the summits of the highest mountains above ca. 3000 m (Spence et al. 1995).

METHODS

The data set consists of monthly, yearly, and total record means for minimum, maximum, and annual temperature (T), and precipitation (PCP). Climate stations and basic data are listed in Table 1, along with information on duration of record and elevation. Figure 1 shows the area under consideration and the station locations. In all, 27 stations with records of 10 years or greater were utilized. Data were taken from the World Wide Web site maintained by the Desert Research Institute at the University of Nevada, Reno (www.wrcc.dri.edu/summary). Data was first inspected for gaps in records. If a particular monthly value was missing, the missing value was estimated as the mean monthly value of the previous year and following year. Data were then converted to metric values. Seasons were used for certain comparisons. Seasons are defined as follows: winter (December-February), spring (March-May), summer (June-August), and fall (September-November). Growing season (April-September) and winter season (October-March) were also compared. Latitude and longitude for each station were recorded, and two vectors were calculated using the pythagorean theorem, one from the southeast to northwest (135° to 315°), the

Table 1. Climate data for selected stations on the central Colorado Plateau. PCP=precipitation, Tann=annual mean temperature, and POTE=Thornthwaite potential evapotranspiration. The recording period and duration in years for each station is also listed.

Station	Elevation[1]	PCP[2]	Tann[3]	POTE[2]	Record	Yrs
(1) Page	1372	164	14.5	853	1959-1998	39
(2) Lee's Ferry	978	153	16.9	993	1916-1998	82
(3) Wahweap	1136	158	15.7	911	1967-1998	31
(4) Big Water	1250	171	14.7	859	1963-1998	35
(5) Escalante	1773	278	9.4	622	1901-1998	97
(6) Bullfrog	1165	152	15.2	899	1967-1998	31
(7) Hite	1058	144	16.2	941	1949-1962	13
(8) Hite Marina	137	136	16.0	942	1968-1978	10
(9) Hite Ranger Station	1220	214	15.5	919	1978-1998	20
(10) Hans Flat	2012	248	10.6	667	1981-1998	17
(11) Mexican Hat	1265	159	13.6	810	1948-1998	50
(12) Natural Bridges NM	1982	320	10.3	652	1965-1998	33
(13) Hanksville	1313	138	11.8	745	1948-1998	50
(14) Boulder	2034	272	9.3	614	1954-1998	44
(15) Sandy Ranch	1615	193	10.1	660	1963-1988	25
(16) Bryce Canyon Airport	2312	307	4.4	474	1948-1983	35
(17) Bryce Canyon NP	2412	405	5.1	484	1959-1998	39
(18) Henrieville	1832	264	9.2	605	1963-1979	16
(19) Monu. Valley Mission	1616	188	13.4	783	1961-1989	18
(20) Betatakin	2222	310	9.9	628	1948-1998	50
(21) Navajo Mountain	1835	233	9.8	635	1956-1975	19
(22) Capitol Reef NP	1679	193	12.1	731	1967-1998	31
(23) Fruita	1677	174	11.7	711	1948-1967	19
(24) CANY-Needles	1536	214	11.8	727	1965-1998	33
(25) CANY-Neck	1808	231	11.4	713	1965-1998	33
(26) Kayenta	1735	195	11.5	698	1915-1978	63
(27) Green River	1241	159	11.4	773	1893-1998	105

[1] Elevation in meters

[2] Precipitation and POTE in millimeters

[3] Temperature in °C

second from southwest to northeast (225° to 45°). The position of each station was determined along these two vectors, which roughly correspond to Gulf of California and Gulf of Mexico air masses and storm tracks. After the effects of elevation were removed, a series of regressions were run among latitude, longitude, two vectors 45° off the vertical-horizontal coordinates, and climate variable residuals.

Potential evapotranspiration (POTE) rates were calculated for each station. POTE determines the potential annual loss of water for a region from evaporation and plant transpiration. Thornthwaite's POTE was used because it is widely applied in North America, and its weaknesses and strengths are well known. The principal

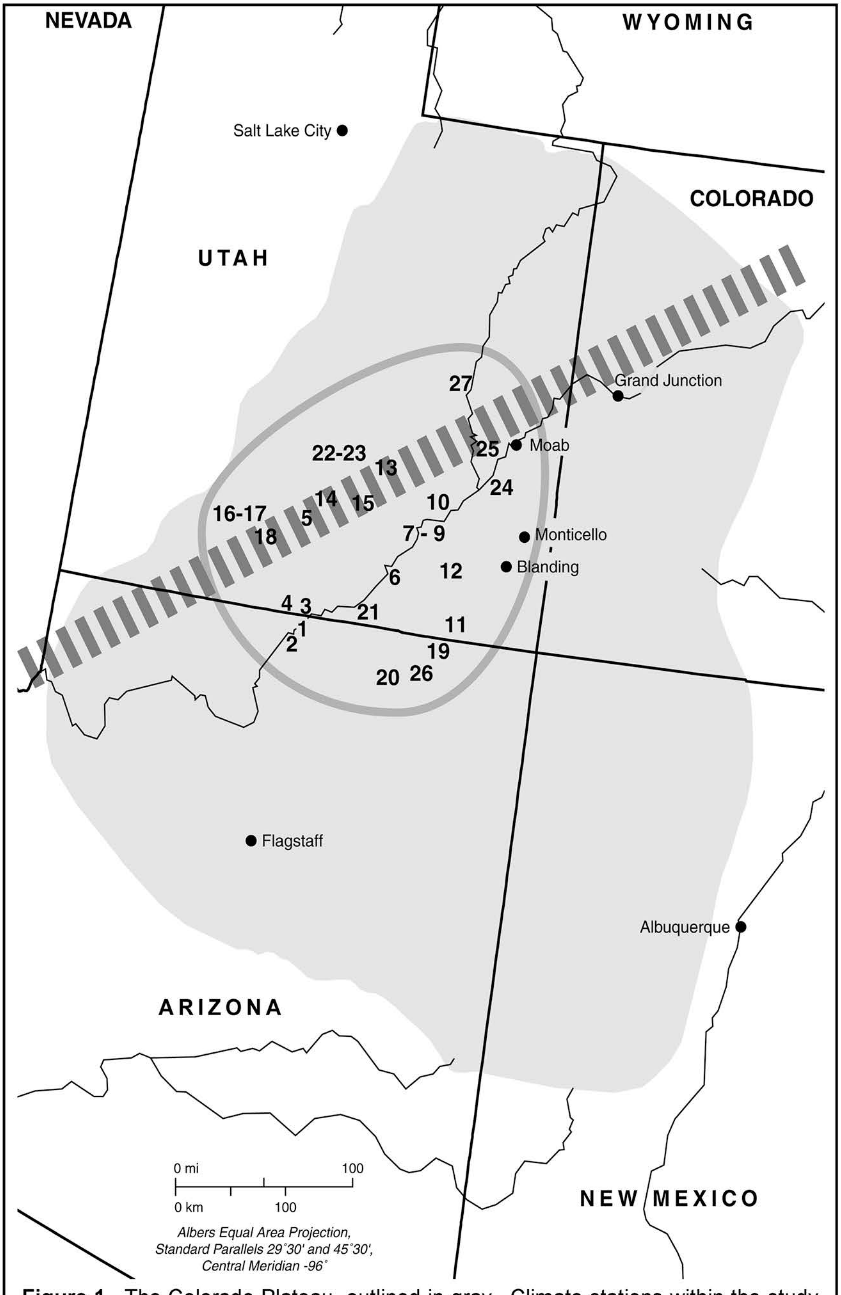

Figure 1. The Colorado Plateau, outlined in gray. Climate stations within the study area, encompassed in dark grey circle, are numbered (see Table 1). The heavy, dashed line represents the approximate boundary of regional air masses and the average northern limit of the summer monsoon season in the region (from Mitchell 1976, Petersen 1994).

weakness is that it tends to underestimate values in extremely arid regions. Thornthwaite's POTE (*e*) is calculated as:

$$e = 1.8(10t/I)a \tag{1}$$

where: a = a constant,
t = monthly mean temperature in °C, and
I = annual temperature index obtained by summing the monthly values.

An assumption was made that climate variable means and variances were stationary throughout the duration of each station's record. This may not be the case, particularly for stations with long term records (e.g., Escalante, 98 years). Generally, this is a reasonable assumption (Rowlands 1993), particularly given the relatively short period of time under consideration (e.g., 30-50 years).

For analysis of trends in climate variables, a subset of nine of the 27 stations were selected. These were selected because of relatively complete records back to 1966, and because they represent an elevational gradient. This elevational gradient ranges from 978 m at Lee's Ferry to 2412 m at Bryce Canyon National Park. These nine stations were analyzed in relation to three T and three PCP variables. Trends were examined for the period 1966-1998 (33 years) using linear regression. For those stations with longer records, a second set of analyses was completed for the duration of each record.

RESULTS

Characterization

Summary climate data can be found in Table 1. Mean annual temperature (T) varies from a high of 16.9° C at Lee's Ferry to 4.4° C at Bryce Canyon Airport. Precipitation (PCP) is generally low at most stations, ranging from 136 mm at the Hite Marina to 405 mm at Bryce Canyon National Park. Because of the generally low PCP and hot summers, POTE rates are relatively high, ranging from 993 mm at Lee's Ferry to 474 mm at Bryce Canyon Airport. POTE exceeds PCP for all stations. Even at the highest elevations around Bryce Canyon National Park (2300-2400 m), POTE exceeds PCP, on average, seven months of the year. For all stations, however, winter season (December-February) PCP exceeds POTE.

There is strong seasonal control for all T and PCP variables. A breakdown of PCP by season shows that, for most stations, it peaks in fall (September-November). For all stations, 30% of summed yearly PCP occurs in fall, followed by 27% in summer. Winter and spring are somewhat lower, with 22% and 21%, respectively. A weakly bimodal pattern occurs for most stations, with a late summer-early fall peak, and a second smaller peak in late winter. The driest months of the year tend to be May and June, and the wettest months July and August. At intervals of every two-three years, September and October tend to have the heaviest PCP.

Climate diagrams for three stations, Page (1372 m), Escalante (1773 m), and Bryce Canyon National Park (2412 m) are depicted in Figure 2.

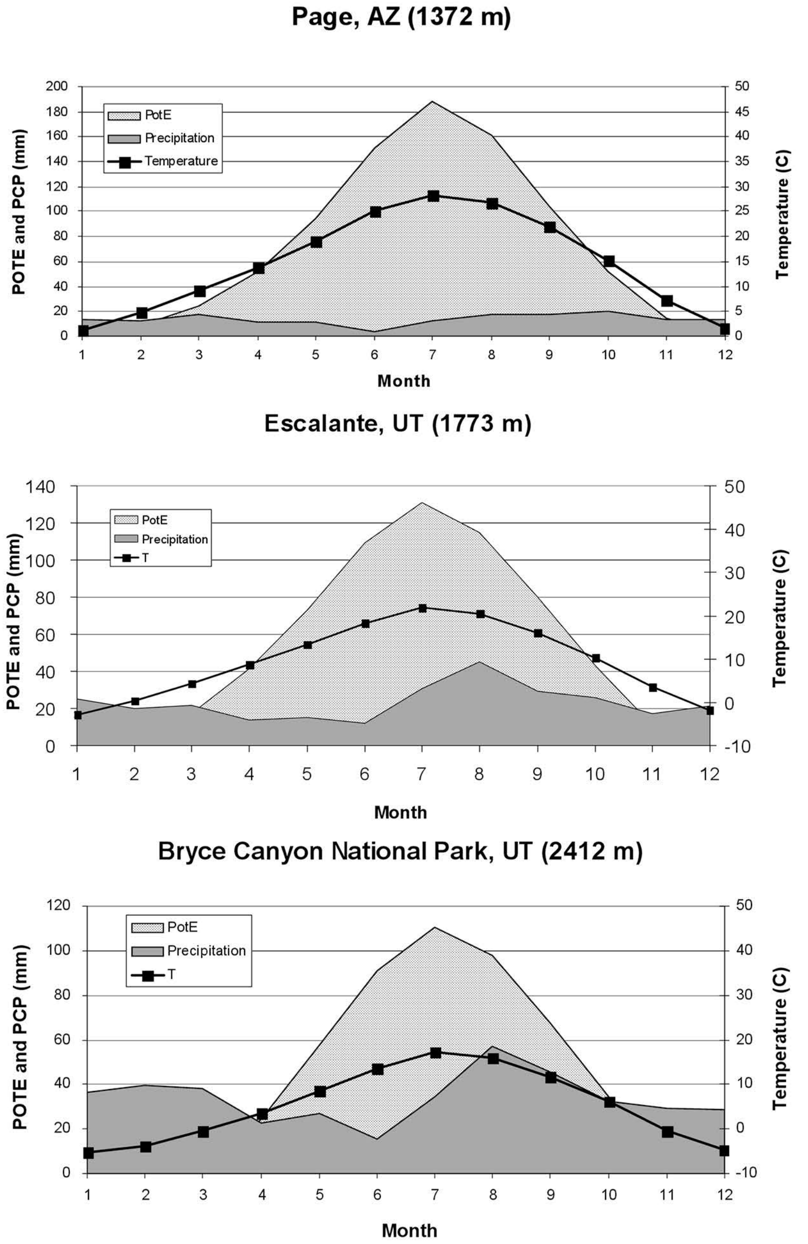

Figure 2. Simplified climate diagrams plotting mean monthly temperature (°C), mean precipitation (mm), and potential evapotranspiration rates for three climate stations on the central Colorado Plateau. The year starts in January (month 1) and goes to December (month 12). **a**. Page, Arizona (1372 m); **b**. Escalante, Utah (1773 m); **c**. Bryce Canyon National Park, Utah (2412 m).

Elevational Relationships

All climate variables are strongly controlled by elevation. The regression equations for PCP, annual T, and POTE are:

Precipitation (mm) = 0.1498*elevation in meters - 25.7 (r^2=0.802) (2)
Annual T (°C) = -0.007*elevation in meters + 23.168 (r^2=0.817) (3)
POTE (mm) = -0.3148*elevation in meters + 1244.5 (r^2=0.847) (4)

Figure 3 shows the relationship among elevation, PCP, and POTE. As elevation increases, PCP increases and POTE decreases in a linear manner. The point at which the two lines intersect is known as the arid-humid boundary, where the PCP/POTE ratio is one. On the central Colorado Plateau, this boundary, based on where the two lines intersect in Figure 3, is estimated to lie at ca. 2730 m.

The relationship among annual maximum and minimum T, and elevation is similar, with T decreasing as elevation increases. All three curves are essentially identical, with the same slopes. The regression equations for maximum and minimum annual T are:

Maximum annual T (°C) = -0.007*elevation in meters + 30.817 (r^2=0.935) (5)
Minimum annual T (°C) = -0.007*elevation in meters + 15.577 (r^2=0.596) (6)

The relationship between annual minimum T and elevation is much weaker than that for annual and maximum T. This may result from influences by local topographic factors, such as depressions or valleys, that can cause winter temperature inversions. The adiabatic lapse rate, using mean annual T, is -0.70° C for each 100-meter increase in elevation.

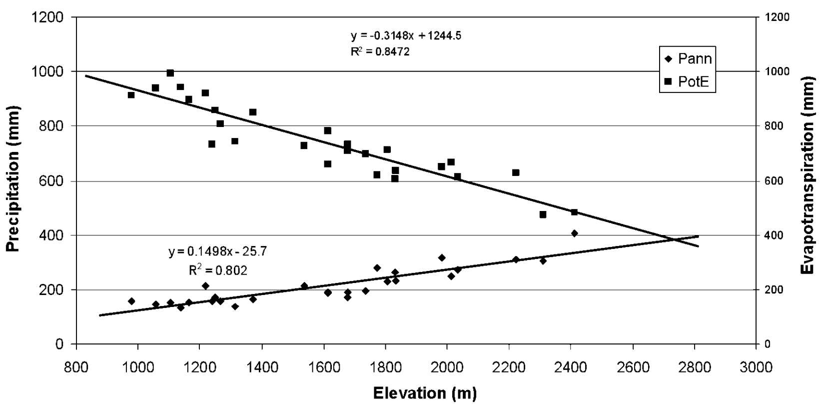

Figure 3. The relationship among precipitation (PCP), potential evapotranspiration (POTE), and elevation on the central Colorado Plateau. The regression curves, regression equations, and variance are noted for the two curves.

Summer PCP increases more rapidly with elevation than winter PCP, although the differences are rather slight (winter PCP regression slope = 0.038, summer PCP slope = 0.047). PCP increases at almost the same rate for both growing (April-September) and winter (October-March) seasons (growing season regression slope = 0.076, winter season slope = 0.074).

Geographic Relationships

Regression analysis indicates that elevation shows the strongest relationship with climate variables (Table 2). Regressing the residuals against latitude shows a trend of increasing winter PCP at higher latitudes, as one would expect. Winter PCP declines along a southwest to northeast vector in the study area. Growing season PCP shows a weak relationship with longitude, decreasing from east to west. Spring PCP exhibits a weak southeast to northwest increase.

All three T residuals show some relationships with geographic position, including both latitude and the SE to NW vector (Table 2). Both annual and maximum T

Table 2. Summary of linear regressions of climate residuals after the effects of elevation are removed against latitude, longitude, and two 45° vectors, a southeast to northwest vector, and a southwest to northeast vector. The arrows indicate the direction of the trends. As the vector value increases northward (↑) the value of the climate residual either increases (↑) or decreases (↓) in value. The results of the regression are also displayed (ns=not significant, *P*>0.15).

	Latitude	Longitude	SE→NW	SW→NE
Precipitation				
Annual	ns	ns	ns	ns
Growing Season	ns	p=0.154	ns	ns
Vector/PCP		↑/↓		
Winter Season	ns	ns	ns	ns
Winter	P=0.025	ns	ns	p=0.038
Vector/PCP	↑/↑			↑/↓
Spring	ns	ns	p=0.102	ns
Vector/PCP			↑/↑	
Summer	ns	ns	ns	ns
Fall	ns	ns	ns	ns
Temperature				
Annual	p=0.034	ns	p=0.029	ns
Vector/T	↑/↓		↑/↓	
Maximum	p=0.001	ns	p=0.020	ns
Vector/T	↑/↓		↑/↓	
Minimum	ns	ns	p=0.070	ns
Vector/T			↑/↓	
POTE	p=0.022	ns	ns	ns
Vector/POTE	↑/↓			

decline as latitude increases, as expected, but minimum T does not change along this gradient. All three T variables exhibit significant declines along the SE to NW vector.

Climate Trends

Regression analysis reveals numerous significant trends in T variables for most stations (Table 3). With few exceptions, T has increased over the last 33 years. Many of these increases are statistically significant. For minimum T, all stations show either an increase, or no trend. For those stations showing this trend, the change in minimum T varies from approximately 0.5 to 1.9° C, depending on the station. Minimum T at Wahweap, on Lake Powell, has not changed in the last 33 years. However, January mean minimum T at Wahweap has shown strong increases (p=0.020). The largest increases in minimum T since 1966 have been at Page, the CANY-Needles, and Escalante. The smallest changes have been at Lee's Ferry, Wahweap, and Bryce Canyon National Park. Although there is only a weak, nonsignificant trend towards increasing minimum T since 1966 at Lee's Ferry, a significant increase has occurred (p=0.050) since 1944 (there are numerous gaps prior to this year). Only the two highest elevation stations, Bryce Canyon National Park and Betatakin, show weak increases or no trends in minimum T. Annual mean T parallels minimum T, with trends in the same direction. However, maximum T has decreased at two high-elevation stations since 1966, Natural Bridges National Monument and Bryce Canyon National Park. At the same time, however, maximum T has increased at Betatakin. Overall, maximum T shows fewer definite trends compared with annual and minimum T.

PCP trends are more variable in the study area (Table 4). There is a weak trend towards increasing PCP among the nine stations. Five stations show increases in annual PCP, while the other four show no trend. Most of the increases in PCP are in the winter months rather than the summer months; few are significant.

Table 3. Mean temperature trends in the last 33 years (since 1966) at selected climate stations on the central Colorado Plateau. Trends ($p \leq 0.25$) are indicated as either increasing (↑) or decreasing (↓) using regression. Significance of each regression is shown (ns=not significant, $p > 0.25$, no trend (→)).

	Annual Mean		Annual Maximum		Annual Minimum	
Station	Trend	Significance	Trend	Significance	Trend	Significance
Lees Ferry	↑	p=0.226	↑	p=0.174	↑	p=0.256
Wahweap	→	ns	↑	p=0.156	→	ns
Mexican Hat	↑	p=0.017	↑	p=0.070	↑	p=0.033
Page	↑	p<0.001	↑	p=0.140	↑	p<0.001
Needles	↑	p=0.016	→	ns	↑	p=0.008
Escalante	↑	p=0.001	↑	p=0.054	↑	p<0.001
Natural Bridges	→	ns	↓	p<0.001	↑	p=0.002
Betatakin	↑	p=0.089	↑	p=0.008	→	ns
Bryce Canyon	→	ns	↓	p=0.043	↑	p=0.118

Table 4. Mean precipitation trends in the last 33 years (since 1966) at selected climate stations on the central Colorado Plateau. Trends ($p \leq 0.25$) are indicated as either increasing (↑) or decreasing (↓) using regression. Significance of each regression is shown (ns=not significant, $p>0.25$, no trend (→)).

	Annual		Winter Season		Growing Season	
Station	Trend	Significance	Trend	Significance	Trend	Significance
Lees Ferry	↑	p=0.124	↑	p=0.198	→	ns
Wahweap	↑	p=0.111	↑	p=0.124	→	ns
Mexican Hat	→	ns	→	ns	→	ns
Page	↑	p=0.165	→	ns	↑	p=0.028
Needles	→	ns	→	ns	→	ns
Escalante	→	ns	→	ns	→	ns
Natural Bridges	→	ns	→	ns	→	ns
Betatakin	↑	p=0.105	↑	p=0.174	→	ns
Bryce Canyon	↑	p=0.028	↑	p=0.071	→	ns

Four stations have longer records that are fairly complete: Lee's Ferry, Escalante, Mexican Hat, and Betatakin. Table 5 displays the results of linear regression of climate variables over time for these four stations. For Lee's Ferry, the long-term record reveals a highly-significant increase in minimum T since 1944, but no changes in annual or maximum T. The trend towards increasing winter season PCP, since 1966, becomes significant when extended back to 1944 (Fig. 4). For Mexican Hat,

Table 5. Mean temperature and precipitation trends for four stations with long-term records on the central Colorado Plateau. Trends ($P \leq 0.25$) are indicated as either increasing (↑) or decreasing (↓) using regression. Significance of each regression is shown (ns=not significant, $P>0.25$, no trend (→)).

			TEMPERATURE			
	Annual Mean		Annual Maximum		Annual Minimum	
Station	Trend	Significance	Trend	Significance	Trend	Significance
Lees Ferry[1]	→	ns	→	ns	↑	$P=0.054$
Mexican Hat[2]	↓	$P=0.142$	↓	$P=0.055$	→	ns
Escalante[3]	↑	$P<0.0001$	↑	$P<0.0001$	↑	$P<0.0001$
Betatakin[4]	→	ns	↑	$P=0.174$	↓	$P=0.099$

			PRECIPITATION			
	Annual		Growing Season		Winter Season	
Station	Trend	Significance	Trend	Significance	Trend	Significance
Lees Ferry[1]	→	ns	→	ns	↑	$P=0.072$
Mexican Hat[2]	↑	$P=0.061$	→	ns	↑	$P=0.038$
Escalante[3]	↓	$P=0.009$	↓	$P=0.005$	→	ns
Betatakin[4]	↑	$P=0.065$	→	ns	↑	$P=0.079$

[1] Years 1944-1998; [2] Years 1949-1998; [3] Years 1925-1998; [4] Years 1951-1998

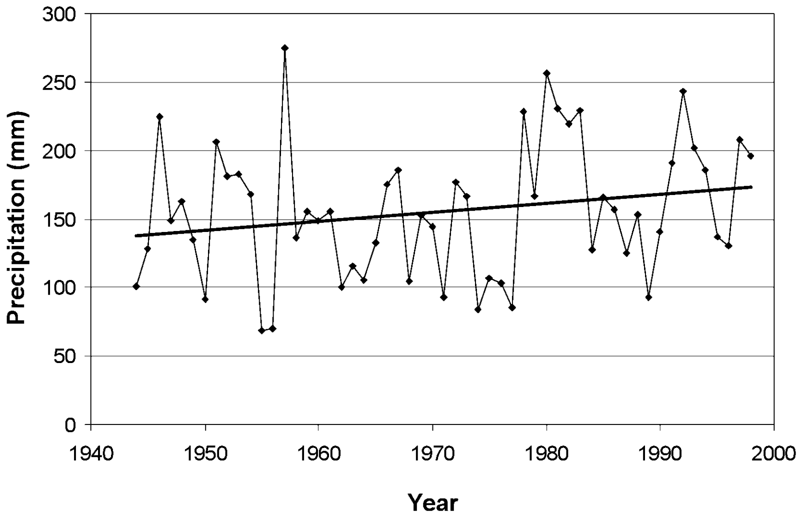

Figure 4. Mean annual precipitation in millimeters for Lee's Ferry, Arizona, between 1944-1998. The linear regression curve is also displayed (slope=0.65).

extending the record back to 1951 reveals a slight cooling trend overall and significant increases in winter PCP. The longest record, Escalante, reveals a highly-significant increase in all T variables since 1925 (Fig. 5), while at the same time PCP has decreased significantly during the growing season (April-September). Finally, T at Betatakin shows an unusual trend of decreasing minimum T and slightly increasing maximum T. Winter season PCP has increased significantly since 1951.

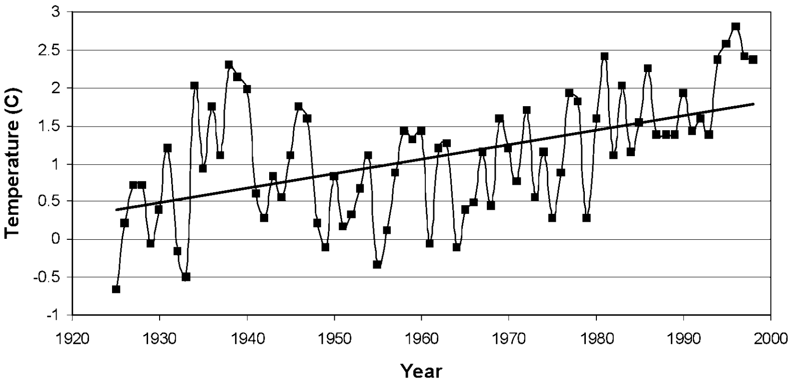

Figure 5. Mean annual minimum temperature in °C for Escalante, Utah, between 1925-1998. The linear regression curve is also displayed (slope=0.02).

Changes in both T and PCP will affect POTE rates. Combining the general trend towards increasing temperature, with no or minor increases in PCP, POTE rates will increase in the study area. Figure 6 plots current POTE rate curves against elevation for the 27 stations, and future conditions based on a 3° C increase in annual T with no changes in PCP. The regression curves show that POTE + 3° C does not increase uniformly across the elevational gradient. The slope of the regression line steepens as T increases. POTE increases as much as 15% at some stations under the warming scenario; for example, POTE at Lee's Ferry increases from 993 mm to 1136 mm. By comparison, the current POTE rate at Tucson in the Sonoran Desert is 1100 mm.

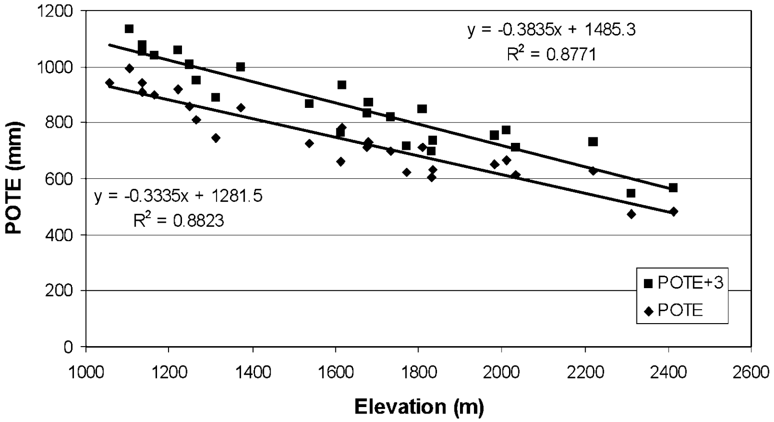

Figure 6. The relationship between current evapotranspiration rates (POTE) in millimeters and potential POTE rates with a 3° C increase in mean annual temperature is plotted against elevation for the central Colorado Plateau. The regression curves and equations for the two relationships are also displayed.

DISCUSSION AND CONCLUSIONS

Climate

This study has presented an analysis of the climate of the central Colorado Plateau, and has examined recent trends in precipitation and temperature for selected climate stations. The study area comprises a relatively uniform climate region based on an analysis of geographic variables. Other than expected relationships between temperature and latitude, there are few changes in climate across the study area. The principal exception to this is a significant southeast to northwest decline in temperature. This may reflect the change across the boundary of the two air masses that separate the southern and eastern portions of the Colorado Plateau from the northern and western portions (Mitchell 1976). This boundary is much broader than implied by Figure 1, as its position shifts along this vector from year to year.

Figures 4 and 5 illustrate, at single stations, the extremely high year to year variability in temperature and precipitation for all stations in the region. The Lee's Ferry precipitation record reveals a cycle of high precipitation episodes followed by low periods at ca. 10-year intervals since 1944. This pattern is similar at other stations, with changes between high and low precipitation at cycles of ca. every 8-12 years. The pattern for temperature is somewhat more variable, but again, a strong cyclic pattern can be discerned with climate records that have been analyzed in detail. This variability is typical of arid climates throughout the world (Evenari et al. 1985). Coefficients of variation are high for most stations, ranging from 20-50% for climate variables.

Two principal global circulation models are the Goddard Institute for Space Science (GISS) and the Geophysical Fluid Dynamics Laboratory (GFDL). With a predicted doubling in CO_2 content, the GISS model predicts a 4.7° C increase and an 8% precipitation increase in the western U.S. (Hansen et al. 1988). For the GFDL model, the comparable predictions are 4.2° C and 30% increase (Manabe and Wetherald 1987). Both are in agreement that much of the precipitation increase is likely to result from a strengthening of the summer monsoon rather than increases in winter precipitation. More recently, two other models, the Hadley Centre and the Canadian Climate Centre models, have been analyzed with respect to the western U.S. (NAST 2000). The Canadian model predicts larger increases in temperature (4.5-6.0° C), while the Hadley model is similar to the GFDL and GISS models. Both models also predict increases in precipitation of 25-50%, but differ from the GISS and GFDL models in that the increases are predicted to be in winter precipitation rather than summer precipitation.

The climate data suggest two principal trends in the last 30-40 years in the study area: (1) significantly increasing minimum temperatures, and (2) slight increases in winter precipitation. The first trend is consistent with all GCM models, while the second is consistent with predictions of the Hadley and Canadian models, but not with predictions of the GISS and GFDL models. For the central Colorado Plateau, there is no evidence for a strengthening of the summer monsoon since 1966. Escalante, at the northwestern edge of the study area, has experienced a significant decline in summer precipitation (Table 3). Mexican Hat, at the southeastern edge of the study area, where the effects of a strengthened monsoon should become apparent first in the region, has had no significant changes in summer precipitation since 1951 (Table 3).

These trends may reflect one of two possible climate scenarios: global warming or short-term (decadal) climatic oscillations and variability. During the last 100 years, there have been several episodes of warming and cooling. For example, the 1930's and 1940's were relatively warm in the study area, and were followed by relatively cool conditions in the 1960's and 1970's. Hence, the high temperatures recorded in the last 20 years may be part of this cyclic phenomenon. At present, the regional and global climate data are inadequate to clearly differentiate these two possibilities, at least at the regional level. Assuming that the trends presented in this study continue, and are early signs of global warming, a variety of hypotheses can be presented on the potential responses of vegetation as well as individual species.

Potential Effects on the Vegetation of the Colorado Plateau

One effect of increasing temperatures, with little or no increase in precipitation, is increased evapotranspiration rates over time. Although the effects of this are probably not discernable at present, due to the high variability in climate, this trend could have consequences in both the short- and long-term future of the Colorado Plateau vegetation. Recent studies in the shortgrass steppe of the Great Plains have shown that increases in minimum temperatures can be linked with changes in abundance and productivity of herbaceous species. Alward et al. (1999) showed that the dominant native warm-season C_4 grass, blue grama (*Bouteloua gracilis*), may have declined as a result of warming. Consequences of increased minimum temperatures include earlier spring growth of cool season C_3 species, including exotics, that can then deplete soil moisture prior to the green-up or germination of warm season species like blue grama. Competition for available nutrients may also change with increased growth of cool season species. Given the current trend of increasing winter precipitation discernable on the central Colorado Plateau, the most likely short-term effect on arid vegetation would be increases in cool-season herbaceous and woody species, and declines in warm season species, most of which are grasses. Long-term predictions for all models are that grasslands and woodlands on the Colorado Plateau will increase, while arid scrub vegetation will decrease substantially.

Effects in higher elevation, semi-arid and humid vegetation are less well understood. Increased evapotranspiration stress during the summer may cause declines in growth and recruitment at the lower limits of pinyon-juniper woodlands. Warmer temperatures, without an increase in the summer monsoonal precipitation, could reduce growth rates and seedling recruitment, and increase mortality in Ponderosa pine, a species that is closely tied to warm season precipitation. Over the long term, an increase in annual temperature of 3° C, without significant increases in precipitation, will raise the arid-humid boundary by approximately 90 m, from 2730 m to 2820 m (estimate based on intersection of POTE and precipitation lines for a 3° C increase scenario, not illustrated). This could significantly reduce the extent of high elevation coniferous forests, subalpine meadows, and alpine tundra, on the Colorado Plateau. However, this scenario seems unlikely based on the predictions of increased precipitation found in all models.

A combination of increases in temperature and precipitation is likely to have complex effects on the vegetation of the Colorado Plateau. Long-term shifts in vegetation boundaries and changes in temperature and precipitation may have significant impacts on populations of relict plant species and the many rare and often edaphically-restricted plant species that are characteristic of the Colorado Plateau (Spence 1995, TNC 1993). Also, the GCMs predict increased variability in precipitation, with dry and wet years alternating. This could change fire regimes, as fuel loads would build up during wet phases. If a drought period subsequently followed, there would be an increased chance of potentially destructive stand-replacing fires in the forest, woodland and grassland communities of the Colorado Plateau.

Although all the GCM models discussed predict increases in precipitation in the western U.S., the differences between them are relatively large. The consequences of an 8% increase in precipitation, compared with a 50% increase, are likely to be very different for arid and semi-arid vegetation in the region. Also important is the timing of these increases, because many dominant plant species on the Colorado Plateau, and elsewhere in the Southwest, differentially utilize warm-season and cool-season moisture (Ehleringer et al. 1991, Comstock and Ehleringer 1992). Although it will be some time before we better understand the potential changes in timing and extent of precipitation in the region brought about by global warming, enough climate data are currently available to model these potential future climates, based on global warming and different scenarios of precipitation changes.

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LITERATURE CITED

Alward, R.D., J.K. Detling, and D.G. Milchunas. 1999. Grassland vegetation changes and nocturnal global warming. Science 283: 229-231.

Ashcroft, G.L., D.T. Jensen, and J.L. Brown. 1992. Utah climate. Utah Climate Center, Utah State University, Logan.

Comstock, J.P., and J.R. Ehleringer. 1992. Plant adaptations in the Great Basin and Colorado Plateau. Great Basin Naturalist 52: 195-215.

Ehleringer, J.R., S.L. Phillips, W.S.F. Schuster, and D.R. Sandquist. 1991. Differential utilization of summer rains by desert plants. Oecologia 88: 430-434.

Evanari, M., I. Noy-Meir and D.W. Goodall. 1985. Hot deserts and arid shrublands, A. Ecosystems of the World 12A. Elsevier, New York.

Hansen, J., I. Fung, A. Lacis, S. Lebedef, D. Rind, R. Ruedy, G. Russel, and P. Stone. 1988. Global climate changes as forecast by the Goddard Institute for Space Studies three-dimensional model. Journal of Geophysical Research 93: 9341-9364.

Petersen, K.L. 1994. Modern and pleistocene climatic patterns in the west. Pages 27-54 *in* Harper, K.T., L.L. St. Clair, K.H. Thorne, and W.M. Hess, (eds.) Natural history of the Colorado Plateau and Great Basin. University Press of Colorado, Niwot.

Manabe, S., and R.T. Wetherald. 1987. Large scale changes in soil wetness induced by an increase in carbon dioxide. Journal of Atmospheric Research 44: 1211-1235.

Mitchell, V.L. 1976. The regionalization of climate in the western United States. Journal of Applied Meteorology 15: 920-927.

National Assessment Synthesis Team (NAST). 2000. Climate change impacts on the United States. The potential consequences of climate variability and change. U.S. Global Change Research Program. Cambridge University Press, New York.

Rowlands, P.G. 1993. Climatic factors and the distribution of woodland vegetation in the southwest. Southwestern Naturalist 38: 185-197.

Spence, J.R. 1995. Characterization and possible origins of isolated Douglas Fir stands on the Colorado Plateau. Pages 71-82 *in* Waugh, W.J., (ed.) Proceedings of a symposium, Sept. 12-14, 1994. Climate change in the Four Corners and adjacent regions: implications for environmental restoration and land-use planning.. U.S. Dept. Energy CONF-9409325, Grand Junction, CO.

Spence, J.R., W.H. Romme, L. Floyd-Hanna and P.G. Rowlands. 1995. A preliminary vegetation classification for the Colorado Plateau. Pages 193-213 *in* van Riper, C. III, (ed.) Proceedings of the second biennial conference on research in Colorado Plateau National Parks, Oct 25-28, 1993. National Park Service Transactions and Proceedings Series NPS/NRNAU/NRTP-95/11.

The Nature Conservancy (TNC). 1993. The potential effects of climate change on the native vascular flora of North America. A preliminary climate envelopes analysis. Electric Power Research Institute EPRI TR-103330.

Walter, H. 1985. Vegetation of the earth and the ecological systems of the geo-biospehere. 3rd ed. Springer-Verlag, Berlin.