Proceedings of the 22nd Biennial Pronghorn Workshop

2006

Edited by
Dale E. Toweill

Idaho Department of Fish and Game
Shilo Inn, Idaho Falls, Idaho
May 16 – 19, 2006

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Western Association of Fish and Wildlife Agencies

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Section I Workshop Agenda

22nd Biennial Pronghorn Workshop
May 16-19, 2006
Idaho Falls, Idaho

Sanctioned by:
Western Association of Fish & Wildlife Agencies

Hosted by:
Idaho Department Fish & Game

Tuesday, May 16

4:00 – 8:00 PM **Registration**

6:00 – 8:00 PM **Social** (Sponsored by ***Bear River Sales***)

Wednesday, May 17

7:00 – 8:30 AM **Registration**

8:30 – 8:45 AM **Welcome to Idaho!**

8:45 – 8:55 AM **Workshop announcements**

Technical Session #1 *(Moderator – Jeff Short)*

8:55 – 9:20 AM ***Are pronghorn vital rates affected by habitat?***
John Byers, University of Idaho, Moscow

9:20 – 9:45 AM ***Evaluation of pronghorn productivity relative to broad-scale habitat variables in Wyoming (1978-2003).***
Timothy Smyser, University of Idaho, Moscow
Archie Reeve, PIC Technologies, Laramie, Wyoming
Edward Garton, University of Idaho, Moscow

9:45 – 10:10 AM ***Influences of vegetation on pronghorn numbers in the Intermountain West.***

Jim Yoakum, Western Wildlife Consultants, Verdi, Nevada

10:10 – 10:30 AM **Break** (Sponsored by ***Lotek Engineering***)

Technical Session #2 *(Moderator – Daryl Meints)*

10:30 – 10:55 AM ***Broad-scale landscape changes relative to pronghorn abundance in West Texas.***
Aaron Sides, Sul Ross State University, Alpine, Texas
Louis Harveson, Sul Ross State University, Alpine, Texas
Clay Brewer, Texas Parks & Wildlife Department, Fort Davis

10:55 – 11:20 AM ***Relationship between soil chemistry and pronghorn fawn recruitment in Arizona.***
Kirby Bristow, Arizona Game & Fish Department, Phoenix
Shelli Dubay, Arizona Game & Fish Department, Phoenix
Richard Ockenfels, Arizona Game & Fish Department, Phoenix

11:20 – 11:45 AM ***Population productivity and pronghorn nutrition during lactation.***
Timothy Smyser, University of Idaho, Moscow
Mark Hurley, Idaho Department Fish & Game, Salmon
Edward Garton, University of Idaho, Moscow

11:45 – 12:10 ***Comparison of diet characteristics of two pronghorn herds in North Central Arizona.***
William Miller, Arizona State University Polytechnic, Mesa
Melissa Drake, Arizona State University Polytechnic, Mesa
Lauren Colliver, Arizona State University Polytechnic, Mesa

12:10 – 1:30 PM **Lunch** (on your own)

Technical Session #3 *(Moderator – Richard Guenzel)*

1:30 – 1:55 PM ***Effects of diet habits on pronghorn recruitment in Arizona.***
Kirby Bristow, Arizona Game & Fish Department, Phoenix
Shelli Dubay, Arizona Game & Fish Department, Phoenix
Stan Cunningham, Arizona Game & Fish Department, Phoenix
Daniel McDonald, Texas Tech University, Lubbock
Jaimie Warren, Arizona Game & Fish Department, Phoenix
William Miller, Arizona State University, Mesa
Richard Ockenfels, Arizona Game & Fish Department, Phoenix

1:55 – 2:20 PM ***An evolutionary history of pronghorn habitats and its effect on species differentiation.***
David Brown, Arizona State University, Tempe

2:20 – 2:45 PM ***Petroleum development and pronghorn: where are the break points?***
Jon Beckmann, Wildlife Conservation Society, Victor, Idaho

	Joel Berger, Wildlife Conservation Society, Victor, Idaho *Kim Murray Berger*, Wildlife Conservation Society, Victor, Idaho
2:45 – 3:10 PM	***Effects of a species-level trophic cascade on pronghorn fawn survival in Grand Teton National Park.*** *Kim Murray Berger*, Wildlife Conservation Society, Victor, Idaho
3:10 – 3:30 PM	**Break** (Sponsored by ***Wildlife Conservation Society***)

Technical Session #4 *(Moderator – Jon Rachael)*

3:30 – 3:55 PM	***Use of infrared thermography to detect signs of diseases in pronghorn antelope.*** *Mike Dunbar*, U.S. Dept. of Agriculture, Ft. Collins, Colorado *Jack Rhyan*, U.S. Dept. of Agriculture, Ft. Collins, Colorado
3:55 – 4:20 PM	***Dispersal of yearling pronghorns in western South Dakota***. *Christopher Jacques*, South Dakota State University, Brookings *Jonathan Jenks*, South Dakota State University, Brookings
4:20 – 4:45 PM	***Long distance migration and the challenges of protection.*** *Joel Berger*, Wildlife Conservation Society, Victor, Idaho *Kim Murray Berger*, Wildlife Conservation Society, Victor, Idaho *Steve Cain*, Grand Teton National Park, Moose, Wyoming
4:45	**End of Session, Workshop Announcements**
5:00 – 7:00 PM	**Social** (Sponsored by ***Bear River Sales***)
	Dinner (on your own)

Thursday, May 18

8:30 – 8:45 AM	**Workshop announcements**

Technical Session #5 *(Moderator – Bill Jensen)*

8:45 – 9:10 AM	***Two heads are better than one: a paired observer evaluation of pronghorn line transect surveys.*** *Timothy Smyser*, University of Idaho, Moscow *Richard Guenzel*, Wyoming Game & Fish Department, Laramie *Edward Garton*, University of Idaho, Moscow
9:10 – 9:35 AM	***A non-invasive technique to weigh wild pronghorn: prospects and problems.*** *Leigh Baker Work*, Wildlife Conservation Society, Victor, Idaho

9:35 – 10:00 AM ***A comparison of pronghorn body measurements throughout western North America.***
David Brown, Arizona State University, Tempe
Christine Maher, University of Southern Maine, Portland
Carl Mitchell, U.S. Fish & Wildlife Service, Wayan, Idaho

10:00 – 10:20 AM **Break** (Sponsored by ***Idaho Chapter The Wildlife Society***)

Technical Session #6 *(Moderator – Tom Keegan)*

10:20 – 10:45 AM ***Activity budgets of Sonoran pronghorn in a semi-captive enclosure.***
Ryan Wilson, University of Arizona, Tucson
Paul Krausman, University of Arizona, Tucson
John Morgart, U.S. Fish & Wildlife Service, Albuquerque, New Mexico

10:45 – 11:10 AM ***State Status Reports.***
Bruce Ackerman, Idaho Department Fish & Game, Boise
Bradley Compton, Idaho Department Fish & Game, Boise

11:10 – 11:35 AM ***Thirty year history of the "Pronghorn Management Guides."***
Jim Yoakum, Western Wildlife Consultants, Verdi, Nevada

11:35 – 1:45 PM **Business Meeting** (see agenda, lunch provided)

Technical Session #7 *(Moderator – Don Whittaker)*

1:45 – 2:10 PM ***Movement and distribution patterns of pronghorn in relation to roads and fences in Wyoming.***
Daly Sheldon, Wyoming Game & Fish Department, Cheyenne

2:10 – 2:35 PM ***Evaluation of pronghorn fawn hiding cover availability for a central Arizona population.***
Dana Warnecke, Arizona Game & Fish Department, Mesa
Jesse Brunner, Institute for Ecosystem Studies, Millbrook, New York

2:35 – 3:00 PM ***Improvements in aerial line transect surveys to estimate pronghorn abundance in Wyoming: where do we go from here?***
Richard Guenzel, Wyoming Game & Fish Department, Laramie

3:00 – 3:25 PM ***Temporal and spatial variation in pronghorn distribution and population dynamics in Alberta.***
Katherine Sheriff, University of Calgary, Calgary, Alberta
C. Cormack Gates, University of Calgary, Calgary, Alberta
Dale Eslinger, Alberta Sustainable Resource Development, Medicine Hat
Paul Jones, Alberta Conservation Association, Lethbridge
Mike Suitor, University of Calgary, Calgary, Alberta

3:25 – 3:45 PM **Break** (sponsored by ***Idaho Chapter Safari Club International***)

Panel Discussion *(Moderator – Brad Compton)*

3:45 – 5:00 PM	*A panel of invited experts will discuss future research and management needs related to pronghorn conservation.*
5:00	**End of Session, Workshop Announcements**

Banquet/Awards Ceremony

5:30 – 6:30 PM	No Host Social
6:30 PM	Dinner Served
7:30 – 8:30 PM	Awards Ceremony (*Richard Ockenfels*)

Friday, May 19

7:00 – 7:00 PM	Field tour of Yellowstone & Teton National Parks (sack lunch provided)

Section II Status Report

Pronghorn State and Province Status Report

22nd Biennial Pronghorn Workshop, Idaho Falls, ID, May 16-19, 2006

Bruce B. Ackerman, Biometrician, Idaho Department of Fish and Game, P.O. Box 25, Boise ID 83707-0025, USA

Abstract: A standardized questionnaire was provided to 16 western states in the United States, 2 Canadian provinces, and Mexico, to collect 2004/2005 pronghorn population, survey, and hunting information. These data are summarized, and compared to previous results collected for 2003 and 1993 (Stillings 2004). Wyoming remains the core of the global pronghorn population with an estimate of 512,000 animals. All states and provinces except Baja California Sur have a pronghorn rifle season. Total harvest decreased substantially in 2005 versus 1993. Wildlife/Landowner conflicts are often mitigated through hunting permits for landowners, transferable licenses, depredation payments, and hunter access programs.

These data are summarized, and compared to previous results collected for 2003 and 1993 (Stillings 2004). A database of these survey results will be placed on a web site, to be added to every 2 years for the biennial workshops.

Introduction

A standardized questionnaire was provided to all states and provinces in the United States, Canada, and Mexico which are known to have free-ranging pronghorn populations. Surveys asked for information on pronghorn population size and estimation methods, hunting seasons and harvest estimates, and information about ongoing research projects. Questionnaires were completed by all states and Canadian provinces surveyed, as well as Baja California Sur in Mexico. These data were entered into a database for future use, along with data from 1993 and 2003 collected 2 years ago (Stillings 2004).

Population Estimates and Survey Methodology

Pronghorn population estimates ranged from 512,000 in Wyoming to 68 in Baja California Sur in Mexico. Jensen et al. (2004) provided the first detailed map of pronghorn distribution and densities at a county level. Almost all states and provinces have conducted aerial surveys to sample population sizes in at least part of their pronghorn ranges. Sex and age data were collected using aerial and/or ground surveys. Aerial line transects were the most common survey method.

Pre-season buck-to-doe ratios ranged from a low of 36 bucks per 100 does in Arizona to a high of 61 bucks per 100 does in Texas. Pre-season fawn-to-doe ratios ranged from a low of 36 fawns per 100 does in Alberta to a high of 91 fawns per 100 does in South Dakota.

Hunting Season Structure

Hunting season structure varied substantially by jurisdiction. Many muzzleloader seasons occurred in conjunction with rifle or archery seasons. Some locations had separate muzzleloader seasons following the rifle hunt. Most archery seasons opened prior to firearm season.

Harvest Summary

The tables below summarize harvest data from western states, and Alberta, and Saskatchewan. Some locations reported 2004 or 2005 harvest data, while some reported both. The percent of the estimated population that was harvested varied from 3-4% in Saskatchewan and Texas to 14-28% in North Dakota. Bucks comprised the majority of the harvest, ranging from 47-49% in South Dakota to 100% of the harvest in several states. Does and fawns were not harvested in Arizona, California, and Texas. In locations where does and fawns were harvested, the percent of total harvest ranged from 3-7% in Nevada to 51-53% in South Dakota.

The total harvest in most areas was higher in 2004/2005 compared to 2003 (Stillings 2004). The number of rifle hunters and harvest generally decreased in 2004/2005 compared to 1993. Rifle hunter success remains very high, averaging 81% (range 68% to 96%). Only 9 states had a muzzleloader season, with hunter success averaging 54% (range 44% to 63%).

The number of archers and harvest has remained relatively stable among states and provinces reporting data since 1993. The biggest change in archery hunters occurred in Idaho (86% increase in resident hunters, large change in hunting season structure, general season was changed from rifle to archery) and New Mexico (60% decrease in total archers). Archery success was lowest of the 3 kinds of weapons; averaging 26% (range 9% to 50%).

Non-Resident Hunting Opportunity

All states/provinces impose restrictions on the number of non-resident rifle and muzzleloader licenses. The percentage of non-resident rifle hunters varied from 0% in California, Nebraska, and Oklahoma to 53% in Wyoming. North Dakota and Kansas were the only states that did not allow non-residents to hunt with a rifle.

Wildlife/Landowner Partnerships

Most states/provinces have a partnership program aimed at reducing wildlife/landowner conflicts. Programs generally either provided direct monetary compensation, licenses for the landowner, licenses that can be sold, or provided payment in return for hunter access to private land.

Results in Online Database

The results of this survey will be placed in an on-line database, along with previous results collected for 2003 and 1993 (Stillings 2004). The intention is that these results will be added to every 2 years for the biennial workshops. Results will be available on a web site.

References:

Jensen, W. F., B. M. Hosek, and W. J. Rudd. 2004. Mapping continental range distribution of pronghorn using Geographic Information Systems technology. Pages 18-36 in Proceedings Pronghorn Workshop, May 1-4, 2004. Bismarck, ND, USA.

Stillings, B.A. 2004. Pronghorn province and state status report. Pages 5-17 in Proceedings Pronghorn Workshop, May 1-4, 2004. Bismarck, ND, USA.

Table 1. List of state and provincial contacts for pronghorn status survey, May 2006

State/ Province		Contact Person	Title	Agency	Address	City	State	Zip	Country	Ph Number	Email Address
1	AB	D. Edward (Ed) Hofman	Area Wildlife Biologist	Alberta Sustainable Resource Development, Fish and Wildlife Division	201 Centre St, Provincial Bldg.	Drumheller	AB	T0J 0Y0	Canada	403-823-1670	ed.hofman@gov.ab.ca
2	SK	Al Arsenault	Provincial Ungulate Population Biologist	Saskatchewan Environment	112 Research Dr	Saskatoon	SK	S7K 2H6	Canada	306-933-5797	Aarsenault@serm.gov.sk.ca
3	OR	Don Whittaker	Species Coordinator	Oregon Dept. Fish and Wildlife	3406 Cherry Ave. NE	Salem	OR	97303	USA	503-947-6325	don.whittaker@state.or.us
4	ID	Bruce Ackerman	Wildlife Staff Biologist	Idaho Dept. Fish and Game	P.O. Box 1525	Boise	ID	83707	USA	208-287-2753	backerman@idfg.idaho.gov
5		Survey not received									
6	ND	Bruce Stillings	Big Game Biologist	North Dakota Game and Fish Dept.	225 30th Ave. SE	Dickinson	ND	58601	USA	701-227-7431	bstillings@nd.us
7	SD	John Wrede	Regional Wildlife Manager	South Dakota Game, Fish, and Parks	3305 W. South St.	Rapid City	SD	37702	USA	605-394-2394	John.Wrede@state.sd.us
8	WY	Reg Rothwell	Supervisor of Biological Services	Wyoming Department of Game and Fish	5400 Bishop Blvd	Cheyenne	WY	82006	USA	307-777-4588	Reg.Rothwell@wgf.state.wy.us
9	NE	Survey not received									
10	CA	Joe Hobbs	Elk and antelope coordinator	California Dept. of Fish and Game	1812 9th Street	Sacramento	CA	95814	USA	916-445-9992	jhobbs@dfg.ca.gov
11	NV	Mike Cox	Big Game Staff Biologist	Nevada Department of Wildlife	1100 Valley Road	Reno	NV	89512	USA	775-688-1556	mcox@ndow.org
12	UT	Craig McLaughlin	Big Game Coordinator	Utah Division of Wildlife Resources	PO. Box 146301	Salt Lake City	UT	84114	USA	801-538-4777	craigmclaughlin@utah.gov
13	CO	Bruce Watkins	Terrestrial Analyst	Colorado Division of Wildlife	2300 S. Townsend Ave	Montrose	CO	81401	USA	970-252-6025	bruce.watkins@state.co.us
14	KS	Matt Peek	Pronghorn Program Coordinator	Kansas Dept of Wildlife and Parks	P.O. Box 1525	Emporia	KS	66801	USA	620-342-0658	mattp@wp.state.ks.us
15	AZ	Brian Wakeling	Big Game Management Supervisor	Arizona Game and Fish Department	2221 West Greenway Road	Phoenix	AZ	85023	USA	602-789-3385	bwakeling@azgfd.gov
16	NM	Survey not received									
17	TX	Duane Lucia	Natural Resource Specialist V	Texas Parks and Wildlife Department	1702 Landmark Ln Ste. 3	Lubbock	TX		USA	806 761-4971	duane.lucia@tpwd.state.tx.us
18	OK	Survey not received							USA		
19	MEX	Survey not received							Mexico		

Table 2. Population estimation methods, by state and province, 2005.

				Pre-Season B:D ratio	Pre-Season F:D ratio	Survey Type				How often covered by Air?		How often covered by Ground?		Survey Method		Time of Year	
State/ Province		Population Estimate	Percent Observed			Heli-copter	Fixed-Wing	Ground	Land-owner	Specific area	Entire range	Specific area	Entire range	Aerial	Ground	Aerial	Ground
1	AB	17,807	8 to 15	42	36	**X**				Annual	Annual	---	---	Strip, Line Transect		Post-Fawn	
2	SK	18,858	Varies	39	51	**X**	**X**			2-3 years	55% of core each year; 25% all	---	---	Line Transect, Targeted Search & Count		Pre-Fawn, Post-Fawn	
3	OR	~25,000	Unknown			**X**	**X**	**X**		Annual	Annual			Targeted Search & Count, Haphazard/Random Search & Count	Trend Routes, Targeted Concentration Areas	Post-Fawn, Winter	Winter
4	ID	13,000				**X**	**X**	**X**		Occasional	Never	Occasional	Never	Line Transect, Targeted Connect Future areas	Targeted Concentration Areas	Pre-Fawn, Post-Fawn	Post-Fawn
5	MT	N/A					**X**							Strip Transect		Post-Fawn	
6	ND	15,267	90	37	65		**X**			1-3 years	3 years	---	---	Targeted Search & Count		Post-Fawn	
7	SD	49,500	33	55	91		**X**			Annual	Annual	Annual	Annual	Strip Transect	Targeted Concentration	Pre-Fawn	Post-Fawn
8	WY	512,117	Unknown	14 to 93	36 to 95		**X**			3 years	3 years	Annual	Annual	Line Transect		Pre-Fawn	Post-Fawn
9	NE	6,000 - 7,000	9				**X**	**X**	**X**					Strip Transect	Trend Routes, Targeted Concentration	Post-Fawn, Winter	Post-Fawn
10	CA	4,254	97				**X**			Annual	Annual			Line Transect, Targeted Search & Count		Winter	
11	NV	21,500	40	45	52	**X**		**X**		Annual	Never	Annual	Never	Targeted Search & Count, Haphazard/Random Search	Targeted Concentration	Fall	Fall, Post-Fawn, Winter
12	UT	12,000	50 to 75	58	60		**X**	**X**		1-2 years	1-2 years	Annual	Annual	Strip Transect	Targeted Concentration	Pre-Fawn	Post-Fawn
13	CO	70,800	17	60	56	**X**	**X**	**X**		Usually 1-3 years				Strip Transect, Line Transect, Haphazard/Random Search & Count	Targeted Concentration Areas	Post-Fawn	Post-Fawn
14	KS	2,100	60 to 70	40	80		**X**			Twice per year	N/A			Line Transect		Post-Fawn, Winter	
15	AZ	8,000 - 10,000	75	36	41		**X**			Annual	Annual	n/a	n/a	Strip Transect		Post-Fawn	
16	NM	N/A	Various				**X**							Strip Transect		Pre-Fawn	
17	TX	16,730	40 to 50	61	70	**X**	**X**	**X**		Annual	Annual	Annual	Never	Strip Transect	Targeted Concentration	Post-Fawn	Post-Fawn
18	OK	1,500	60				**X**	**X**						Strip Transect	Targeted Concentration	Winter	Winter
19	MEX1	68	60				**X**	**X**						Strip Transect, Haphazard/Random Search & Count	Trend Routes	Winter	Fall, Pre-Fawn, Post-Fawn

Table 3. Hunting season structure, by state and province, 2005.

		Number of permits is limited?			Rifle		Muzzleloader		Archery		Special Status Hunts			
State/ Province		Rifle	Muzzle-loader	Archery	Dates	Days	Dates	Days	Dates	Days	Type	Dates	Days	Comments
1	AB	Yes	No season	Yes	9/26 to 10/22 (split season)	12	None		9/7 to 9/25	19	None			
2	SK	Yes	Yes	Yes	10/24 to 11/5 (no Sundays)	12	10/1 to 10/31 (no Sundays)	26	9/1 to 10/31 (no Sundays)	52	None			
3	OR	Yes	Yes	Yes	Late August	10	Late August	10	Late August	10	Youth only	August	31??	
4	ID	Yes	Yes	No	9/25 to 10/24	30	9/25 to 10/24	30	8/15 to 9/15	32	Short range weapon	9/25 to 10/24	30	
4	ID										Youth	9/25 to 10/24	30	
5	MT	Survey not received												
6	ND	Yes	No Season	No	9/30 to 10/16	16	None		9/2 to 10/9	38	None			
7	SD	Yes	No season	No	10/1 to 10/14	14	None		8/20 to 10/31	58	None			
8	WY	Yes	Yes	Yes	9/1 to 12/31, varies	14-106	8/20 to 9/20	16-30	8/15 to 9/30	46	None			
9	NE	Survey not received												
10	CA	Yes	No Season	Yes	8/19 to 8/27, 9/2 to 9/10	9	None		8/5 to 8/13	9	Junior antelope	8/19 to 8/27	9	
10	CA										Fund Raising	7/29 to 9/17	51	
11	NV	Yes	No Season	Yes	8/27 to 9/5	10	None		8/6 to 8/21	16	Nevada Heritage tag (bid tag), 2 statewide	7/15 to 10/31	Many	
12	UT	Yes	No season	Yes	9/17 to 9/27; 10/8 to 10/16 (1 unit)	11	None		8/20 to 9/16	27	Doe Only	varies; Sept-Dec.	10 to 61	limited entry; few units hunted;dates vary by unit
13	CO	Yes	Yes	Some Areas	10/7 to 10/13	7	10/21 to 10/29	9	8/15 to 9/20	37	Auction & Raffle Licenses	8/15 to 1/31		2 auction & 2 raffle licenses are offered each year
13	CO										Ranching for Wildlife	Varies	Varies	Private & public (resident only) licenses available
13	CO										Damage Hunts	Varies	Varies	As needed basis.
14	KS	Yes	Yes	No	10/7 to 10/10	4	10/3 to 10/10	8	9/24 to 10/2 and 10/15 to 10/31	26	None			
15	AZ	Yes	Yes	Yes	9/8 to 9/20, 2006	13	9/8 to 9/17, 2006	10	8/11 to 9/7, 2006	14	Juniors only	N/A	N/A	Discontinued in 2005, offered prior to that.
15	AZ										Special Big Game License Tag	8/1 to 7/31	365	3 tags offered, auction or raffle for fundraising
16	NM	Survey not received												
17	TX	Yes	No Season	No Season	10/1 to 10/9	9	None		None		None			
18	OK	Survey not received												
19	MEX1	Survey not received												

Table 4. Harvest estimation methods, by state and province, 2005.

State/ Province		Harvest Estimation Method	Other, please describe
1	AB	Questionnaire, Phone Survey	
2	SK	Questionnaire, Mail Survey with Permits	
3	OR	No Harvest Estimates	
4	ID	Mail Survey with Permits, Phone Survey	Mandatory harvest report, with mail and phone follow-up in non-reporting.
5	MT	Survey not received	
6	ND	Questionnaire, Mail Survey with Permits	
7	SD	Questionnaire, Mail Survey/Random	
8	WY	Questionnaire, Mail Survey/Random, Carcass Check In	Carcasses for age structure of harvest.
9	NE	Survey not received	
10	CA	Mail Survey with Permits	Harvest estimates are based upon tag returns and follow up letters to any hunter that did not return a tag (all tags are required to be returned)
11	NV	Mail Survey with Permits	Most hunt questionnaires are entered by hunters via website
12	UT	Phone Survey	Buck pronghorn hunters must report their success within 30 days of end of season, by phone or via internet through Division web site. Doe pronghorn success is calculated through a post-hunt phone survey, there is no reporting requirement for hunter.
13	CO	Questionnaire, Phone Survey	
14	KS	Questionnaire	Mail to all permit holders, but not with permits. Achieve near 100% response rates.
15	AZ	Questionnaire, Mail Survey/Random	
16	NM	Survey not received	
17	TX	Mail Survey with Permits	
18	OK	Survey not received	
19	MEX1	Survey not received	

Table 5. Total harvest (all weapon types), by state and province, 2004 and 2005.

State/ Province		#Bucks Harvested		#Does/ Fawns Harvested		#Total Harvest		%Bucks in Harvest		%Does/Fawns in Harvest		% of Population Harvested	
		2004	2005	2004	2005	2004	2005	2004	2005	2004	2005	2004	2005
1	AB	XXXX	674	XXXX	623	XXXX	1,297	XXXX	52	XXXX	48	XXXX	7
2	SK	XXXX	524	XXXX	93	XXXX	617	XXXX	85	XXXX	15	XXXX	3
3	OR	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX
4	ID	994	1,148	262	260	1,256	1,408	79	82	21	15	10	XXXX
5	MT	Survey not received		XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX
6	ND	1,527	2,108	551	2,093	2,078	4,201	73	50	27	50	14	28
7	SD	3,590	4,509	3,704	5,054	7,294	9,563	49	47	51	53	15	19
8	WY	24,590	25,784	11,790	14,282	36,380	40,066	68	64	32	36	7	8
9	NE	Survey not received		XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX
10	CA	206	213	0	0	206	213	100	100	0	0	5	5
11	NV	1,283	1,489	40	119	1,323	1,608	97	93	3	7	6	7
12	UT	XXXX	603	XXXX	492	XXXX	1,095	XXXX	55	XXXX	45	XXXX	9
13	CO	3,111	3,584	2,364	2,646	5,475	6,230	57	58	43	42	8	9
14	KS	94	127	10	14	104	141	90	90	10	10	5	7
15	AZ	406	471	0	0	406	471	100	100	0	0	4-5	5-6
16	NM	Survey not received		XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX
17	TX	542	688	0	0	542	688	100	100	0	0	3	4
18	OK	Survey not received		XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX
19	MEX1	Survey not received		XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX

Table 6. Rifle harvest of pronghorns, by state and province, 2004 and 2005.

State/ Province		#Bucks Harvested		#Does/ Fawns Harvested		#Resident Hunters		#Non-Resident Hunters		#Resident Days		#Non-Resident Days		%Hunter Success	
		2004	2005	2004	2005	2004	2005	2004	2005	2004	2005	2004	2005	2004	2005
1	AB	XXXX	608	XXXX	623	XXXX	1,618	XXXX	---	XXXX	2,783	XXXX	---	XXXX	82
2	SK	XXXX	524	XXXX	93	XXXX	750	XXXX	0	XXXX	XXXX	XXXX	0	XXXX	89
3	OR	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX
4	ID	747	806	216	184	1,334	1,387	35	60	3,736	4,051	125	179	68	68
5	MT	Survey not received		XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX
6	ND	1,361	1,851	504	2,032	2,272	4,917	0	0	4,606	9,469	0	0	82	79
7	SD	3,349	4,118	3,683	5,022	5,783	7,150	448	659	11,970	17,017	927	1,568	71	66
8	WY	23,434	24,605	11,236	13,615	16,259	17,047	19,726	23,303	53,037	58,378	60,274	74,247	96	93
9	NE	Survey not received		XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX
10	CA	196	201	0	0	231	242	0	0	693	726	0	0	85	83
11	NV	1,194	1,402	40	119	1,396	1,707	99	258	4,041	5,442	258	644	79	77
12	UT	XXXX	544	XXXX	492	316	449	28	43	XXXX	939	XXXX	---	XXXX	90
13	CO	2,815	3,209	2,329	2,596	6,528	6,967	437	444	10,979	11,667	690	671	74	77
14	KS	70	81	7	5	106	121	0	0	146	159	0	0	73	71
15	AZ	283	356	0	0	334	399	19	23	780	923	45	53	82	86
16	NM	Survey not received		XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX
17	TX	542	688	0	0	638	822	0	0	9	9	0	0	85	84
18	OK	Survey not received		XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX
19	MEX1	Survey not received		XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX

Table 7. Muzzleloader harvest of pronghorns, by state and province, 2004 and 2005.

State/ Province		#Bucks Harvested		#Does/ Fawns Harvested		#Resident Hunters		#Non-Resident Hunters		#Resident Days		#Non-Resident Days		%Hunter Success	
		2004	2005	2004	2005	2004	2005	2004	2005	2004	2005	2004	2005	2004	2005
1	AB					---	---	---	---	---	---	---	---	---	---
2	SK					---	---	---	---	---	---	---	---	---	---
3	OR	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX
4	ID	52	85	10	19	139	214	4	17	632	826	12	71	44	45
5	MT	Survey not received		XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX
6	ND					---	---	---	---	---	---	---	---	---	---
7	SD	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8	WY	231	212	111	120	160	150	195	205	---	---	---	---	---	---
9	NE	Survey not received		XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX
10	CA					---	---	---	---	---	---	---	---	---	---
11	NV	0	0	0	0	0	0	0	0	0	0	0	0	---	---
12	UT					---	---	---	---	---	---	---	---	---	---
13	CO	60	61	19	32	164	152	6	12	442	418	8	38	46	57
14	KS	14	22	2	2	30	38	0	0	51	89	0	0	53	63
15	AZ	50	56	0	0	87	92	5	5	276	281	16	17	56	62
16	NM	Survey not received		XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX
17	TX	0	0	0	0	0	0	0	0	0	0	0	0	0	0
18	OK	Survey not received		XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX
19	MEX1	Survey not received		XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX

Table 8. Archery harvest of pronghorns, by state and province, 2004 and 2005.

State/ Province		#Bucks Harvested		#Does/ Fawns Harvested		#Resident Hunters		#Non-Resident Hunters		#Resident Days		#Non-Resident Days		%Hunter Success	
		2,004	2,005	2,004	2,005	2,004	2,005	2,004	2,005	2,004	2,005	2,004	2,005	2,004	2,005
1	AB	XXXX	66	XXXX		XXXX	189	XXXX	---	XXXX	638	XXXX	---	XXXX	43
2	SK					---	---	---	---	---	---	---	---	---	---
3	OR	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX
4	ID	195	250	36	54	1,059	1,178	15	25	5,368	4,966	63	116	31	25
5	MT	Survey not received		XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX
6	ND	166	257	47	61	1,237	1,302	94	88	6,561	6,179	6,561	6,179	16	23
7	SD	241	391	21	32	837	993	278	262	3,984	4,279	1,323	1,129	23	34
8	WY	925	967	443	547	642	685	778	936	---	---	---	---	---	---
9	NE	Survey not received		XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX
10	CA	10	12	0	0	20	24	0	0	60	72	0	0	50	50
11	NV	89	87	0	0	333	378	14	50	1,420	1,784	40	152	27	21
12	UT	XXXX	59	XXXX		66	90	2	5	XXXX	377	XXXX	60	XXXX	---
13	CO	236	314	16	18	1,369	1,571	115	168	6,261	7,710	492	752	17	19
14	KS	10	24	1	7	120	153	0	0	392	458	0	0	9	20
15	AZ	73	59	0	0	393	392	23	23	2,479	2,318	143	134	19	15
16	NM	Survey not received		XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX
17	TX	0	0	0	0	0	0	0	0	0	0	0	0	0	0
18	OK	Survey not received		XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX
19	MEX1	Survey not received		XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX

Table 9. Current research projects on pronghorns, by state and province, 2005.

State/ Province		Program Description	Funding	Results
1	AB	Migration and movement study, using GPS collars, visual identity collars, and radio-telemetry collars. Ongoing (Alberta Conservation Association)		
2	SK	None		
3	OR	None		
4	ID	Landscape evaluation, population monitoring. No current program of coordinated aerial surveys.		
5	MT	Survey not received		
6	ND	Determine home range, habitat-use, and survival rates of adult pronghorn in North Dakota.		
7	SD	Field investigations recently completed and thesis in draft stage, 1) comparing movements, reproduction, recruitment of two different antelope populations in Harding and Fall River counties, and 2) evaluation of present survey methodology with emphasis on development of a new, more accurate, cost-efficient, and less labor-intensive survey protocol for monitoring pronghorn populations in the state.		
8	WY	1. Survival Study. 2. High/Pronghorn passage study. 3. Physiology of stress.		
9	NE	Survey not received		
10	CA			
11	NV			
12	UT	None		
13	CO	1. Evaluate distance sampling methods using a known population of radio-marked pronghorn. 2. Determine survival rates of radio-marked pronghorn. 3. Movements and dispersal of radio-marked pronghorn.		
14	KS			
15	AZ	1. Impact of Arizona Highway 89 and mitigation to facilitate movements. 2. Pronghorn use of Camp Navajo (habitat, disturbance). 3. Sonoran pronghorn habitat, captive rearing. 4. Planning for additional predation impacts.		
16	NM	Survey not received		
17	TX	To determine the relationship between landscape level changes in pronghorn habitat in Trans-Pecos ecoregion. Specific objectives are (1) use GIS to map historic management units and evaluate habitat changes relative to pronghorn trends (2) evaluate precipitation indices relative to pronghorn trends; and (3) re-delineate herd units that reflect current physical boundaries and aggregations of pronghorn herds.		
18	OK	Survey not received		
19	MEX1	Survey not received		

Table 10. Other items of interest from pronghorn management programs, by state and province, 2005.

State/ Province		Items of interest
1	AB	Antelope populations appear to be doing well in all areas, although coyote predation (particularly on fawns) in some areas is significant. Weather factors in the past few years have been negligible, due to above-average temperatures and below-average precipitation during past winters. Wet springs (June) in 2005 and 2006 may have had an impact on fawn survival. Next survey planned for July 6-12, 2006.
2	SK	Looking at expanding pronghorn movement/migration study in Alberta and Montana to Saskatchewan.
3	OR	Oregon has hopes of initiating new research, because funding is becoming available through an auction and raffle tag for pronghorn.
4	ID	None
5	MT	Survey not received
6	ND	
7	SD	It is difficult, both administratively and practically, to develop a long-range management plan for pronghorn in S.D. and establish long-term population goals and objectives.
8	WY	1) Herd classifications done by aerial and ground. 2) August post-fawning ground classification. 3) % of population observed from POP-II Model 4) B:D, F:D range provided from across state 5) Season dates: many different hunt areas and seasons, these are the outside dates, depends on license type and hunt area.
9	NE	Survey not received
10	CA	
11	NV	We only collect and generate post-season buck and fawn ratios so I added 5 points onto our statewide averages to give you preseason values in the survey. We continue to work on building water developments in water deficient habitats and capture and transplant antelope where carrying capacity has not yet been met in release sites and from capture sites where extensive winter range habitat has been lost. One more thing about survey efforts. I didn't mark any option because we don't count/census, we classify for ratios, but they are truly directed search survey and not statistically randomized over landscape.
12	UT	1)#Bucks harvested 2005 includes all hunters (public and CWMU) (=tags to landowners) [Cooperative Wildlife Management Units (CWMU)] 2) Number Res/Nonres hunters 2005 DO NOT include CWMU hunters 3) Number of hunter days and success is for Bucks, it includes Res/NonRes 4) Season dates reported are for 2005 5) 2005 Does: public harvest=381,%success=90% (depends if at least 1 taken on 2 doe permit), permits =252 (including 200 2-doe permits); 6) Population Estimate is 12,000 to 15,000 7) Rifle season is Any Weapon CWMU harvest = 111, success=73%, permits=177 Total doe harvest=492,success=80%,permits=429 (200 2-doe permits, potential for 629 harvest if 100% of permits were filled.)
13	CO	Population estimates are obtained by spreadsheet modeling using preseason sex & age ratios, harvest estimates, and survival estimates. Trend counts are often used to adjust models. There is currently no standardized procedure for pronghorn inventory in Colorado.
14	KS	The info provided pertains to 2005 where not specified (i.e. season dates, survey data).
15	AZ	
16	NM	Survey not received
17	TX	1) We don't keep track of non residents hunting pronghorns, we issue permits to landowners who then sell the right to trespass on their property. 2) We don't have multiple seasons for different weapons but our hunters are allowed to use any legal means and methods for harvesting pronghorns in Texas.
18	OK	Survey not received
19	MEX1	Survey not received

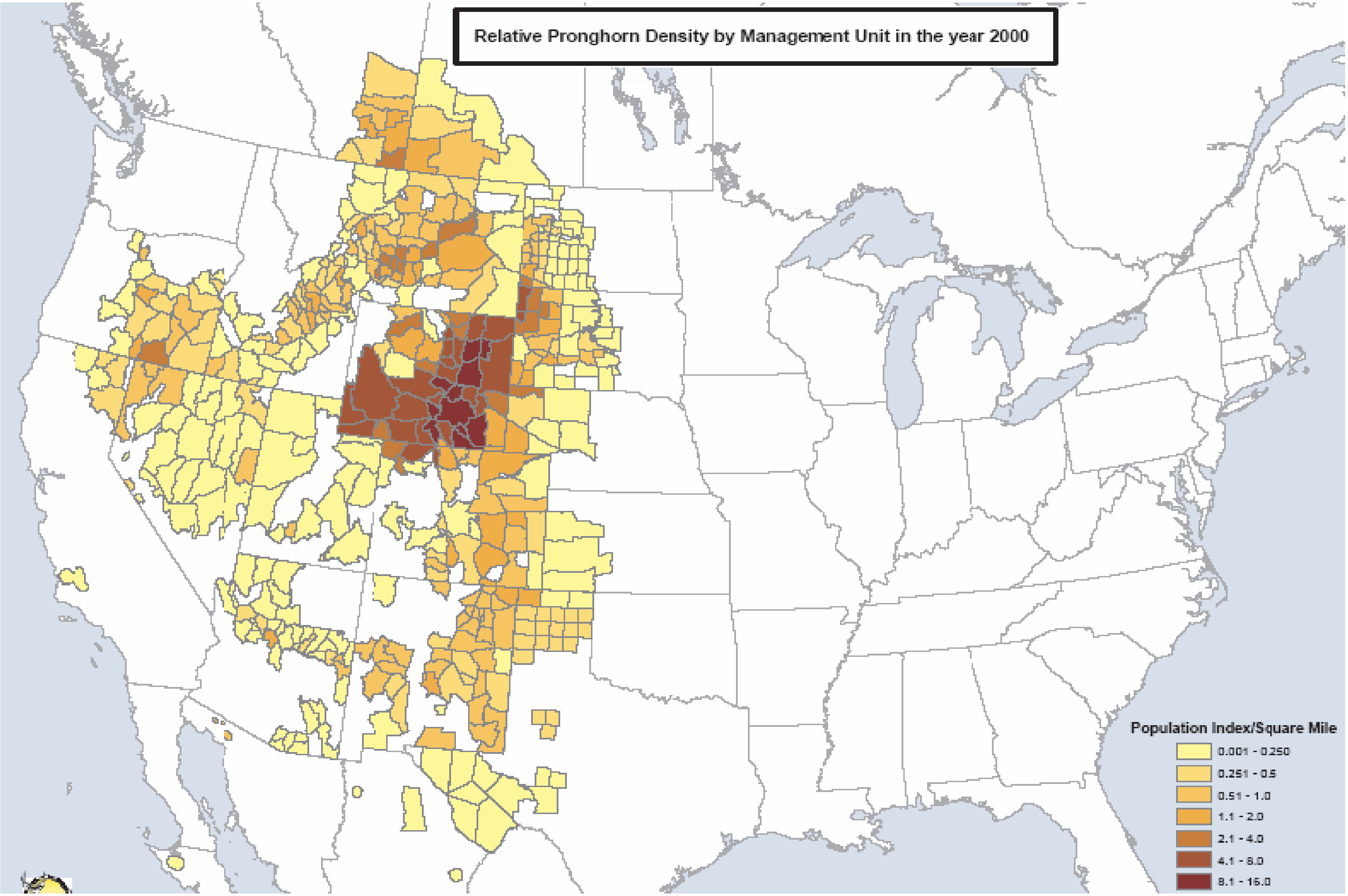

Figure 1. Pronghorn density, by management unit, 2000, from Jensen, Hosek, and Rudd (2004).

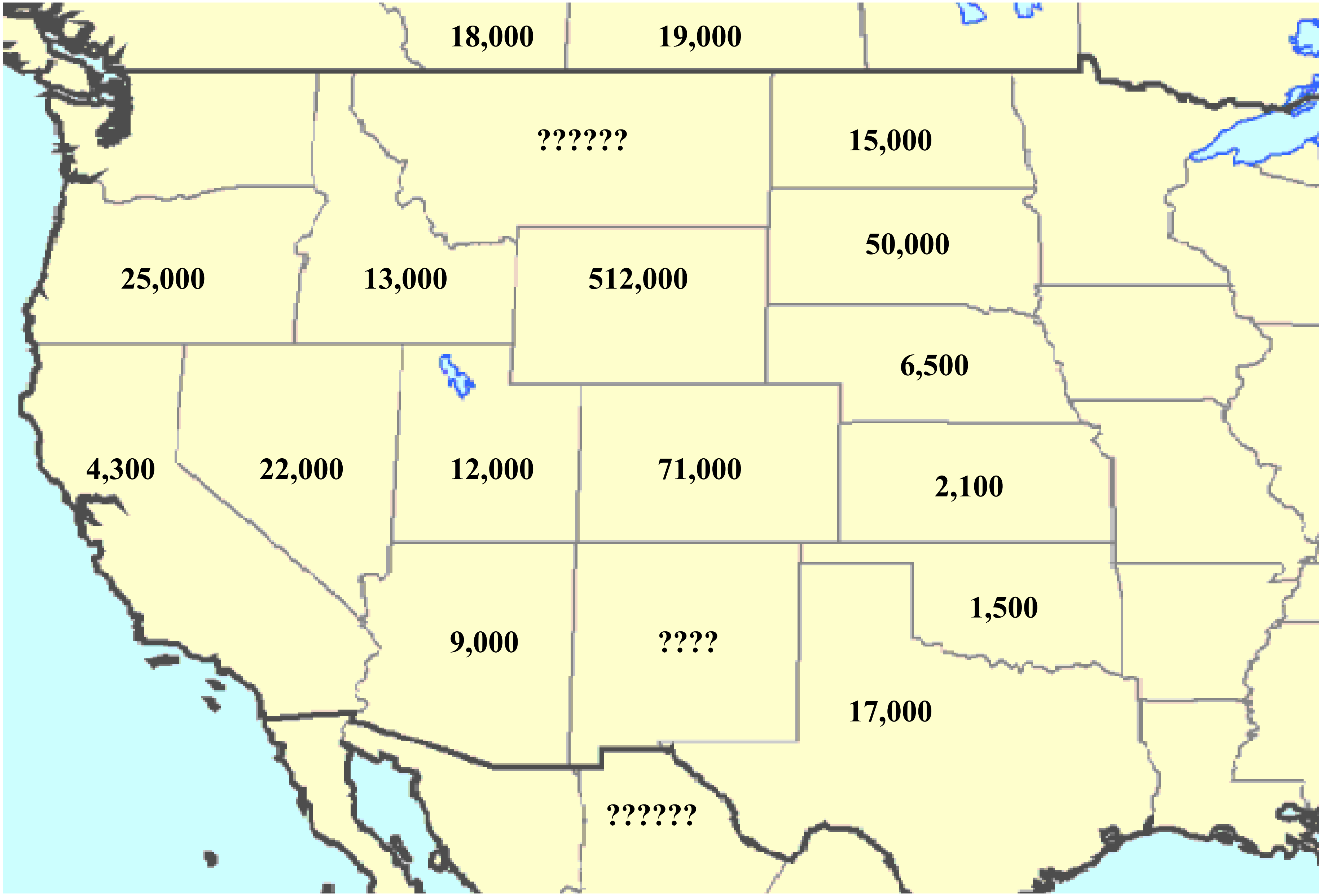

Figure 2. Map of most recent pronghorn population estimates, by state and province, 2003 to 2005.

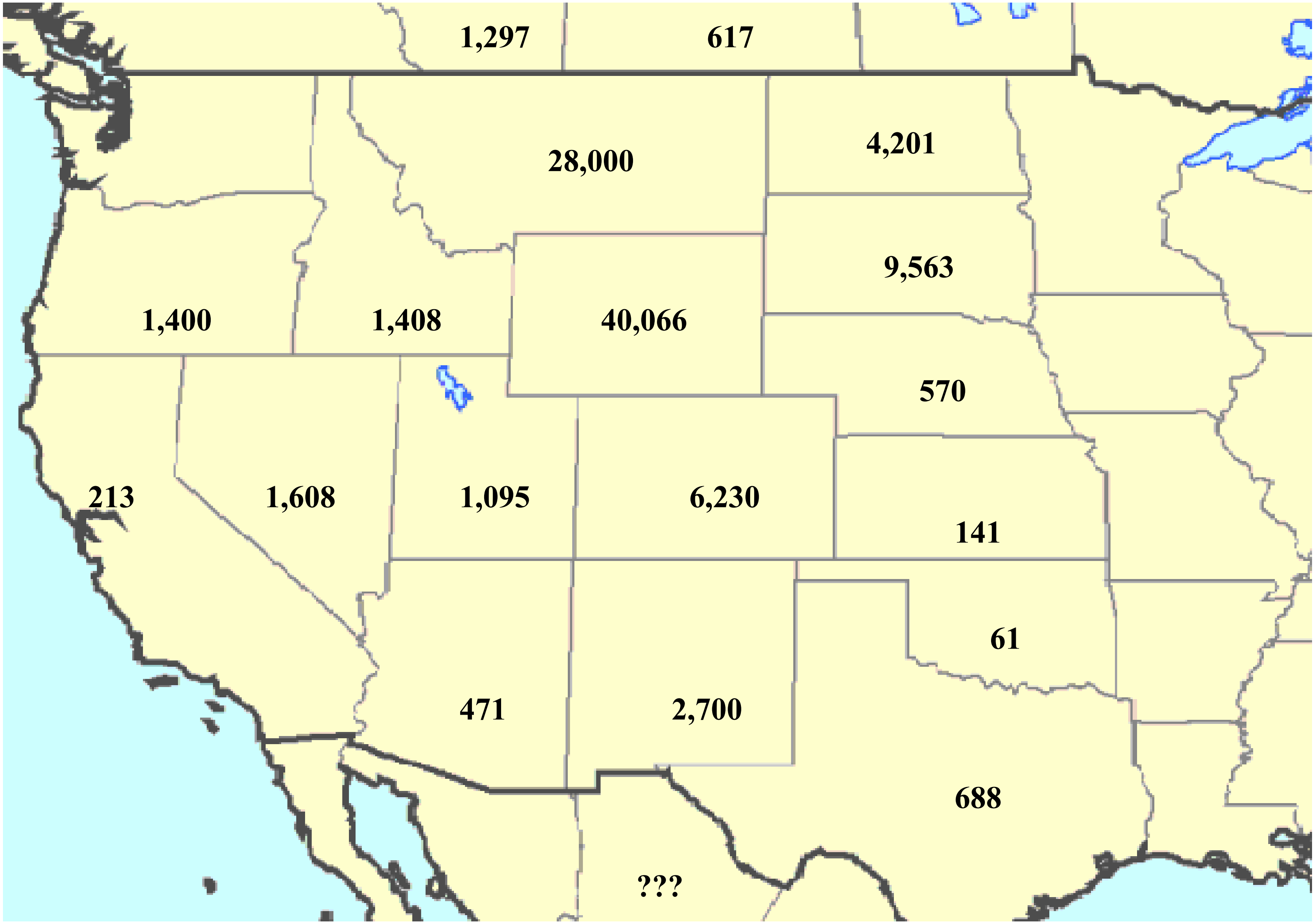

Figure 3. Map of most recent pronghorn harvest estimates, by state and province, 2003 to 2005.

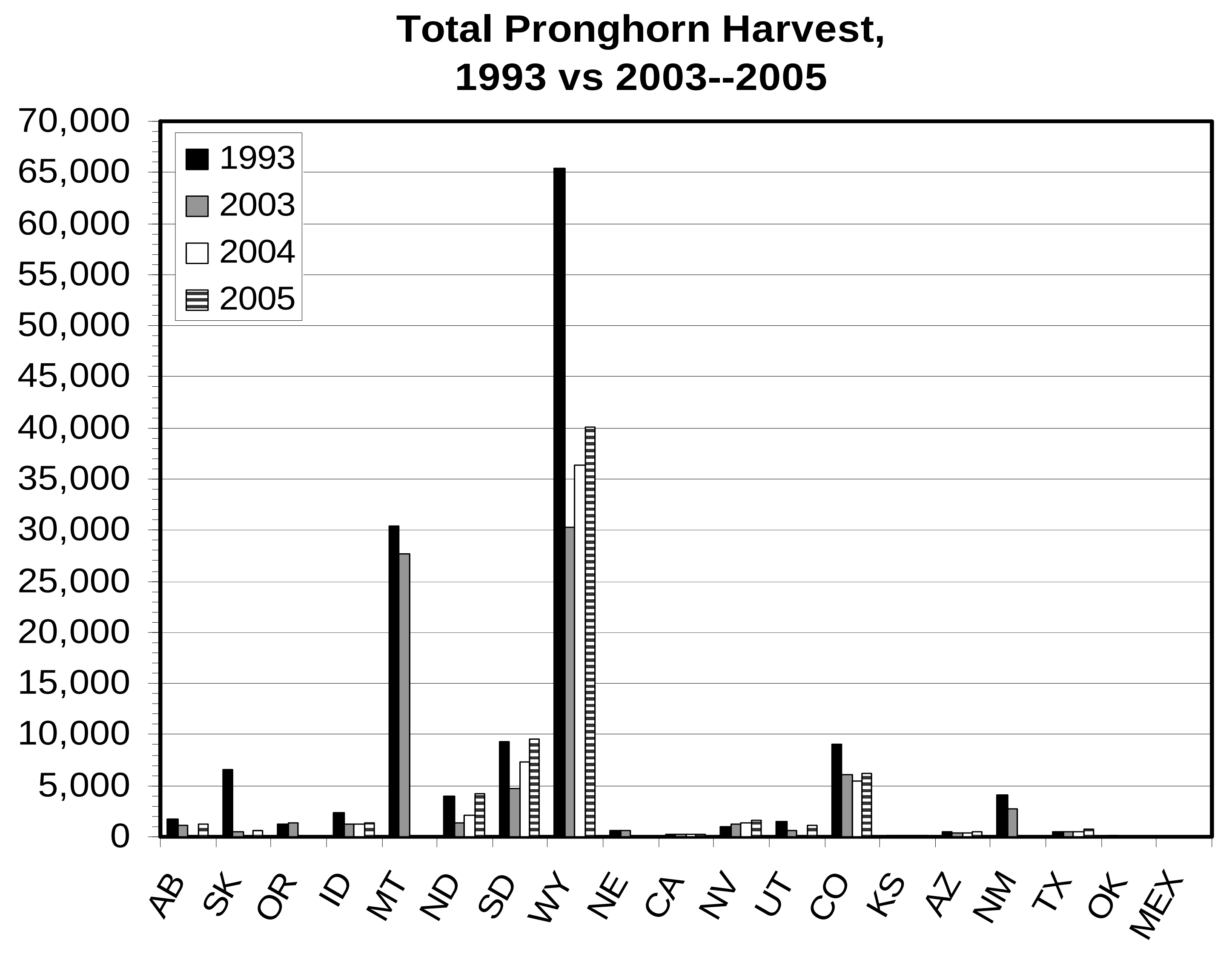

Figure 4. Histogram of pronghorn harvest estimates, by state and province, 1993 vs. 2003-2005.

Section III Submitted Papers

Are Pronghorn Vital Rates Affected by Habitat Quality?

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83844-3051

Abstract: I compared pronghorn condition and reproductive effort at the National Bison Range (NBR), a site with a mild climate and high quality forage, to condition and reproductive effort in Yellowstone National Park (YNP), a site with harsh winters and poor winter range. NBR pronghorn are descended from a sample of individuals moved from YNP about 50 years ago, so significant genetic differences between the 2 populations are unlikely. Pronghorn adult females and fawns were heavier at the NBR than at YNP, but the condition of fawns at the 2 sites did not differ. Also, maternal reproductive expenditure, measured as litter mass/maternal mass, was identical at the 2 sites. Pronghorn are unusual mammals in that they have very high annual reproductive expenditure, yet little detectable cost of reproduction. Several years after this comparative study ended, the NBR experienced a severe summer drought. Range condition was obviously poor, and for the first time since 1981, there were pronghorn individuals in visibly poor condition. In the rut of that year, most females abandoned the typical mate-sampling behavior. Over the following winter, there was substantial, male biased, mortality, and in the following spring widespread resorption of litters by females. One can find environmental limits on pronghorn reproduction, but those limits appear to occur only in extremely poor environments. This relative insensitivity of female reproductive performance to environmental conditions can lead to erroneous conclusions about the meaning of fawn: doe ratios.

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Key Words: vital rates, habitat quality, National Bison Range, Yellowstone National Park, Fawn: Doe Ratios

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Part I – A paradox and a hypothesis test

Among mammals, the ungulates have some of the highest known rates of maternal reproductive expenditure (Case 1978), and among ungulates, the highest known level of maternal expenditure is found in pronghorn (Robbins and Robbins 1979, Byers 1997a). In pronghorn, the mass of the litter is about 13% of maternal mass and, during lactation, the 45 kg mother supports 2 young that each grow at close to one-quarter kg/day. High birth weights and growth rates in ungulates in general, and in pronghorn in particular, are considered to be an evolved consequence of historically high levels of predation on young (Byers 1997a).

Reproduction is often considered to have a cost, where cost is expressed as decreased future fecundity or survival that result from current reproductive expenditure (Stearns 1992). Such a cost of reproduction exists in several ungulate species (Clutton-Brock et al. 1983, Clutton-Brock 1991, Green and Rothstein 1991, Festa-Bianchet et al. 1995). A cost of reproduction in ungulates should not be surprising, because the levels of maternal expenditure in the group are so high. Therefore, I was surprised to find, in my long-term study of pronghorn at the National Bison Range (NBR), that a cost of reproduction was not detectable. In this population, I recognized all individuals and showed that each female, from the age at first reproduction at 1.5 years to death produced twin fawns each spring. In addition, the level of effort of a female (weaning 0, 1, or 2 fawns) had no effect on her subsequent gestation length or litter mass (Byers 1997a). These findings seemed paradoxical. Pronghorn have levels of maternal reproductive expenditure that are about the highest known in mammals, yet show no cost of reproduction. Other mammals with lower levels of expenditure do show a cost of reproduction (Byers and Hogg 1995).

One possible explanation of the paradox was that the ecology of my study site was unrepresentative. The NBR comprises a native short grass prairie on which the density of bison is low. The NBR is on the western side of the continental divide in Montana and has a relatively mild climate. Perhaps I had failed to detect a cost of reproduction in pronghorn at the NBR because the animals there enjoyed abundant high quality food and little energetic stress in winter.

I decided to test this hypothesis by comparing vital rates of pronghorn on the NBR to vital rates in populations where forage quality was lower and winter energetic stress was higher. The first comparison population that I selected was that of the Northern Range in Yellowstone National Park (YNP). This comparison was ideal, because the NBR pronghorn are descended from transplants from YNP in the 1950s (Dow and Wright 1962, Byers 1997a). Thus, any differences in individual condition or vital rates between the 2 populations can be attributed to environmental effects; this is the hypothesis under test.

Materials and Methods

Study Sites. The NBR is an enclosed, 7504 ha National Wildlife Refuge that was established in 1908 to save bison from extinction. Descriptive detail may be found in Byers (1997a). The NBR is dominated by Palouse Prairie grassland. Pronghorn on the NBR are descended from transplants from YNP in 1951, 1952 and 1956 (Dow and Wright 1962), with occasional introductions of a few individuals from other Montana populations (Byers 1997a). The YNP pronghorn population is a remnant of a once larger indigenous population that moved up and down the Yellowstone River valley, from the high grasslands of what is now YNP in summer to lower elevation sites near the current location of Livingston, Montana in winter. The northern fall migration of pronghorn in YNP is now halted by the fences of private landowners, so pronghorn and other ungulates of the Northern Range of YNP now spend the winter in the vicinity of Gardiner, Montana, where soils are poor and herbaceous vegetation is scant. Figure 1 shows a comparison of annual temperature and precipitation at the NBR and at Gardiner, and Table 1 summarizes Boccadori's (2002) recent description of YNP winter range.

Adult Mass. In YNP we captured 30 female pronghorn by helicopter net gunning in February 1999. At capture, we attached a conventional VHF radio collar and weighed the animal to the nearest kg. At the NBR, we captured 49 females in November 1999 by driving them into a corral trap with a helicopter. We weighed each female to the nearest kg.

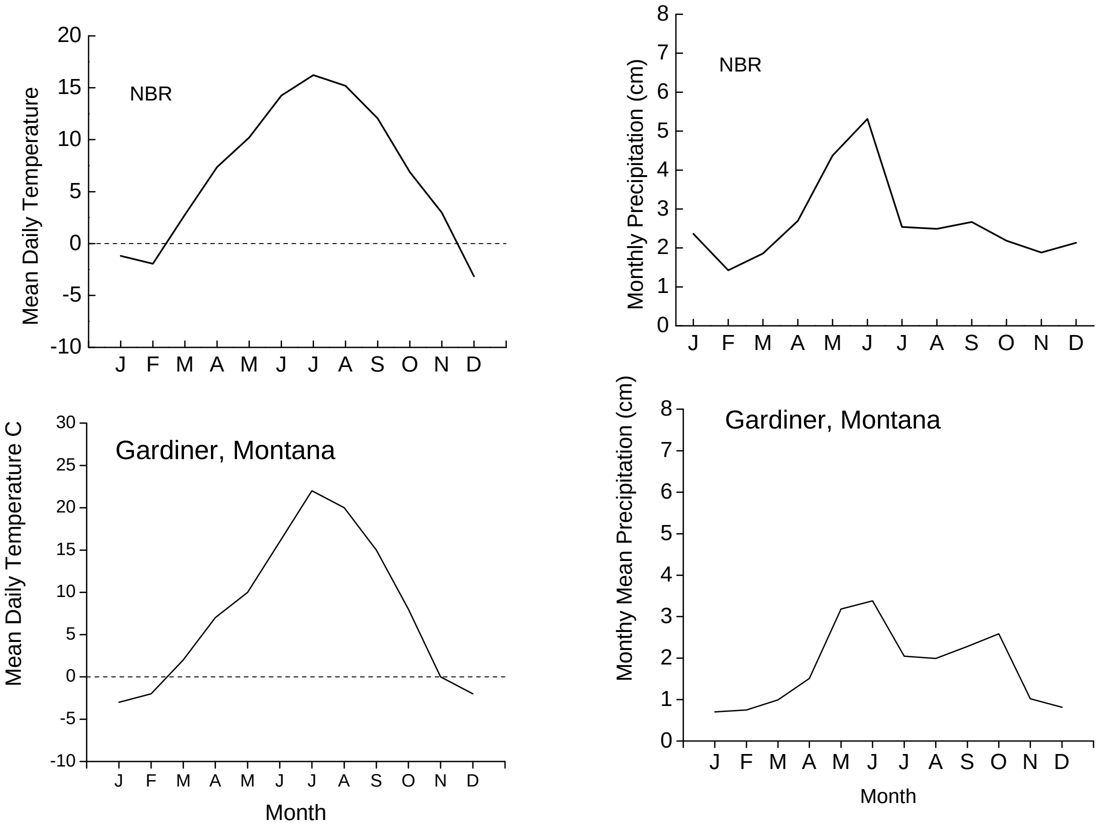

Figure 1. Average annual temperature and precipitation at the National Bison Range and at the Yellowstone National Park winter range near Gardiner, Montana.

Table 1. Summary of Yellowstone National Park winter range vegetation (from Boccadori, 2002).

Cover Type	Percent of Winter Range	% Herbaceous Cover	Other
Grassland	40	8.8	Much bare soil, gravel
Old Fields/Current Pasture	16	17.8	Abundant crested wheatgrass
Grassland-Sagebrush	11	Canopy 15.8	
Sagebrush	25	17.6	
Rabbitbrush	4	23.3	Understory: crested wheatgrass, alyssum, dandelion, stickseed
Greasewood	1	15.2	

Fawn Mass and Condition. At both sites, we captured fawns using methods described by Byers (1997b). We weighed each fawn to the nearest 0.10 kg and measured the length of the right tarsus to the nearest mm. As an index of condition, we plotted mass against tarsus length for each population and calculated the least-squares slope. Mass vs. tarsus length gives an indication of how heavy an individual is for a given skeletal size.

Pregnancy Status. In both populations in May and June of each year we located all study females each day or as frequently as possible and recorded whether or not each female was obviously pregnant.

Litter Size. Byers (1997a) reported that litter size on the NBR is always 2. To estimate litter size in YNP we relied on earlier reports by O'Gara (1968), necropsy of 2 late term females, and observation of 13 births.

Yellowstone Pronghorn Birth Locations. In the May-June birth season in YNP, we located radio-collared pronghorn females daily or as frequently as possible. Each time that we recorded the location of a collared female, we also recorded the number of other females in that female's group. We recorded the UTM (NAD 83) coordinates of birth sites to the nearest 100 m using 1: 24000 topographic maps. We used the birth site locations of radio-collared pronghorn females (2000-2001 $N = 26$ and 20, representing 17 and 13 percent, respectively, of the total number of adult females in this largely closed population) to identify the 7 major areas (Winter range, Blacktail Plateau, West Specimen Ridge, East Specimen Ridge, West Lamar Valley, Center Lamar Valley, East Lamar Valley) where 95% of fawns were born and to estimate the total numbers of females that gave birth in each of these locations. We calculated the estimated number of births in each location as the proportion of radio-collared females that gave birth in this location times the total number of un-collared females in the population.

Fawn age at death. In YNP we attached solar powered ear tag radio transmitters with mortality sensors to 27 fawns. We monitored signals from fawns daily to detect the age at death. When ear tag transmitters indicated mortality, we attempted to recover the tag and to record information on its location, presence of bite marks, and whether any remnants of the fawn's carcass were present. When we failed to capture the fawn of a radio-collared female, we located that female daily and assessed, based on her behavior (solitary or in a group; calm or wandering and calling for a fawn) and the size of her udder, whether her fawn was alive. We obtained estimates of the age at death for another 38 fawns in this way.

Estimates of fawn survival. Female pronghorn with surviving fawns are sedentary close to the birth site until late August (Byers 1997a). Thus in mid-August, a surviving fawn is found in the same general area where it was born. In YNP over 2 days in mid-August, 2000 and 2001, we located all radio-collared pronghorn females and counted the total number of fawns in groups that contained these females. Because pronghorn coalesce into larger groups at this time of year, this was likely a total count of all fawns recruited into the YNP northern range pronghorn population.

Wolf Density. During the years of this study, 6 wolf packs occupied the northern grassland of YNP, and approximately one-half of the individuals in each pack wore conventional radio collars. Signals from radio collars allowed Wolf researchers to make visual sightings from fixed-wing aircraft. When the aircraft was directly above the wolf, researchers recorded the Universal Transverse Mercator (NAD 83) coordinates using a handheld GPS unit. Locations of wolf den sites were recorded in the same manner. To reflect the presence of wolves during the period in which pronghorn fawns were vulnerable to coyotes, we used locations from 1 March to 31 August in 2000 and 2001 in all analyses of wolf density

Wolf density and fawn survival. For each of the 4 major birth areas, we divided the estimated total number of births by the number of known births (to radio-collared females). We then randomly seeded this number of estimated birth sites around each known birth site. The coordinates of each seed were created using a random number generator to choose values within ± 400 m latitude and ± 400 m longitude of the known site. We then used ArcView 3.2 to draw a Jennrich-Turner ellipse that comprised 95% of all birth sites (known and seeded) on each of the 7 principal areas where fawns were born. Although Jennrich-Turner ellipses tend to overestimate home range size, we considered them to be ideal for our analysis, in which we wanted to obtain a global estimate of wolf influence in the general area where a fawn was born. We then used the Spatial Analyst extension in ArcView to create, using Krieger methods, a color-based display of wolf density (using all point locations of wolves from March through August in 2000 and 2001) over the same view. We imported the resulting image into Sigma Scan Pro 5.0, converted to grayscale, and measured the average color intensity within each Jennrich-Turner ellipse as well as in a blank area (an area of the view where wolves did not occur). For each ellipse, the index of wolf density was the value of blank (white - the maximum possible color intensity) minus the average color intensity within the ellipse. This gave an index in which the lightest ellipses (those with low wolf density) had low values, and the darkest ellipses (high wolf density) had high values.

Results

The main results are shown in Table 2. Litter size was very close to 2 in both populations. In YNP, one radio collared female was not pregnant in any study year and the pregnancy status of individuals in 4 other instances was undetermined; all other YNP females were pregnant each year. YNP females were significantly lighter than NBR females and there was a corresponding difference in fawn mass. However, fawn condition in the 2 populations was not different (ANCOVA $t = 0.164$, df = 82, $P > 0.50$), and maternal expenditure, measured as litter mass/maternal mass, was not different.

In summary, although pronghorn in YNP are exposed to more severe winters and have poorer quality forage, their patterns of reproductive performance are essentially identical to those of females on the NBR. These results suggested that pronghorn fecundity is not very sensitive to variation in habitat quality. As on the NBR, fawn survival in YNP seemed to be mostly a function of coyote density (assuming that coyote density varies inversely with wolf density)

Table 2. Comparison of vital rates, fawn condition, and maternal expenditure of pronghorn at Yellowstone National Park (YNP) and the National Bison Range (NBR). Asterisks (*) show the significantly larger of 2 mean values in a column.

Population	Pregnancy Rate	Litter Size	Female Body Mass (kg)	Fawn Birth Mass (kg)	Fawn Condition (size-mass slope)	Maternal Expenditure: Litter Mass/Maternal Mass
YNP	90%	2	46.6	3.05	0.411	0.131
NBR	98%	2	54.1*	3.60*	0.442	0.133

In YNP fawn survival had a bimodal age distribution (Figure. 2). Fawn survival to weaning was not associated with fawn birth mass (*t* = 0.70, df = 26, *P* = 0.49), nor was fawn age at death (Pearson *r* = 0.17, df = 22, *P* = 0.42). Fawn survival to weaning in YNP was associated with birth location. Across the 7 major birthing areas, there was a significant positive relationship between the proportion of fawns surviving and wolf density (Figure. 3: Pearson *r* = 0.76, *P* = 0.04).

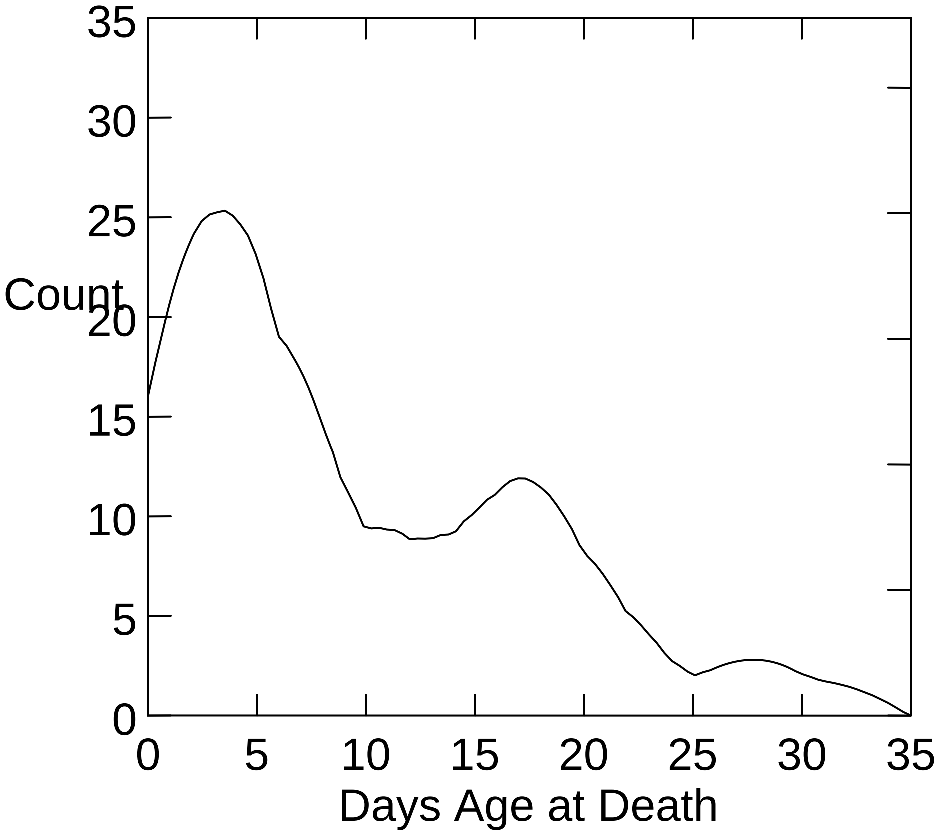

Figure 2. Kernel-smoothed estimates of the age of death of 65 pronghorn fawns that did not survive to weaning in Yellowstone National Park.

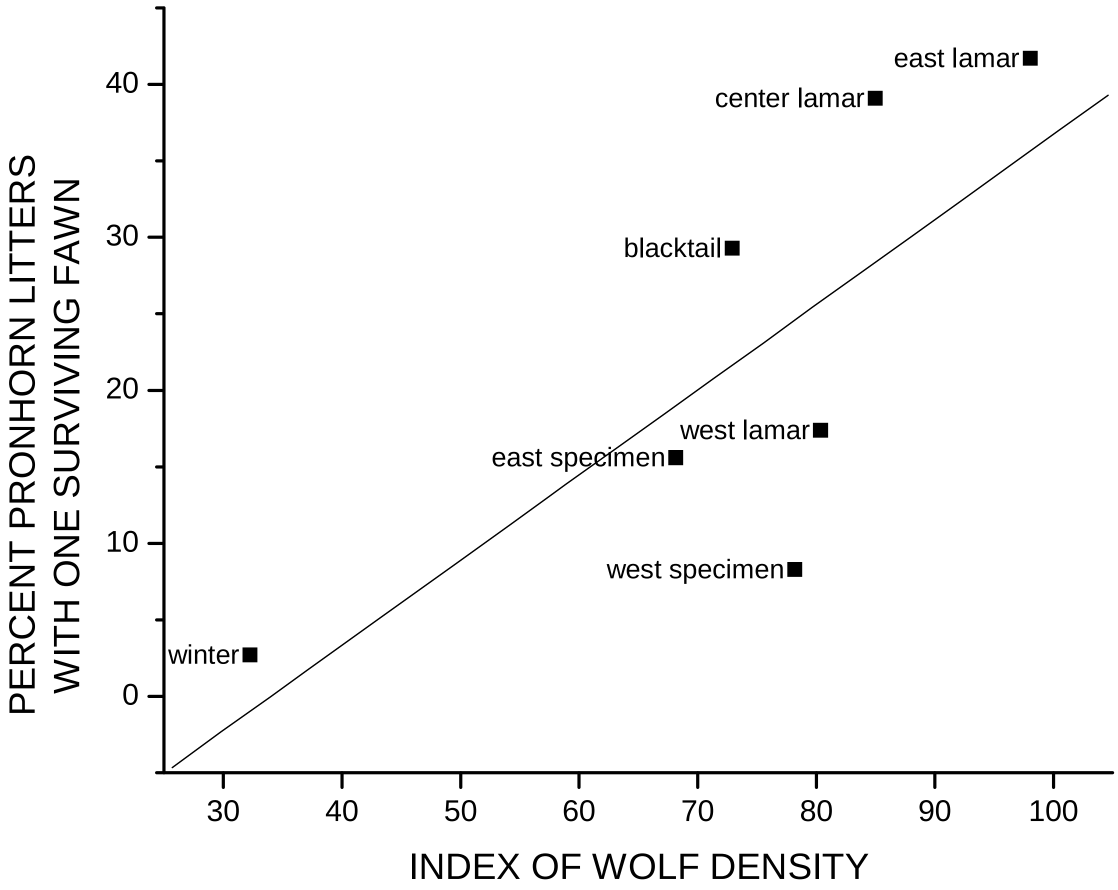

Figure 3. Estimated proportion of fawns that survived to weaning plotted against wolf density in the 7 major areas where fawns were born in the Yellowstone National Park Northern Range.

Part I Conclusion

In summary, although pronghorn in YNP are exposed to more severe winters and have poorer quality forage, their patterns of reproductive performance are essentially identical to those of females on the NBR. These results suggested that pronghorn fecundity is not very sensitive to variation in habitat quality. As on the NBR, fawn survival in YNP seemed to be mostly a function of coyote density (assuming that coyote density varies inversely with wolf density).

Part II – 2003 -2004 drought on the NBR

Events in 2003-2004 caused me to modify my conclusion that pronghorn fecundity is not affected by environmental quality. Figure 4 shows how NBR temperature and precipitation, expressed as deviations from the 30-year mean, changed in the summer of 2003. During this summer, grasses senesced early and snapped off at about 4 cm. In contrast to other years, when I walked across the grassland in August-September 2003, there were many patches of bare ground,

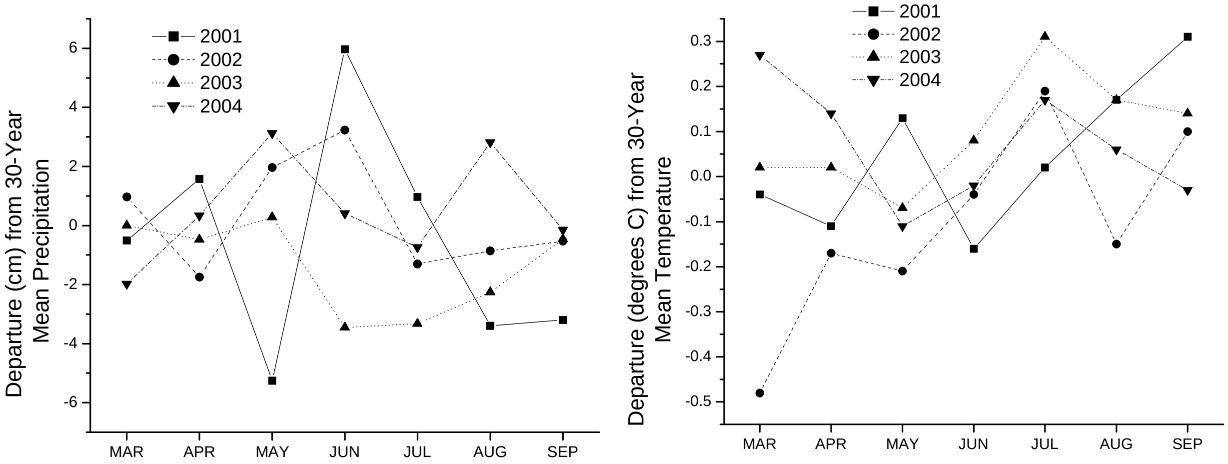

Figure 4. Departures from the 30 year average values for precipitation (upper panel) and temperature (lower panel) at the National Bison Range, 2001-2004. The summer of 2003 was unusually hot and dry.

and forbs were scarce. Many pronghorn by September were in visibly poor condition. In the rut of 2003, most females abandoned the usual, energetically expensive, mate sampling strategy (Byers et al. 2005). In the succeeding winter, 27 of 34 adult males, 25 of 66 adult females, and 8 of 10 fawns died. In spring of 2004, only 7 of 41 females gave birth. In mid-May 2004, other females appeared to be pregnant, but several weeks from parturition. Then most females progressively seemed to be not pregnant. I surmised that these females had reabsorbed their litters. This phenomenon has been reported in other pronghorn populations in severe winters (Martinka 1967). After 23 years of study of pronghorn on the NBR, I had finally detected an effect of forage quality on fecundity.

Part III – The Fawn:doe Ratio as an Indicator of Habitat Quality

My conclusion from the NBR-YNP comparison and from the events on the NBR in 2003-2004 was that although one can detect an effect of forage quality on pronghorn fecundity, the reduction in quality required to detect effects is so severe that in most instances, forage quality will not be important. In other words, I suggest that pronghorn in most habitats across their current range are able to select a diet that provides sufficient energy to permit the annual production of 2 young.

This conclusion raises a question about how fawn:doe ratios are interpreted. The fawn:doe ratio is commonly the dependent variable in studies of forage quality. Several examples of this kind of analysis appear in the proceedings of this workshop. However, given that pronghorn fecundity likely is invariant in most populations, the way that fawn:doe ratios are interpreted may be misleading. The fawn:doe ratio represents the summed effects of female fecundity and fawn survival to weaning. If female fecundity does not vary across habitats, then all of the variation in fawn:doe ratios is explained by variation in fawn survival. Figure. 5 depicts the main causal links, as I see them, between forage quality and the fawn:doe ratio. The effect of forage quality on fecundity is likely to be small in most pronghorn populations. The effect of coyote density on fawn survival is large, and has been convincingly shown in many studies (O'Gara and Yoakum 2004). The links of unknown strength are between forage quality and fawn growth rate, between fawn growth rate and fawn survival, between forage quality and

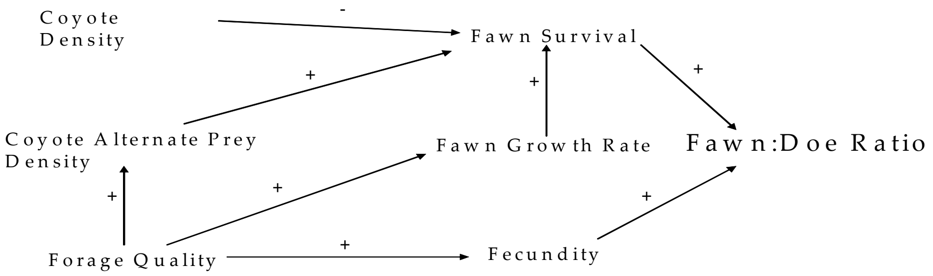

Figure 5. The network of main effects that influence the fawn:doe ratio.

the density of alternative prey for coyotes. Also, the extent to which coyotes switch to alternative prey is unknown. Figure 5 is thus a proposal for research. In several carefully chosen populations, the variables in Figure 5 could be measured simultaneously. This would permit path analysis which would quantify the strengths of the hypothesized connections shown in Figure 5. When path coefficients are known, managers will be in a better position to decipher the meaning of variation in fawn:doe ratios.

I used my long-term data on the NBR pronghorn population to evaluate some of the connections shown in Figure. 5. Figure. 6 shows the fawn:doe ratio on the NBR from 1981 to the present. The values shown represent total counts. These data, from a single population, offer a powerful opportunity to evaluate the strengths of environmental effects on fawn:doe ratios. In regression models, I evaluated the following independent variables: spring (April – June) precipitation, summer (July – September) precipitation, previous year's spring precipitation, previous summer's precipitation, where all precipitation values were expressed as deviations from the 30-year mean, number of coyotes removed by the U.S. Fish & Wildlife Service in spring, number of coyotes removed in the previous year. Table 3 shows AIC evaluation of these models. The best model was that which included number of coyotes removed in the current and in the previous year and spring precipitation, and this model was only slightly better than the one that included only the number of current year coyotes removed and precipitation. Figure. 7 shows a plot of how fawn:doe ratios varied as a function of spring precipitation and number of coyotes removed. These data show that although coyote density certainly has a major effect, there also seems to be a slight effect of spring precipitation. Because these data are from a single population, it is reasonable to infer that spring precipitation is an estimator of spring and early summer forage quality. At this point, data do not exist to evaluate by which path forage quality exerted its effect. It may have been via faster growth rates of fawns, by coyotes switching to alternative prey, or by an interaction of these effects. However, the data do suggest that the path analysis that I propose (Figure. 5) is possible, and should provide for conclusions that are useful to managers.

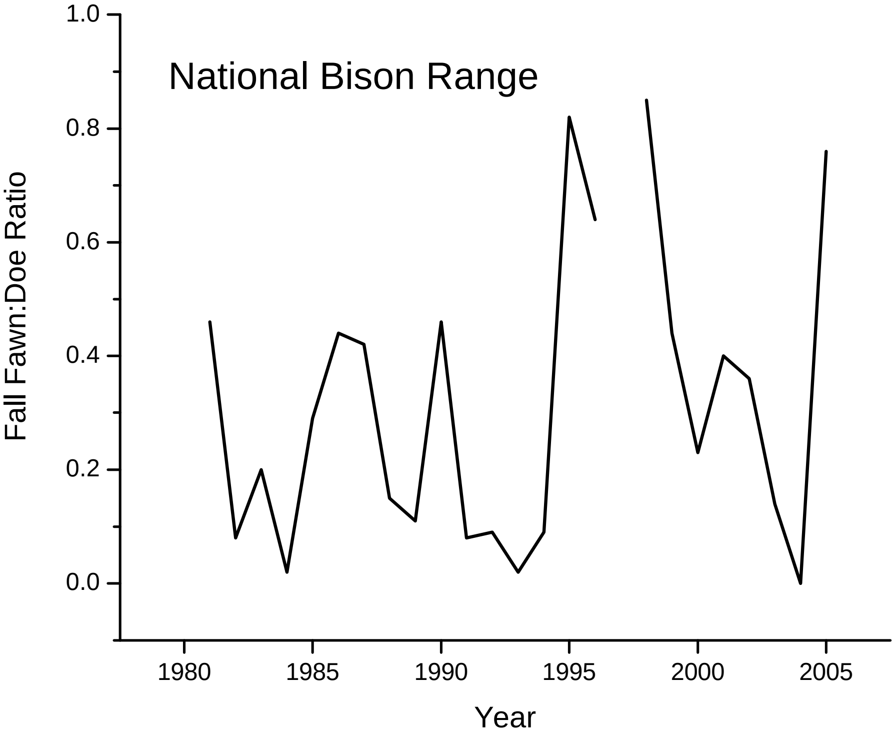

Figure 6. The October fawn:doe ratio on the National Bison Range, 1981-2005.

Table 3. AIC evaluation of regression models to predict the fawn:doe ratio from variables related to forage quality and coyote density

Regression Variables	AIC	**Δ AIC**
Spring Precipitation Coyotes Removed Previous Year Coyotes Removed	-23.266	0
Spring Precipitation Coyotes Removed	-22.341	0.925
Previous Spring Precipitation Spring Precipitation Coyotes Removed Previous Year Coyotes Removed	-21.647	0.694
Coyotes Removed	-20.156	1.491
Previous Spring Precipitation Previous Summer Precipitation Spring Precipitation Coyotes Removed Previous Year Coyotes Removed	-19.825	0.331
Coyotes Removed Previous Year Coyotes Removed	-18.587	1.238
Previous Spring Precipitation Previous Summer Precipitation Spring Precipitation Summer Precipitation Coyotes Removed Previous Year Coyotes Removed	-17.998	0.859

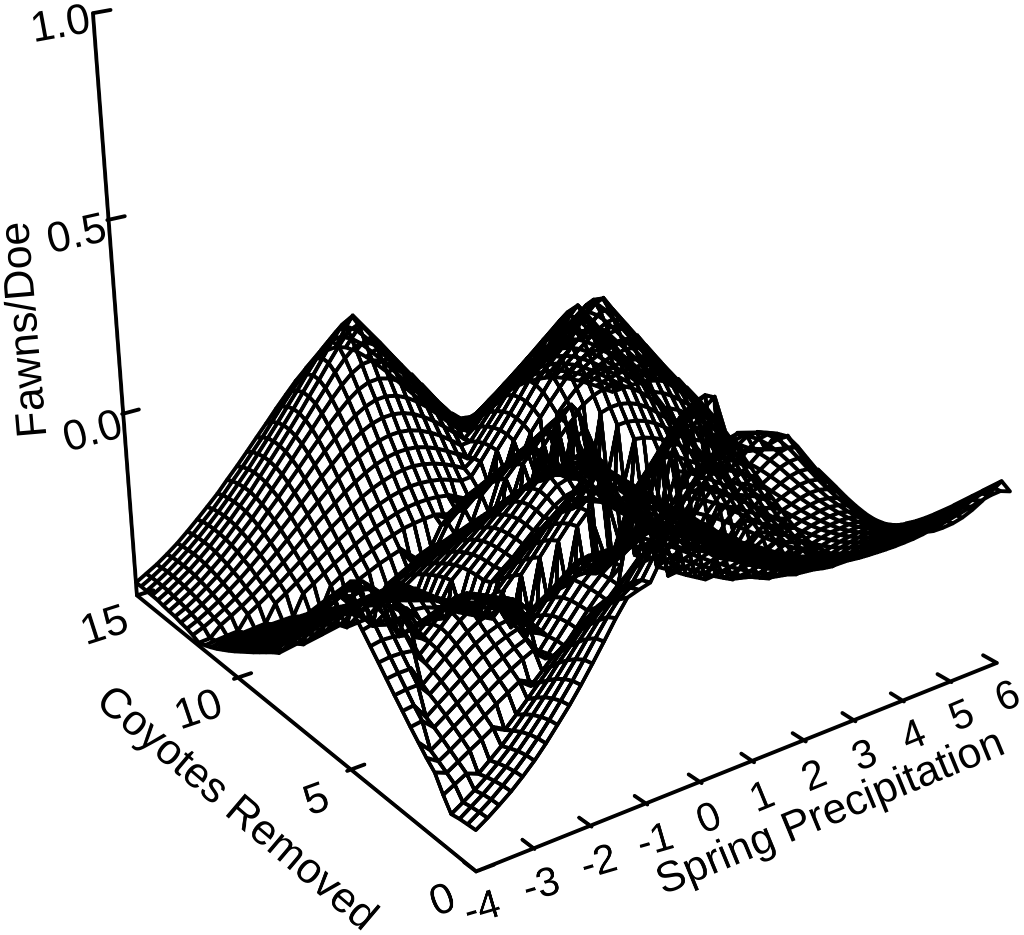

Figure 7. National Bison Range fawn:doe ratio plotted against spring precipitation (deviation from the 30 year mean) and number of coyotes removed in spring by the U.S. Fish & Wildlife Service.

Acknowledgments

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Evaluation of Pronghorn Population Productivity Relative to Broad-scale Habitat Variables in Wyoming (1978-2003)

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Abstract: Intensive studies of pronghorn populations have identified a number of factors that contribute to population dynamics but few have strong effects beyond the local scale or function in a regulatory manner. We used fawn:doe ratios collected from the 44 herd units in Wyoming from 1978-2003 to assess the influence of broad scale habitat variables on population productivity. We evaluated 2 sets of models to: 1) examine the response of productivity to annually varying habitat characteristics and 2) contributions of habitat characteristics to inherent differences between herd units in productivity. The annually varying habitat model identified positive relationships between fawn:doe ratios and previous growing season precipitation, fall precipitation, and previous season's population growth potential. Fawn:doe ratios were negatively related to winter precipitation and growing season precipitation. This model indicated pronghorn populations demonstrate density dependent growth characteristics and highlighted the importance of pre-winter condition on ensuing fawn production. For contributions to inherent differences between herd units, fawn:doe ratios were negatively associated with fall precipitation and positively associated with growing season precipitation. Negative associations with fall precipitation were in discord with previous studies of focal populations. The observed disparity in precipitation relationships both among models and with focal studies and the limited variance in fawn:doe explained by either model set may reflect the inability of variables used in the modeling effort to reflect the response of pronghorn to a heterogeneous environment; alternatively pronghorn population process may occur at the fine scale and productivity as assessed at the scale of the herd unit may reflect a summation of numerous independent population dynamics.

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Key Words: *Antilocapra americana,* growing season, habitat characteristics, precipitation, productivity, pronghorn, Wyoming

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Introduction

Most efforts to understand population processes focus on intense studies of local populations (Bomar 2000). Results from these local populations are then extrapolated across landscapes and occasionally synthesized with other studies to frame concepts of population regulation. Fine scale studies of pronghorn (*Antilocapra americana*) have yielded several complementary and competing hypotheses regarding the mechanisms that regulate populations. Disease (Beale and Smith 1973, Trainer et al. 1983, Dunbar et al. 1999), trace mineral deficiencies (Bodie and O'Gara 1980, Stoszek 1980), severe winter weather (Martinka 1967, Barrett 1982), predation (Smith et al. 1986, O'Gara and Malcolm 1988, Willis 1988, Canon 1993, Byers 1997, O'Gara and Shaw 2004) and nutrition (Hess 1999, Kohlman et al. 1999, Aoude and Danvir 2004, O'Gara and Shaw 2004) have all been shown to contribute to population processes at fine scales. Under typical environmental conditions, adult pronghorn have high survival and pregnancy rates (Byers 1997). For this reason, much of the research on pronghorn population dynamics has focused on fawn survival as a population parameter sensitive to environmental conditions (Eberhart 1977) and important for the persistence of populations.

The incidence of disease can be an important component in the regulation of wildlife populations; however, with low rates of disease reported from pronghorn populations, it is unlikely that pathogens contribute strongly to broad scale processes (O'Gara 2004*a*). Assessing the prevalence of disease in fawns of Hart Mountain National Antelope Refuge, Oregon concurrent with a population decline, Dunbar et al. (1999) found 2% of marked fawns died as a result of pasteurellosis. Other studies have identified similarly low rates of fawn mortality attributable to disease (Beale and Smith 1973 [5% disease related mortality], Trainer et al. 1983 [2% disease related mortality]).

Trace element deficiencies have also been implicated in poor fawn survival in a limited number of studies (Bodie and O'Gara 1980, Stoszek 1980). A subset of radio-marked fawns in the Pahsimeroi Valley, Idaho demonstrated symptoms consistent with those of weak calf syndrome, a condition documented in domestic livestock. Associated symptoms include: hemorrhages, edema, atrophic thymus gland, enlarged lymph nodes, and susceptibility to secondary bacterial enteritis (Bodie and O'Gara 1980). These symptoms were accompanied in pronghorn fawns by pathologically low levels of selenium (Stoszek 1980). While selenium deficiencies may be important within the Idaho batholith (Robbins 1993, Bomar 2000) or other local habitats, trace mineral deficiencies are an issue of habitat suitability and are unlikely to play a major role in regulating pronghorn populations throughout their range.

Because of their sensitivity to snow accumulations, pronghorn populations are susceptible to catastrophic losses during severe winters. High snow accumulations and below normal temperatures can result in population losses in excess of 60%, as deep snows restrict access to winter forage causing individuals to perish from starvation (Martinka 1967 and Barrett 1982). Poor recruitment often follows severe winters because of high rates of fetal absorption and the poor condition in which females leave the winter range (Barrett 1982). In severe winter conditions, access to food resources becomes limited as a function of snow depth rather than through a density dependent mechanism such as intraspecific competition. Therefore, while extreme winter conditions may result in catastrophic losses, such a mortality factor driven by environmental stochasticity rather than density dependence will not serve in a regulatory capacity for population abundance.

Predation is frequently implicated in heavy losses of pronghorn fawns. Predation was the proximate cause of mortality for ≥ 54% of radio marked fawns from O'Gara and Shaw's (2004) summary of 18 neonatal telemetry studies representing 995 fawns. The importance of predation in pronghorn populations is corroborated by the positive population responses elicited following predator control (Smith et al. 1986, O'Gara and Malcolm 1988, Willis 1988, Canon 1993, Byers 1997). While fawn predation is an important driving factor in population dynamics, the effects of predation can vary greatly both spatially and temporally. Coyote densities can vary across fine spatial scales with dramatically different impacts on local pronghorn populations (Trainer et al. 1983). Additionally, the impact of a constant coyote population may vary from one year to the next with the abundance of alternative prey items (Hamlin et al. 1984). Spatial and temporal variability in the intensities of coyote predation prohibits using coyote densities to guide broad scale management action.

While fine scale studies have identified factors influential in local pronghorn population response, application of these factors to broad temporal and spatial scales has limited utility. Alternatively, density dependent forage-limitation has been hypothesized to regulate pronghorn populations (Aoude and Danvir 2004, O'Gara and Shaw 2004) and may function to unify many of these fine scale processes. Further, environmental variables that influence nutrition such as climatic conditions, soil composition, and vegetation characteristics, may function on broader spatial and temporal scales. Auode and Danvir (2004), working in the shrubsteppe habitats of Utah, suggested summer forage quality was the limiting mechanism for pronghorn populations operating in a density dependent manner. Corroborative evidence for density dependent regulation is provided by declines in fawn:doe ratios with increasing population size as documented in this Utah population (Auode and Danvir 2004) and throughout Arizona (O'Gara and Shaw 2004). While predation is undoubtedly an important mortality factor, susceptibility to predation may be a function of an environmental cascade driven by nutrition. The nutritional condition of gravid females as they enter the winter affects both the gestation length and birth weight of the ensuing fawn crop; gestation length increased and birth weight decreased from wet to dry years (Byers and Hogg 1995). Relating these observations to population processes, heavier fawns at birth had a greater probability of survival to weaning (Fairbanks 1993). Similarly, fawns born during the peak fawning period realized higher survival rates to weaning (Gregg et al. 2001). Therefore, poor nutritional condition, which prolongs gestation, may perturb birth synchrony and lead to increased predation risk (Berger 1992, Berger and Cain 1999). Nutritional condition likely continues to influence fawn survival after birth. The response of fawn growth to a range of both natural and artificial levels of energy and protein intake suggests nutrition rather than physiology constrains the rate of development (Martin and Parker 1997). Poor forage quality may depress milk production of lactating does thereby reducing fawn growth rates and prolonging the period in which fawns remain vulnerable to terrestrial predators (Martin and Parker 1997).

If pronghorn population dynamics are regulated by density dependent factors associated with nutrition rather than localized predation levels or stochastic factors such as winter severity, then broad scale patterns should link habitat quality with population productivity. Our objective was to evaluate the response of population productivity to nutritionally-focused habitat variables at broad scales appropriate for management. At the scale of the herd unit, our goals were to evaluate the relationship between population productivity as assessed through fawn:doe ratios and 1) temporally variable habitat characteristics and 2) stable habitat characteristics that differed among herd units.

Study Area

This study spanned the state of Wyoming, encompassing the 44 pronghorn herd units defined by the Wyoming Game and Fish Department (WGFD). The study area excluded populations within Yellowstone and Grand Teton National Parks as management is out of the jurisdiction of WGFD. Within delineated herd units, managers subjectively classified habitat as unsuitable, crucial, spring/summer/fall, winter, winter/yearlong, and yearlong. Our spatial analysis excluded habitats classified as unsuitable habitat. Annual average precipitation (1980-1997) within herd units ranged from 25.2 cm to 72.1 cm with precipitation generally increasing with elevation (Thornton et al. 1997). Irrigated and dryland agriculture (7%) was scattered throughout the state with concentrations in the southeast (Wyoming GAP Analysis 1996).

Methods

Data acquisition

We evaluated fawn:doe ratios as our measure of population productivity relative to spatially and temporally explicit habitat variables. Fawn:doe ratios represent the additive effect of both fecundity and survival; however, pregnancy rates have been shown to be uniformly high across pronghorn populations (O'Gara 2004*b*). Therefore, differences observed in population productivity likely emphasize differences in fawn survival. Preharvest fawn:doe ratios were collected through aerial and ground surveys conducted in late summer by WGFD as part of routine population monitoring from 1978 to 2003. The relationship between fawn:doe ratios and habitat characteristics were assessed through 2 unique model sets intended to identify: 1) the response of fawn:doe ratios to annually varying habitat characteristics and 2) habitat conditions that contribute to inherent differences in population productivity among herd units.

Models evaluating annual fawn:doe ratios (1979-2003) were composed of the temporally dynamic variables: previous year's fall precipitation (fall [August-November]), previous winter's precipitation (winter [December-February]), growing season precipitation (grow [March-July]), previous year's growing season precipitation [grow(-1)], population growth potential (potential), previous year's growth potential [potential(-1)], and the z-score transformation of the previous year's total harvest (harvest). To estimate herd unit precipitation, we constructed a weighted average based on the inverse of distance from the herd unit centroid to the 5 nearest weather stations (National Oceanic and Atmospheric Administration, Western Regional Climate Center). Additional weather stations were incorporated when data from the nearest 5 were inadequate. Months with > 5 missing days of precipitation data were eliminated from weighted averages. Growth potential was defined as: (average population estimate - current population estimate)/(average population estimate). Population estimates were derived from a combination of line transect population estimates and population modeling conducted by WGFD (Reeve et al. 2003). Total harvest values were those published by WGFD (Reeve et al. 2003).

Averaging all available fawn:doe ratios from 1978-2003 for each herd unit, we evaluated herd unit productivity relative to the spatially explicit habitat characteristics: average fall precipitation [fall (August –November 1980-1997)], average winter precipitation [winter (December-February 1980-1997)], average growing season precipitation [grow (March-July 1980-1997)], range production [production], per capita range production [forage], and the proportion of the herd unit not delineated as yearlong habitat [habitat]. Precipitation data were obtained at a resolution of 1 km^2 from Thornton et al. (1997). Using STATSGO data (http://www.ncgc.nrcs.usda.gov), we characterized annual potential production of range forage (lbs/acre) based on the composition of soil types assuming normal precipitation. To represent forage availability to the individual, we divided range productivity by the average density of pronghorn over the study period. To express potential benefits of seasonal migration, our final variable considered the proportion of the herd unit delineated by game managers as not "yearlong" habitat.

Analysis

We used regression models to assess the response of population productivity to annual variation in precipitation and population densities. To isolate the response of population productivity to annual variation in habitat quality from inherent differences in recruitment potential among herd units, we used z-score transformations of annual fawn:doe ratios by herd unit as our response variable. For instance, we subtracted the mean fawn:doe ratio (1978-2003) for herd unit 202 from the observed 1979 ratio for this herd unit, and then divided the difference by the standard deviation of fawn:doe ratios for herd unit 202. We used an information theoretic approach applying Akaike's Information Criterion (AIC) to evaluate a fully-parameterized, main-effects model, and 7 reduced models. The predictor variable 'potential' is based on the current year's population abundance, and given the limited capacity for abundance to change over successive years, 'potential' will be strongly autocorrelated with the variable 'potential(-1),' which is based on the previous year's population abundance. For this reason, we did not simultaneous include both measures of growth potential in either our global or reduced models.

To assess the influence of stable habitat characteristics on population productivity, we used linear regression (PROC REG, SAS 1999) to relate spatially explicit habitat characteristics to fawn:doe ratios averaged over the study period (1978-2003). Prior to model construction, we used the variance inflation factor to screen variables for collinearity. Because of the high collinearity of the fall precipitation variable with growing season and winter precipitation, we eliminated it from the fully parameterized model. We used AIC to evaluate the fully parameterized model, 4 reduced models, and a null model.

Table 1. Models of fawn:doe ratios z-score transformed by herd unit evaluated with linear regression to assess the influence of the temporally variable habitat characteristics: fall precipitation (fall), winter precipitation (winter), growing season precipitation (grow), previous year's growing season precipitation [grow(-1)], population growth potential (potential), previous year's population growth potential [potential(-1)], and previous falls z-score transformation of total harvest [harvest(z)]. The response of 1080 estimates of fawn:doe ratios collected from the 44 pronghorn herd units throughout the state of Wyoming between 1979 and 2003 were used in the analysis.

Models	Variables	AIC	ΔAIC	R-square
Model 1	Fall, Winter, Grow, Grow(-1), Potential(-1)	-222.70	0.00	0.11
Model 2	Fall, Grow(-1), Potential(-1)	-205.88	16.82	0.10
Model 3	Potential(-1)	-199.55	23.15	0.09
Model 4	Fall, Winter, Grow, Grow(-1), Potential	-138.92	83.78	0.04
Model 5	Fall, Grow, Potential	-137.71	84.99	0.04
Model 6	Fall, Winter, Grow, Grow(-1), Potential, Harvest(z)	-136.94	85.76	0.04
Model 7	Fall, Winter, Grow, Grow(-1)	-131.40	91.30	0.03
Model 8	Potential	-111.07	111.63	0.01

Results

For the temporally variable models, 1,080 observed fawn:doe ratios were available from 25 years of surveys across 44 herd units. Evaluation of competing models with an information theoretic approach identified the model incorporating the variables fall, winter, grow, grow(-1), potential(-1) (Model 1) as the AIC best model (Tables 1, 2). This model explained 11% of the variation in the data (Table 1). The ΔAIC score for the next competing model was > 16, indicating there was little support for alternative models. From this best model, the time-lagged potential growth variable was the strongest variable with a predicted increase of approximately 0.27 fawns per does (magnitude of z-score affect across range of predictor values = 1.72; Table 2) from the lowest to the highest growth potential (Table 2). Fawn:doe ratios were positively associated with fall precipitation (magnitude = 0.88, ≈ 0.14 fawns:doe; Table 2), with a weak positive relationship to the time-lagged growing season precipitation (magnitude = 0.16, ≈ 0.02 fawn:doe; Table 2). Winter precipitation was negatively related with fawn:doe ratios (magnitude = -0.45, ≈ -0.07 fawn:doe; Table 2) as was growing season precipitation (magnitude = -0.73, ≈ -0.11 fawn:doe; Table 2).

From the analysis of spatially explicit landscape characteristics, averaged fawn:doe ratios from the 44 herd units were normally distributed (Shapiro-Wilk W = 0.96, P = 0.14, skewness = -0.07). The average ratio was 0.68 fawns per doe (SD = 0.13) with a range from 0.44 to 0.88 fawns per doe. The model including the variables fall precipitation and growing season precipitation was the AIC best model (Model 1, Table 3). The ΔAIC scores from the 2 univariate models evaluated (range production and habitat) indicated that these models should be considered competitive models (Table 3). Model 1 identified a negative relationship between fawn:doe ratios and fall precipitation with predicted fawn:doe ratios decreasing 0.31 fawns per doe from the wettest to driest herd units (Table 4). The second variable, growing season

Table 2. Parameter estimates and the associated magnitude of response for the best regression model relating z-score transformed fawn:doe ratios to annually varying habitat variables. Variables included in the model were fall precipitation (fall), winter precipitation (winter), growing season precipitation (grow), growing season precipitation from the previous year [grow(-1)], and population growth potential from the previous year [potential(-1)]. Magnitude is expressed as the estimated response of z-score transformed fawn:doe ratios to the range of values encountered for a given predictor variable. Z-score magnitudes have been transcribed to represent approximate fawn:doe ratios by evaluating the range of predictor variables against a theoretical herd unit with an average range of variation (standard deviation).

Model	Regression Equation
Model 1	fawn:doe ratio = -0.00526 + 0.0942*fall - 0.107*winter - 0.0463*grow + 0.0101*grow(-1) + 0.803*potential(-1)

Variable	Magnitude of Effects (z-score)	Approximate fawn:doe
fall	0.88	0.27
winter	-0.45	0.14
grow	-0.73	-0.11
grow(-1)	0.16	-0.07
potential(-1)	1.72	0.02

precipitation, was positively related with fawn:doe ratios although the effects were not as strong as fall precipitation (0.16 fawn:doe; Table 4). In the range productivity model (model 3; Table 3), population productivity was positively related with range productivity, as herd units with the most productive rangelands were predicted to produce 0.13 greater fawns per doe than the least productive herd units (Table 4). The habitat model (Model 2; Table 3) identified a positive relationship with the proportion of habitat designated as yearlong habitat, such that herd units composed of 100% yearlong habitat were predicted to have 0.11 greater fawns per doe than those herd units with no yearlong habitat (Table 4).

Discussion

Evaluation of temporally varying habitat characteristics identified a model inclusive of variables related to forage availability and carrying capacity. The positive associations between fawn:doe ratios and both the previous growing season precipitation and fall precipitation highlights the importance of female pre-winter condition on fawn survival (Byers and Hogg 1995, Danvir 2000). Summer and fall forage conditions are important for determining the status of females as they enter the winter season during which much of gestation occurs (Robbins 1993). The positive relationships identified between population productivity and precipitation are likely caused by the effects of summer and fall rains to delay the seasonal decline in protein and energy of forage items (Smith and Malechek 1974) or induce a fall green-up of seasonally important grasses (Pyrah 1987). Similarly, Byers and Hogg (1995) identified a relationship between fall precipitation (July-October) and birth weight of the ensuing fawn crop and associated gestation length, 2 measures sensitive to available energy with impacts on fawn survival (Fairbanks 1993, Gregg et al 2001).

Our model identified a negative relationship associated with winter precipitation and fawn:doe ratios. Winter precipitation may be closely tied with spring forb abundance (Smith and Lecount 1979) which is important to meet the protein and energy demands of late gestation. The benefits of increased forage following a wet winter appear to be offset in the high plains habitats of Wyoming by the energetic stresses and mobility limitation associated with snow accumulations. Deep snows limit access to winter forage resources and severe winter conditions

Table 3. Competing regression models to predict average pronghorn fawn:doe ratios from the 44 herd units encompassing Wyoming. Habitat variables included in the models were average fall precipitation (fall), average winter precipitation (winter), average growing season precipitation (grow), range production based on soil type (production), range production expressed on a per capita basis (forage), and the proportion of habitat designated as not yearlong habitat (habitat).

Models	Variables	AIC	ΔAIC	*R-Square*
Model 1	Fall, Grow	-183.89	0.00	0.15
Model 2	Habitat	-183.31	0.58	0.10
Model 3	Production	-182.06	1.83	0.07
Null		-180.75	3.13	0.00
Model 4	Winter, Grow, Production, Forage, Habitat	-179.47	4.42	0.27
Model 5	Forage	-178.98	4.90	0.01

may cause catastrophic population losses and high rates of fetal absorption (Martinka 1967, Barrett 1982).

Growing season precipitation was negatively related to fawn:doe ratios in our selected model and throughout all models evaluated. Given the positive relationship identified between population productivity and forb abundance (Auode and Danvir 2004), we expected herd units to respond positively to increasing levels of growing season precipitation due to the link between forb biomass and precipitation. While wetter springs may translate to greater forb abundance in the summer, small-bodied fawns on the open plains are susceptible to death by exposure within the first weeks of life in cold, wet environments (Ellis 1970). Additionally, with the majority of fawn mortality occurring during the first 3 weeks of life (Beale and Smith 1973, Bodie and O'Gara 1980, Trainer et al. 1983, Barrett 1984, Dunbar et al. 1999) much of the season's fawn mortality may occur before the potential benefits of growing season precipitation have emerged.

Finally, the strongest variable in our model was the time-lagged growth potential variable. The strength of both growth potential variables in all evaluated models indicated that pronghorn populations responded in a density dependent manner. The strength of models inclusive of the time-lagged growth potential variable relative to the current growth potential variable (Table 1) suggested that conditions prior to conception and through gestation had a stronger influence on fawn survival than pronghorn abundance at birth. If females are able to manipulate their reproductive energy output in response to population levels, conceivably they would cue to the previous year's population level. Alternatively, some of the benefits of abundant resources in a population below carrying capacity may be offset by the benefits of predator swamping in a higher density population (Linnell 1995).

Evaluation of spatially explicit variables yielded a model similarly incorporating precipitation variables although the trends were different than those observed in the temporally dynamic analysis. Fall precipitation was the most influential variable in the selected model with fawn:doe ratios decreasing with increasing precipitation levels. This outcome was surprising given the positive association demonstrated in the annual variation analysis and conclusions drawn from studies of focal populations (Byers and Hogg 1995, Danvir 2000). The negative relationship may be a limitation of our seasonal delineations of precipitation as late fall

Table 4. Parameter estimates and magnitude of effects associated with the 3 competing regression models used to predict the average pronghorn fawn:doe ratios from the 44 herd units in Wyoming. Models were composed of the variables: average fall precipitation (fall), average growing season precipitation (grow), range production based on soil type (production), and the proportion of habitat designated as not yearlong habitat (habitat). Magnitude is expressed as the estimated response of fawn:doe ratios to the range of values encountered for a given predictor variable.

Model	Regression Equation	Magnitude	
Model 1	fd = 0.734 - 0.022*fall + 0.00942*grow	fall = -0.309	grow = 0.162
Model 2	fd = 0.538 + 0.000137*production	production = 0.135	
Model 3	fd = 0.742 - 0.105*habitat	habitat = -0.105	

precipitation may come in the form of snow. Alternatively, fall precipitation may be correlated with some other habitat gradient not incorporated in this analysis. Growing season precipitation was positively associated with fawn:doe ratios. While this trend is opposite of that identified in the annual variation analysis, the outcome falls in accord with our predictions given the positive associations between precipitation, forb abundance, and population productivity.

Two univariate models were identified as competitive models. The first identified a positive relationship between fawn:doe ratios and forage biomass production based on soil conditions in a "normal precipitation year." This variable showed a close positive correlation with growing season precipitation, supporting the connection among precipitation, forb abundance, and population productivity. Further the strength of this model supports the hypothesis of nutritional limitation regulating population dynamics.

The second univariate model identified a positive relationship between the proportion of habitat in a herd unit classified as yearlong habitat and population productivity. Seasonal migrations (Hoskinson and Tester 1980, Berger et al. 2004) may allow populations to utilize seasonably unsuitable habitats that provide more abundant forage resources during times of suitability. For example, snow accumulations may force pronghorn to vacate some habitats, but subsequent snow melt contributes to increased forb abundance through the spring and summer months. Similarly, dense sagebrush may form in habitats too dry to support populations through the fawning season although such areas may provide crucial access to forage through the winter. Based on this rational, we predicted that pronghorn populations which are able to exploit seasonably unsuitable habitats may realize higher levels of forage abundance with a corresponding increase in population productivity. The opposite trend was observed in the data as herd units with higher proportions of yearlong habitats were more productive than herd units dependent upon seasonal habitats. The lower productivity associated with those herd units with reduced amounts of yearlong habitat may reflect the costs associated with migration. Alternatively, there is a general cline in yearlong habitats across the state of Wyoming, with the highest proportions in the northeast declining to the southwest. The positive association along this gradient of yearlong habitats may reflect the response to some other environmental cline.

Both the analysis of temporally dynamic habitat characteristics and the analysis of spatially explicit characteristics failed to identify strong relationships between habitat conditions and population productivity. The strength of the identified relationships may be limited by a number of factors pervasive throughout our analyses. First, fawn:doe ratios are inherently variable, susceptible to fluctuations in the age distribution of the female population. A strong fawn crop in year 1 may depress fawn:doe ratios in year 2 because of the low reproductive potential of yearlings, even if conditions remain ideal (O'Gara 2004*b*). Additionally, large-bodied ungulates integrate environmental variables over a long period of time (Picton 1984). Population productivity may therefore reflect the interaction of habitat characteristics over the past several years rather than an immediate response to current conditions. Second, variables used in the modeling exercise may fail to accurately characterize the response of pronghorn to landscape conditions. For example, characterizing herd unit precipitation through a weighted average of adjacent weather stations may fail to accurately capture the response of landscapes to variation in precipitation or the importance of spatial and temporal variability in precipitation. The challenges associated with simplifying landscapes to single values are exacerbated by a third factor, the habitat selection capabilities of pronghorn. Selection within a heterogeneous landscape further decreases the connection between habitat conditions assessed at the scale of the herd unit and the way in which habitat conditions are perceived by the individual. For example, highly mobile pronghorn are capable of responding to localized weather events or selecting habitats that are more mesic because of soil conditions or elevation in an otherwise dry landscape. Finally, population processes may indeed occur at a finer scale than the herd unit. Populations may function independently across the landscape, responding uniquely to local conditions. Population productivity at the scale of the herd unit would then simply be the sum of these independent population processes. It is likely that a combination of these factors limited the strength of the relationships between population productivity and environmental conditions.

Conclusions

While we failed to identify a model capable of strongly predicting population productivity, our models highlight the positive relationship between range productivity and population response. Our assessment of annually varying habitat characteristics identified a model incorporating variables that depict the condition in which females enter the winter. Further, the strength of both the time-lagged and current growth potential variables indicated that pronghorn populations are under some form of density dependent regulation.

Distilling landscape heterogeneity for the purposes of regression analysis necessitates an oversimplification of natural processes. The strength of our models likely would be improved had this averaging process reflected habitat use rather than habitat availability. Continued incorporation of biological data into competing models will allow managers to better understand biological processes.

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Influences of Vegetation on Pronghorn in the Intermountain West

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Abstract*:* Pronghorn natality and mortality factors have been studied at different sites and times in the Intermountain West. Various natural and human-caused agents affect pronghorn numbers. Of these, 3 appear to have a major impact: weather, neonate predation and vegetation/nutrition. The later has received the least amount of investigation. Vegetative conditions may affect neonate security and habitat productivity in the form of available forage. Knowledge of accurate forage utility is mostly lacking for pronghorn welfare for grasses/forbs/shrubs. In addition, assessment of preferred forage species availability for all seasons of the year needs to be addressed. Managers have recognized the value of shrubs as "survival plants" during severe winters and droughts. Recently the concept has been accepted that certain herbs are "production plants" needed during pregnancy and lactation-- these are predominately forbs. Consequently, diverse and abundant forbs are a key to fawn recruitment and they appear to be one of the most significant factors influencing herd production over long periods. Two basic management principles are involved: effective foraging control of wild and domestic ungulates, and sustaining vegetation in quality condition. An assessment of more than 40 investigations over 60 years indicates that pronghorn density is often regulated by vegetation conditions. Management strategies resulting in favorable vegetation have demonstrated that increases are possible for wild, free-roaming herds in the Intermountain West.

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Key Words *Antilocapra americana,* ecological carrying capacity, forage nutrition, Intermountain West, mortality, natality, pronghorn/vegetation relationships, sagebrush-grasslands, shrubsteppes, vegetative condition/trend.

Healthy pronghorn populations are dependent on vegetation in quality condition (Ellis 1970, Salwasser 1980, O'Gara and Yoakum 2004, and Autenrieth et al. 2006). Plant communities provide security cover for neonates from enemies, and nutrition for adult populations (Yoakum 2004*b*). Population densities are related to the quality and quantity of grasses/forbs/shrubs for various ecosystems (Ellis 1970). Highest herd densities are found in grasslands, followed by shrubsteppes, and the lowest are in deserts (Yoakum 1972, 2004*b*). Information for this report is limited to the Intermountain West--that wide open shrubsteppe and grassland between the Rocky Mountains and the Sierra Nevada Mountains north of the Mojave Desert.

During the early 1950s, mortality factors affecting pronghorn were studied under Arthur S. Einarsen in California, Nevada and Oregon (Hansen 1955, Yoakum 1957, Compton 1958). Similar studies were reported in California (Ackerly and Regier 1956, Hall 1965), Idaho (Folker 1956, Fichter 1962), Nevada (Foree 1960), and Utah (Hinman 1959, Beale and Smith 1966). The major issues for studies under Einarsen were (1) low pronghorn densities, and (2) low recruitment rates. After 5 years of studies, it was obvious that fawn production and survival were influenced by multiple factors: e.g., disease, predation, climate patterns, natural accidents, collisions with trains and vehicles, fences, and others. However, investigators were unable to determine what factor(s) was/were responsible for limiting herd sizes. Note that investigations did not include nutrition or ecological carrying capacities. Today, wildlife managers ask the same questions as to why herd sizes and fawn recruitment ratios are chronically low--especially relative to management programs such as herd translocation, predator control practices, and harvest increases.

Decades passed since the mid-1900 investigations and additional studies on this topic have been accomplished: California (Ellis 1970, Hall et al. 2000), Idaho (Autenrieth 1980, 1984, Bodie 1978), Nevada (Meeker 1979, McNay 1980), Oregon (Good 1977, Herrig and Vohs 1972, Kindschy et al. 1982, Dunbar 1999, 2001), and Utah (Beale 1978, Beale and Smith 1970, 1973, 1980), and others. These later studies investigated causes of productivity and mortality, and reported many similar welfare agents as identified in the 1950-60 investigations; however, they also brought into focus the impacts of habitat disturbances and vegetative condition/trend information. Of the myriad mortality agents identified during >40 survival investigations, 3 were limiting factors: climate patterns, predation on neonates, and forage nutrition (Hansen et al. 2001, Aoude and Danvir 2002, and Yoakum et al. 2004). While reviewing the above investigations and others, I assessed these studies with an objective of identifying the influences of changing vegetation conditions to changing pronghorn population trends. This resulted in the following findings and conclusions.

Ecological Processes, Relationships and Management

Pronghorn population dynamics relative to ecological processes are based on various biological concepts identified by Leopold (1933) and Dasmann (1964). Essentially, wildlife and their numbers are a product of various habitat characteristics--vegetation being a dominant feature for ungulates.

For pronghorn, the following ecological parameters have been identified (Ellis 1970, Kindschy et al. 1982, Yoakum 2004*b*, 2004*c*).

Habitat Characteristics. Each site has multiple biotic and abiotic characteristics. Vegetation is one and is a dominant factor that provides forage, water and cover. Vegetation is a product of soils and weather. It often changes in composition and mass production because of various natural and human-caused disturbances. Grasslands and shrublands can change dramatically over time due to disturbances and plant succession (Kindschy et al. 1982).

Habitat Requirements. Habitat requirements are the biological needs of pronghorn for habitat characteristics. For vegetation, these include composition, diversity, succulence, height (structure) and nutritional forage values. Each to some extent contributes to regulating herd numbers as each effects pronghorn ability to produce and survive. Vegetation is the main source for nutrient and water consumption. Vegetation structure contributes to pronghorn behavior to "see and flee" from enemies. In addition, vegetation provides security cover for neonates. Habitat requirements, including vegetation, for pronghorn in the Great Basin are listed in Yoakum (1974 and 2004*b*).

Interrelations of Habitat Characteristics and Requirements. The interactions of habitat characteristics and habitat requirements for vegetation for pronghorn varies with seasons, site locations and years. In addition to soils, precipitation and temperature control plant species composition and growth, which in turn, affect pronghorn production and survival. As weather patterns change over years, vegetation likewise changes resulting in fluctuating pronghorn numbers.

These are natural ecological processes that have occurred for eons. Recognizing changing ecological parameters helps one understand why pronghorn numbers change over the years. Vegetative communities are dynamic, and affect pronghorn carrying capacities over time (Autenrieth et al. 2006).

Vegetation Dynamics. Vegetative communities are a product of natural processes (i.e. insect damage, climate, plant succession, wildfires, etc.,) and human activities (shrub manipulation, plant seedings, livestock foraging, prescribed fires, etc.). Thus, disturbance processes change vegetation composition slowly over years, or rapidly as after a wildfire or seedings for restoration. These events can be advantageous or disastrous depending on how, when and where accomplished in relation to pronghorn habitat needs. Certain plant community successional stages produce greater diversity and quantity of nutritional plants that are preferred by foraging pronghorn. Such quality plants have been recently linked to pronghorn production and survival (Hansen et al. 2001, Aoude and Danvir 2002).

Management Prescriptions. Habitat management includes conservation and/or protection of quality habitats, and enhancement of abused deteriorated habitats. When properly conducted, management can increase habitat carrying capacity and thus increase herd density. Habitat management is an applied science and needs trained and experienced practitioners. With insidious decreases in quality habitats due to shrub encroachment, noxious plant invasions, and accelerating human demands, traditional pronghorn numbers are decreasing. Consequently, modern management challenges are to save, protect or enhance extant habitats for the perpetuation of reasonable numbers of wild free- roaming pronghorn (Yoakum 2004*c*).

Case Histories of Vegetation Disturbances and Pronghorn Trends

While reviewing the literature, I did not find any research project designed to test the hypothesis that changes in vegetation affected pronghorn numbers. However, >40 case histories (Table l and 2) relative to such interactions were located. A brief review of 7 cases of natural and human-caused habitat perturbances of vegetation resulted in increased or decreased pronghorn numbers follow:

Table 1. Literature pertaining to mortality studies and influences of vegetation conditions relative to pronghorn (PH) populations in the Intermountain West: 1945-2006.

State Site location	Reference citation	Major thrust of investigation	Findings and conclusions
California			
Modoc County	Ackerly & Regier 1956	PH production and mortality investigation	Rangeland vegetation condition poor. Herds static.
Northeast counties	Hall 1965	Effects of insects on sagebrush	Insects kill sagebrush, but for small acreage.
Northeast counties	Ellis 1970	PH/vegetation relations	PH densities affected by climate and plant communities.
Inyo-Mono County	McCarthy & Yoakum 1984	Assessed 5 translocation sites	Habitat rated poor. Release accomplished but

			unsuccessful.
Mono County	Goldsmith 1988	Evaluated translocated herds	Reported on behavior to vegetation types. Also on controlled burns.
Northeast counties	Hall et al. 2000	Compared PH to vegetation communities	High use of moist areas and forbs.
Long Valley	Yoakum 2000	Effects of wildfires on plants and PH	Fires changed plant composition resulting in new PH occupancy.
Idaho			
Owyhee County	Folker 1956	Field study of mortality factors	Unable to determine causes for low recruitment and static herds.
Pahsimeroi Valley	Bodie 1978	Fawning sites and mortality	Fawn success greater in lower height shrubsteppes.
Little Lost Valley	Autenrieth 1984	Fawning sites and mortality	Vegetation height & density of shrubs and herbs related to fawn survival.
Nevada			
Clark County	Yoakum 1978	Evaluation of vegetation and PH transplants	Vegetation not to PH requirements. Transplant failed.
Sheldon National Wildlife Refuge	McNay 1980	Low fawn recruitment and herd numbers	Affected by livestock foraging.
Elko County	Lister 1989	Developed PH plan prior to project to augment herd	Wildfires changed vegetation & PH increased-no transplant needed.
Sheldon National Wildlife Refuge	Gregg 1997	Assessed prescribed burn program	Prescribed burns changed plants favorable to native wildlife needs.
Statewide	Tsukamoto et al. 2003	Management plan for PH	Reports effects of livestock foraging, veg. manipulation projects and fires.
Pony Springs	Yoakum 2004*c*	Evaluated site before and after treatment	Herd use and nonuse changed with plant community changes.
Oregon			
Statewide	Einarsen 1948	Reported on mortality	Coyotes major cause for fawn losses. Noted other factors affecting survival.
Lake County	Hansen 1955	Intensive field investigations of mortality	Noted various causes of mortality for 2 years.
Lake County	Yoakum 1957	Assessed mortality and fawn survival	Noted high densities on sites with greater plant diversity.

Table 1 Continued

Lake County	Deming 1959	Analyzed shrublands and fire	Wildfires naturally changed shrublands to more abundant herbaceous plants.
Hart Mt. National Antelope Refuge	Deming 1964	Evaluated effects of climate and vegetation on PH	Weather related to forage production. Shrubs competed with herbs for production.
Hart Mt. National Antelope Refuge	Reeher 1969	Investigated vegetation in Vale project	Concluded vegetation changes unfavorable for PH.
Hart Mt. National Antelope Refuge	Herrig & Vohs 1972	Use of plant sites used by PH	PH abundant in low veg. communities. Playas heavily used.
Great Basin	Yoakum 1972	Listed habitat requirements for PH	Provided list of biotic and abiotic factors.
Hart Mt. National Antelope Refuge	Good 1977	Use of playas by PH	Varied with plant characteristics. Preferred succulent plants for forage.
Malheur County	Heady & Bartolome 1977	Objectives and results of the Vale project	Provided quantitative data on manipulated vegetation projects.
Malheur County	Kindschy et al. 1982	Rated PH use of habitats and manipulation projects	PH do well in early plant succession. Herds increased after project alterations.
Jackass Mt.	Willis et al. 1988	Reported on vegetation and PH	Identified shrubs as highly important.
Hart Mt. National Antelope Refuge	U.S. Fish & Wildlife 1994	Developed environmental statement and management plan	Reviewed livestock foraging and history of PH on the Refuge.
Hart Mt. National Antelope Refuge	Pyle & Yoakum 1994	Range management changed from livestock use to fire for vegetation	Livestock eliminated. Fires substituted. Forbs increased. Fawn recruitment and herds increased.
Hart Mt. National Antelope Refuge	Gruell 1995	Reviewed extant and historic fire frequencies	Fires have long history of changing plant composition.
Hart Mt. National Antelope Refuge	Gruell 1996	Assessed wildfires to wildlife	Wildfires naturally changed vegetation for native wildlife.
Hart Mt. National Antelope Refuge	Dunbar 1999	Investigated health issues for fawns and adults	Concluded limited problems existed. Did not control herd numbers.
Hart Mt. National Antelope Refuge	Dunbar 2001	Reported on >50 playas used by PH during summer and autumn.	Highest PH densities were on playas than other plant types. Forb use high.

Hart Mt. National Antelope Refuge	Gregg et al. 2001	Correlated fawn losses with mortality	Predation main cause for fawn and herd size.
Hart Mt. National Antelope Refuge	Hansen et al. 2001	Samples collected for 2 years for 5 ungulates	Correlated forage production/ weather/competition.
Hart Mt. National Antelope Refuge	Yoakum et al. 2004	Assessed fawn/predator losses	Predation high but herds increased. Herds controlled by carrying capacity.
Bear Valley	Yoakum 2004*c*	Related PH to changes in vegetation communities	Ranchers manipulated vegetation. PH moved into valley. High fawn recruitment.
Utah			
Deseret Ranch	Aoude & Danvir 2002	Assessed use of natural sites and manipulated vegetation by PH	Herds readily used forb-rich sites, especially altered plant types.
Parker Mountain	Yoakum 2004*a*	Evaluated PH in relation to habitat and management	Plants heavily used by livestock. Forbs/shrubs abundant. Fawn recruitment high and herds increased for >60 years.

Table 2 Continued

Table 2. Literature pertaining to natural and human-caused disturbances of vegetation relative to pronghorn populations in the Intermountain West: 1965-2004.

State Site location	Reference citation	Natural changes[a]			Human-caused changes[a]				
		1	2	3	4	5	6	7	8
California									
Northeast counties	Hall 1965	X	X						
Northeast counties	Ellis 1970	X			X				
Mono/Inyo counties	McCarthy & Yoakum 1984	X			X	X		X	X
Lassen County	Yoakum 2000	X		X		X			X
Idaho									
Little Lost Creek	Autenrieth 1984				X				
Little Lost Creek	McCarty 1982					X	X		X
Oregon									
Lake County	Deming 1959	X		X					
Malheur County	Kindschy et al. 1982	X		X	X	X	X	X	
Hart Mt. National Antelope Refuge	Pyle & Yoakum 1994	X		X	X				X
Hart Mt. National Antelope Refuge	Gruell 1995	X		X				X	
Hart Mt. National Antelope Refuge	Hansen et al. 2001	X			X				
Hart Mt. National Antelope Refuge	Yoakum et al. 2004	X		X	X				X
Bear Valley	Yoakum 2004*c*				X	X		X	
Pony Springs	Yoakum 2000*c*					X		X	
Nevada									
Sheldon National Wildlife Refuge	Gregg 1997								X
Statewide	Tsukamoto et al. 2003			X	X	X		X	
Utah									
Deseret Ranch	Aoude & Danvir 2002	X			X	X		X	X
Parker Mountain	Yoakum 2004*a*				X				

[a] Numbers represent natural and human-caused factors: 1 = weather, 2 = insects, 3 = wildfires; 4 = livestock foraging, 5 = mechanical treatment, 6 = herbicidal treatment, 7 = seeding treatment, 8 = prescribed burn.

Case l: Pony Springs, Nevada. Twenty miles (32 km) north of Pioche, Nevada is an historic pronghorn rangeland named the Pony Springs (Yoakum 2004*c*). It is in the southern part of the Great Basin. From about the later 1800s to the mid-1900s, intensive foraging by cattle and domestic sheep occurred. In the early 1960s, a vegetation survey disclosed plant composition of 16% grasses, 2% forbs and 82% shrubs, with an average shrub height of 32 inches (81 cm). Prior to treatment, pronghorn occupied the valley but not the treatment site. During the late 1960s the U.S. Bureau of Land Management rehabilitated 6,000 acres (2,428 ha) by plowing and seeding the site with a mixture of some 20 species of grasses/forbs/shrubs. Five years following treatment, the plant community was estimated to be 60% grasses, 20% forbs and 20% shrubs with plant height averaging 18 inches (46 cm). Pronghorn moved into the treatment project for foraging and fawning.

After seeding, the vegetation was protected from livestock for 3 years, and then heavily utilized for the next 2 decades. By the early 1990s, the plant community had changed to 36% grasses, 14% forbs and 50% shrubs averaging 22 inches (56 cm) height. Pronghorn ceased using the area. The last vegetative survey in 2004 disclosed 12% grasses, 3% forbs and more than 75% shrubs averaging 31 inches (79 cm)--vegetative characteristics similar to pretreatment. Pronghorn have not been observed on the treatment site for the last 15 years although the species occupies adjacent rangelands.

Case 2: Bear Valley, Oregon. In the 1940s, pronghorn did not occupy Bear Valley north of Burns, Oregon; however, they were permanent residents in nearby valleys (Polenz 1976). Bear Valley is primarily private lands used for cattle ranching. During the 1950-1960s, ranchers manipulated hundreds of acres by plowing dominant shrublands and planting them to a mixture of crested wheatgrass (*Agropyron cristatum*) and dryland alfalfa (*Medicago spp.*) primarily to increase forage for livestock. Thus the ranchers changed the rangeland vegetation from a native, dominant, tall shrub community to an exotic grass/forb structure with islands of native shrubs.

Continued vegetative manipulation during a 25-year period changed plant characteristics from unfavorable to favorable conditions for pronghorn--not by design but by practices. Thus the carrying capacity for livestock and pronghorn were simultaneously enhanced by ranchers (Yoakum 2004*c*).

Soon after treatment and growth of herbaceous plants, small herds of pronghorn pioneered into the Valley for short periods of time, then returned to nearby traditional rangelands. As additional acreage was treated and winters remained mild, pronghorn remained in the valley and became permanent residents. The population expanded to >600 animals within 20 years and experienced some of the highest fawn to doe ratios in Oregon (Torland 1980).

During August 2004, I again surveyed the site. Herbaceous plants averaged around 80% in seedings. Evidently >40 years of moderate foraging by livestock did not greatly decrease grasses and forbs as was experienced at Pony Springs, Nevada. Two pronghorn herds of a dozen each were observed in the seedings.

Case 3: Vale, Oregon. One of the most extensive rehabilitation projects, was conducted during the 1960s by the U.S. Bureau of Land Management, Vale, Oregon, and labeled the Vale Project (Heady and Bartolome 1977). It was primarily designed to increase livestock carrying capacities but included habitat improvements for wildlife. The Vale Project lasted 11 years and encompassed 10,500 square miles (27,350 square kms) of public lands in Malheur County.

Approximately $10 million was spent for 506,000 acres (204,670 ha) of shrub control, 267,000 acres (108,000 ha) of artificial seedings, 200 miles (322 km) of fences, and 600 water developments. Approximately 9% of the county was treated by shrub control and artificial seedings. Crested wheatgrass was the primary grass seeded; however, 26 sites were planted to 10 dryland alfalfa for pronghorn and other wildlife (Kindschy et al. 1982).

Fifteen years late, adjacent untreated sites to the Vale Project averaged 52% grasses, 3% forbs and 45% shrubs with a mean height of 28 inches (71 cm). Plowed and seeded sites had 76% grasses, 11% forbs and 13% shrubs, indicating the restoration of herbaceous plants had been successful (Yoakum 2004*c*). Estimated pronghorn numbers for the project were obtained from the Oregon Department of Fish and Wildlife. Prior to treatment during 1962-64, numbers averaged 1,400. Following vegetation treatment projects (1972-74), the herd increased to >2,600 (Oregon State Game Commission 1962-1974). Herd counts completed in February 2006 totaled >6,400 (Walt Van Dyke, Oregon Department Fish and Wildlife, personal communication).

Case 4:. Long Valley, California/Nevada. Long Valley, in northeastern California and Nevada, is a shrubsteppe ecosystem within the northern Great Basin. Prior to the 1970s, the Valley was dominated by dense, tall, shrubs and an understory of sparse herbaceous plants. During the summer of 1973, a series of wildfires burned approximately 40,000 acres (16,188 ha) of land mainly under U.S. Bureau of Land Management (BLM) administration. Following the burns, favorable sites were seeded to a mixture of grasses, forbs and shrubs (Yoakum 2000).

Long Valley has been historic pronghorn habitat; however, they have been extirpated from the valley. Small herds occupied rangelands to the north and east with no physical or manmade barriers restricting access to the Valley. A group of 6 was first observed during autumn 1975 (Syd Kahre, California Department Fish and Game, personal communication). Within a decade, they were permanent year-long residents and the herd increased to >50 animals (Fred Hall, California Department Fish and Game, personal communication).

The pre-1973 ecosystem contained physiographic and climatic characteristics suitable for pronghorn habitat (Yoakum 1974). However, the prevalence of tall, dense shrubs apparently did not provide preferred pronghorn habitat--probably the reason they did not occupy the area during the previous century. Only 1% of the pre-burn plant community was forbs which are needed to support fawn recruitment.

The influence of the 1973 wildfires on the shrubsteppe was evaluated for its impact on pronghorn habitat quality (Yoakum 2000). A habitat suitability model developed by the U.S. Bureau Land Management (1980) was used to conduct an assessment. Results are provided in Table 3. The rating for unburned sites was "poor", whereas the rating for burned/seeded sites was "good". Apparently, the wildfires followed by artificial seeding changed the vegetation to favor pronghorn habitat requirements (Yoakum 1974). Primary reasons for this change were: (1) decreases in shrub densities and increases in herbaceous plants for forage, and (2) decreases in vegetation height and density, thereby improving the ability of pronghorn to see enemies. Increased

Table 3. Ratings for pronghorn habitat quality in burned/seeded and unburned sites, Long Valley, California and Nevada, based on criteria in the Pronghorn Habitat Suitability Model (U.S. Bureau of Land Management 1980).

Parameter	*Unburned ratings*	*Burned/seeded ratings*
Vegetation quality:		
Forbs	2	15
Grasses	5	5
Shrubs	3	5
Vegetation height	5	10
Vegetation density:		
Forbs	6	12
Grasses	4	8
Shrubs	4	6
Water availability	10	10
Water quality	10	10
Limiting factors	-20	-20
Total	29	61
Overall rating	Poor	Good

Source: Yoakum 2000

forb production may have contributed to favorable fawn recruitment by providing needed quality nutrition during pregnancy and lactation as noted previously for herds elsewhere in the Great Basin (Ellis 1970). Plant composition was checked in 2005 and remains similar although shrubs have increased some 5 percent. Pronghorn continue to occupy the site and have provided hunting opportunities for the harvest of adult bucks.

Parker Mountain, Utah Pronghorn on the Parker Mountain area in central Utah were investigated and assessed for trends (Yoakum 2004*a*). The site includes land administered by the U.S. Forest Service and the U.S. Bureau Land Management as well as state school lands and private owned ranches. Currently, vegetation was largely a buffalo grass (*Buchloe dactyloides*) type rated in fair to poor ecological condition due to intensive foraging by cattle and domestic sheep for >100 years. Buffalo grasslands often contain >75% grasses, however, the current site plant composition was estimated at 20% grasses, 20% forbs and 60% shrubs--ideal forage percentages for pronghorn in the Intermountain West. Plant height averaged 15 inches (38 cm)--again ideal for pronghorn habitat.

Pronghorn were native to the area but were decimated by hunting during the late 1800s. Forty years ago, the area received a translocation of some 50 pronghorn, and now the herd is >3,000. More than 10,000 adult pronghorn have been removed via sport hunting and translocation over the last 4 decades. The herd averaged 80 fawns per 100 does for 4 decades--one of the highest long-term ratios recorded for the Intermountain West. The area is a "pronghorn factory" due in part to ideal forage class composition and availability, plus structure height. These vegetation characteristics appear to be the result of intensive livestock foraging in past and current years that have changed the dominant buffalo grassland to abundant shrubs with near equal quantities of forbs and grasses. Intensive long-term domestic ungulate foraging appears to have changed the plant community to favor pronghorn habitat requirements.

Deseret Ranch, Utah. A relatively closed pronghorn herd occupies the Deseret Ranch of predominantly private land in northeastern Utah. The Ranch maintains healthy vegetation conditions and abundant drinking water sources for pronghorn, mule deer (*Odocoileus hemionus*), elk (*Cervus elaphus*), moose (*Alces alces*), cattle and domestic sheep. Numbers for both wild and domestic ungulates were maintained below carrying capacity (Aoude and Danvir 2002).

Through natural dispersal and a series of mild winters in the mid-1980s a herd of around 90 pronghorn was established on the Ranch. It has increased to >740 by 2002. Equal numbers of bucks and does are harvested annually. Average recruitment ratios are 40 fawns per 100 does (Aoude and Danvir 2002).

Based on observations during the early 1990s, wildlife biologists speculated that forb-poor habitat and tall (>61 cm), 14 dense shrublands (>25%) reduced pronghorn habitat quality, thereby limiting fawn recruitment and population size. To test this hypothesis, forb abundance and shrub structure on 18 burned or seeded sites totaling 10,550 ac (4270 ha) from 1995 to 2001 were investigated by Aoude and Danvir (2002). The authors concluded: "Both fawn production and population size correlated positively with cumulative hectares treated (r =0.81, p=0.005 and r =0.65, p=0.03 respectively). While pretreatment fawn production correlated negatively with population size (r =0.89, p=0.0001), suggesting density dependent production, fawn production correlated positively with population size post-treatment (r =0.70, p=0.04) suggesting increased habitat quality and carrying capacity. Burned or planted areas were the only habitat types used preferentially by doe groups post-treatment" (Aoude and Danvir 2002:124).

Aoude and Danvir (2004:132) further stated "Our data support the hypothesis that sagebrush steppe communities dominated by dense, decadent sagebrush or crested wheatgrass lack adequate nutritional resources to maintain high pronghorn densities and fawn production. Sagebrush steppe communities lacking periodic disturbance to create early-mid seral forbs may also lack reproductive nutrition for species such as sage grouse and mule deer (*Odocoileus hemionus)*. Our experience thus far suggest grazing strategies based on intermittent herbivory and rest (Augustine and McNaughton 1998) coupled with occasional shrub thinning and (if necessary) planting desirable forbs can benefit pronghorn and other species. Since mature sagebrush stands also provide cover and winter forage for pronghorn and many other sagebrush-dwelling wildlife species, the interspersion, arrangement and connectivity of sagebrush patches must be considered when manipulating landscapes. Results of this experiment suggest treating as little as 2% of the range/year increased pronghorn production and carrying capacity."

Hart Mountain National Antelope Refuge, Oregon. Pronghorn population and ecological data are available from the Hart Mountain National Antelope Refuge (HMNAR) for >50 years (U.S. Fish and Wildlife Service 1994). Herd numbers have fluctuated from lows of <300 in the 1950s to highs of >2,400 in the 2000s (Figure 1). There have been decades with and without predator control programs. Weather data are available for the past 60 years. Permitted and feral livestock numbers have been recorded since 1936. Over the years, numerous studies of various durations were conducted on pronghorn, other wildlife, and habitat conditions (Table 1).

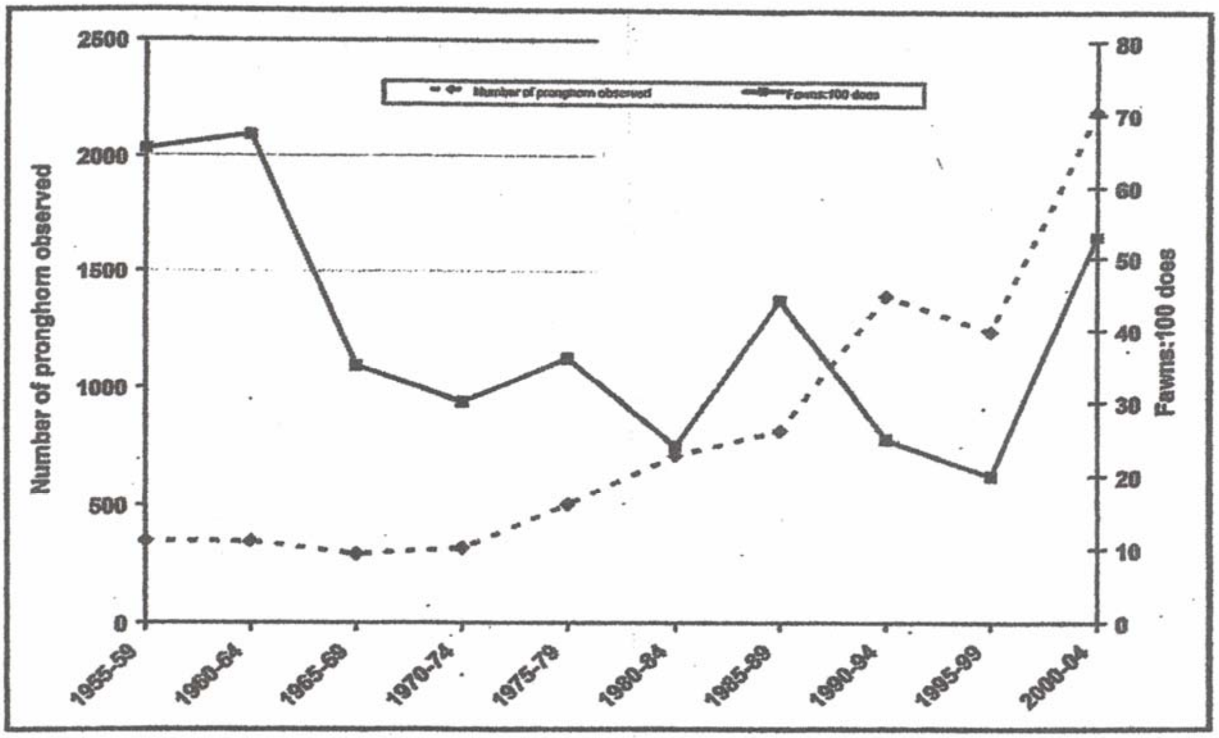

Figure 1. Number of pronghorn and fawn:doe ratios in 5-year increments during summer surveys from 1955 to 2004, Hart Mountain NAR. Predator control practices were conducted from 1955 to 1968, but not thereafter. (Source: U.S. Fish and Wildlife Service 1994, Yoakum)

An environmental impact statement (EIS) was developed during the early 1990s that estimated >90 percent of shrublands were in late succession, and riparian sites and meadows were seriously deteriorated; these areas were not considered quality habitats for pronghorn (U.S. Fish and Wildlife Service 1994). Because long-term poor ecological condition of vegetation noted in the EIS, livestock foraging was terminated, feral horses were eliminated and a new fire management program was incorporated. Prescribed burns were conducted to simulate natural disturbances increasing early- and mid-succession vegetation stages that are favorable to pronghorn and other wildlife (Pyle and Yoakum 1994).

A product of the Refuge EIS was a comprehensive food habit study for pronghorn, mule deer, bighorn sheep (*Ovis canadensis*), and feral horses from 1993 to 1996 (Hansen et al. 2001). Fortunately the study experienced back-to-back years of above and below average precipitation levels. Diet composition varied considerably for the study with a greater variety of plant species being available during years of higher rainfall (thus resulting in increased diversity of plants consumed) than the following year of less precipitation.

During the mid-1990s, pronghorn numbers decreased and fawn recruitment was below alleged maintenance levels for a short period, resulting in the assumption that predation was the controlling factor (Gregg et al. 2001). This prompted a research project on mortality of neonates that has continued for 11 years (Yoakum et al. 2004). Results indicated that forb diversity and abundance had increased >200 percent: thus critical nutritional forage for neonate survival increased. The number of pronghorn observed during summer surveys in 2003 and 2004 was respectively 2,444 and 2,474. Evidently the influence of changing ecological factors during the last decade on the refuge has changed vegetation conditions. Apparently increasing the carrying capacity through various vegetation management practices resulted in higher fawn ratios and herd size (Figure. l).

Conclusions and Management Implications

An assessment of management practices for pronghorn over the last 60 years indicates that natural and human-caused disturbance of vegetation are a limiting factor affecting pronghorn production and survival in the Intermountain West. Results support the contention that vegetation changes can be deleterious or beneficial to pronghorn population trends. Disturbances such as droughts and wildfires are natural ecological events that have affected herds for centuries. However, human-caused agents during modern times are more prevalent factors influencing population trends, although they have been infrequently recognized in management strategies and plans.

Pronghorn numbers have been sustained or increased when vegetation characteristics include: mixed forage classes with composition percentages approximately 20 to 40 each of preferred, succulent, nutritious grasses/forbs/shrubs; diverse number of species (5 to 15 grasses, 20 to 60 forbs, and 5 to 10 shrubs); plants in early- to mid-successional stages of climax; and heights of 15 to 25 inches (38 to 64 cm) (Yoakum 2004*b*).

When vegetation conditions are inadequate to support a healthy pronghorn population, no amount of predator control practices or herd augmentation/translocation will result in long-term increased herd density.

Many pronghorn rangelands today sustain chronic low neonate and herd densities because vegetation is in unhealthy ecological condition. As Leopold (1933) informed us years ago, we can use the same tools that aided resource exploitation (plow, axe, and fire) to rehabilitate wildlife habitats. These techniques are available to enhance pronghorn rangelands and increase herd size.

Substantial evidence now indicates that vegetation management practices to sustain plant conditions favorable to pronghorn habitat requirements or to enhance preferred, succulent, nutritional forage can increase pronghorn fawn recruitment and population density.

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Relationship Between Soil Chemistry and Pronghorn Fawn Recruitment in Arizona

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Abstract: Pronghorn (*Antilocapra americana*) numbers, like all wildlife, are greatly affected by recruitment of young into the population. Nutrition provided by plants can greatly impact recruitment by affecting development of fawns and the condition of does during gestation and lactation. Plant nutrition is generally affected by 3 major factors: 1) sunlight, 2) available moisture, and 3) nutrients in the soil. Previous authors have investigated the relationship between rainfall patterns and available plant nutrition to pronghorn recruitment and productivity; however, similar investigations with respect to soil conditions have not been conducted. We conducted a preliminary investigation into the relationship between soil composition and long-term pronghorn fawn recruitment across sites in Arizona. We measured soil chemistry and mineral composition (14 soil components) across 8 study sites throughout Arizona, and then used linear regression to compare these to long-term pronghorn recruitment estimates from each site. Levels of organic matter, K, and, Zn in the soil were correlated with pronghorn fawn recruitment. We calculated a linear regression model using K levels in the soil that explained 50% of the variation in average fawn recruitment throughout 8 study sites and other, less parsimonious models explained 80% of the variation. When we removed potential outliers, we calculated a linear regression model using percent organic matter estimated in the soil that explained 65% of the variation in average fawn recruitment throughout 6 study sites. Long-term overuse of range resources by ungulates may affect mineral and organic matter availability and subsequently affect the productivity of the habitat. Land-use practices that could affect long-term soil health could also greatly affect pronghorn numbers. Our effort illustrates the need for further investigations into relationships between soil conditions and wildlife population parameters.

Proceedings Pronghorn Workshop 22:69-82

Key Words: antelope; *Antilocapra americana;* copper; fawns; iron; minerals; nutrition; organic matter; potassium; recruitment; selenium; soil; trace elements; zinc.

Over the last 15 years, American pronghorn (*Antilocapra americana*) have declined throughout several areas in Arizona. In 1987, the statewide population of pronghorn was estimated at 12,000 individuals, but the estimate declined to less than 8,000 by 2000 (Arizona Game and Fish

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Department 2001). Several potential causes of pronghorn declines have been identified, including dietary overlap with cattle and sheep, fences that prevent movement, human development, water availability, predators, parasites, and diseases (Lee et al. 1998). In Arizona, decreased fawn recruitment has been identified as a major contributor to the pronghorn decline (Arizona Game and Fish Department 2001). Possible reasons for low fawn recruitment are numerous; nutritional and mineral deficiencies have been considered as potential contributing factors (Lee et al. 1998).

Mineral deficiencies have contributed to low recruitment of young in ungulate populations (Stoszek et al. 1980, Flueck 1994, O'Hara et al. 2001), and mineral supplementation has been shown to increase conception rates of cattle in Arizona (Sprinkle et al. 2000). While several studies have been conducted to investigate the relationship between rainfall patterns and available plant nutrition to pronghorn recruitment and productivity (Hailey and DeArment 1972, Stephenson et al. 1985), similar investigations with respect to soil conditions have not been undertaken (O'Gara and Yoakum 2004). We compared estimates of pronghorn fawn recruitment from several areas in Arizona to site-specific mineral levels, organic matter, and soil chemistry measurements to determine if fawn recruitment differs with soil composition.

Study Areas

We conducted this study at 8 sites in 5 grassland regions in Arizona, based on average pronghorn fawn recruitment numbers in the areas (Figure 1). Sites 1 and 2 encompassed approximately 423 and 432 km^2, respectively, in northeastern Arizona. Site 1 was in the White Mountain Grassland Wildlife Area, 7 km west of Springerville (34° 10' N, 109° 28' W) at an elevation of 2,070 m. Site 2 extended 20 km north from Springerville to the northern boundary of the Tucson Electric Power coal-fired generating station, 3 km southeast of Lyman Lake (34° 15' N, 109° 18' W) at an elevation of 2,015 m.

Predominant vegetative communities in the northeastern study sites were Great Basin grasslands, with sections of Petran montane conifer forest and Great Basin conifer woodland (Brown 1994). Temperatures ranged from below zero (0°C) in the winter to 18°C in summer, with a mean annual temperature of 8°C, and precipitation of 30.0 cm (NOAA 2003). Despite similarities in climate, habitat quality for the 2 northeastern study sites varied dramatically between the sites (Ockenfels et al. 1996), and in the past decade mean pronghorn fawn recruitment was greater in Site 1 (25.9 fawns/100 does) than in Site 2 (15.7 fawns/100 does).

4 sites were located in north-central Arizona; Site 3 encompassed approximately 128 km^2 in Garland Prairie, 7.2 km south of Parks (35° 12' N, 111° 57' W) at an elevation of 2,072 m; Site 4 encompassed approximately 86 km^2 on Anderson Mesa, 11 km east of Mormon Lake (34° 58' N, 111° 22' W) at an elevation of 2,194 m; Site 5 encompassed approximately 344 km^2 in Lonesome Valley, 15 km east of Prescott (34° 44' N, 112° 18' W) at an elevation of 1,550 m; and Site 6 encompassed approximately 159 km^2 near Fain Ranch, 5 km east of Prescott Valley (34° 37' N, 112° 15' W) at an elevation of 1,550 m.

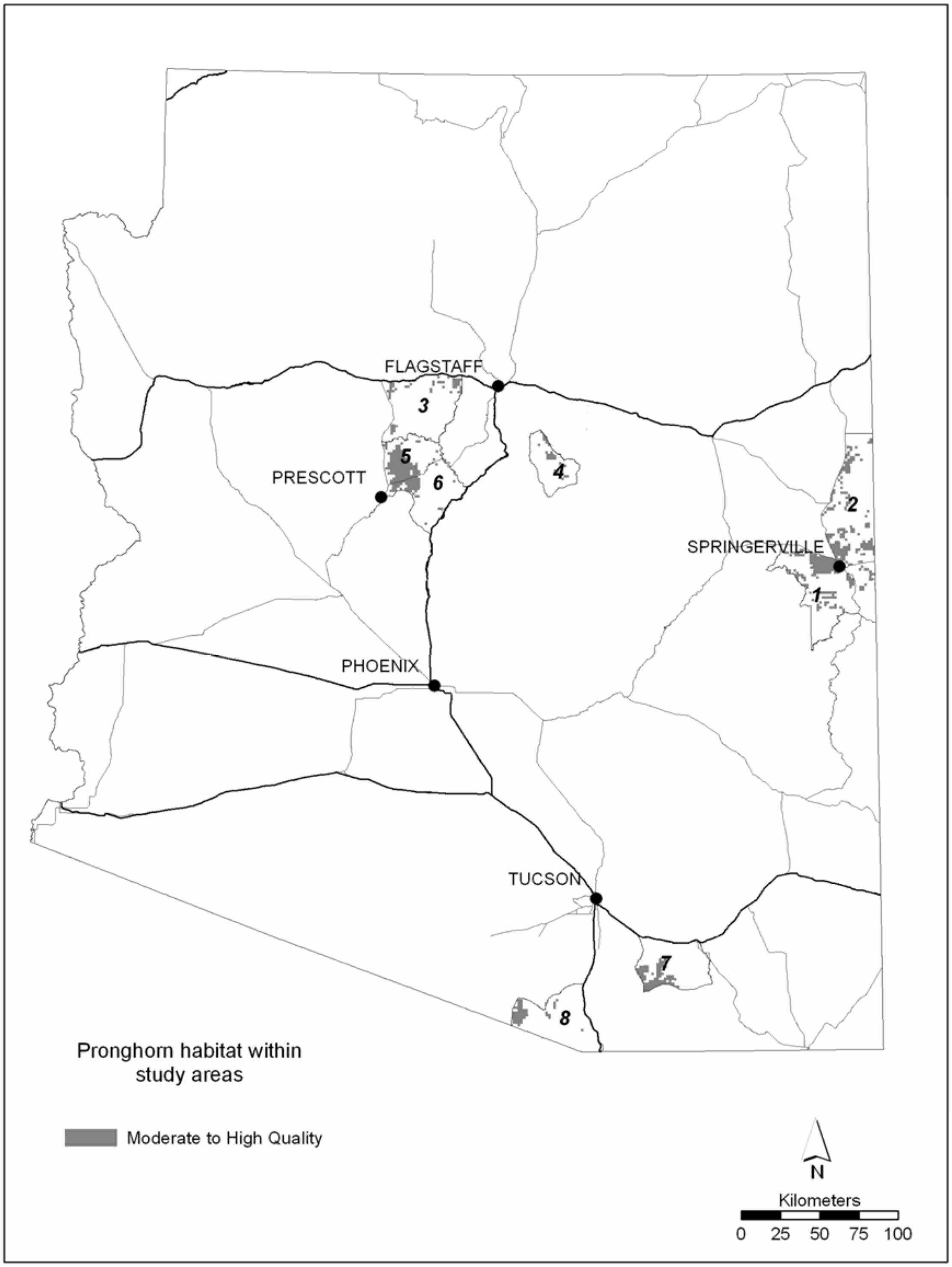

Figure 1. Arizona study sites showing areas of moderate to high-quality pronghorn habitat quality where estimates of pronghorn fawn recruitment (fawns:100 does) and soil samples were collected, 2003.

Predominant vegetative communities in the north-central study sites were Great Basin and Plains grasslands, with some patches of Great Basin conifer woodland (Brown 1994) that were more abundant at Site 4 than other sites. Temperatures ranged from below zero (0°C) in the winter to 18°C in summer, with an annual average of 9°C and an annual average precipitation of 55.0 cm. Habitat quality for the 4 north-central study sites varied substantially among sites (Ockenfels et al. 1996), and in the past decade mean pronghorn fawn recruitment was 37.1 (fawns/100 does) at Site 3, 11.7 at Site 4, 37.7 at Site 5, and 41.8 at Site 6.

The remaining 2 sites were located in southeastern Arizona; Empire Ranch (Site 7), 8.2 km west of Greaterville (31° 46' N, 110° 139' W), encompassed approximately 215 km^2 at an elevation of 1,462 m; and the Buenos Aires National Wildlife Refuge (Site 8), 97 km southwest of Tucson (31° 33' N, 111° 29' W), encompassed approximately 128 km^2 at an elevation of 1,096 m.

Predominant vegetative communities in the southeastern study sites were semidesert grasslands, with some remnants of Sonora savannah grassland at Site 8 (Brown 1994). Temperatures ranged from 9°C in the winter to 26°C in summer, and the mean annual temperature was 18°C in both sites. Mean precipitation was greater at Site 7 (50.0 cm) than at Site 8 (44.0 cm). Habitat quality for the 2 southeastern study sites varied substantially between the sites (Ockenfels et al. 1996), and in the past decade mean pronghorn fawn recruitment was greater at Site 7 (23.2 fawns/100 does) than at Site 8 (12.9 fawns/100 does).

Methods

Field Sampling

We estimated annual pronghorn recruitment in each study site by calculating fawn/doe ratios (number of fawns:100 does) using data collected during standard fixed wing, aerial herd composition surveys conducted each Autumn by the Arizona Game and Fish Department. We averaged annual fawn/doe ratios from 1995-2004 for each study site as an estimate of long-term fawn recruitment. We visually located pronghorn between April and August (late gestation through parturition) 2002-2003 on the 8 sites, then delineated 4 soil sampling areas associated with concentrated pronghorn use at each study site.

We collected soil samples from each of the 4 sampling areas within each study site in August 2003. Soil characteristics do not change significantly over months (Stu Buck, and Dr. Steven Hart, Northern Arizona University, personal communication), so we assumed that collecting samples in August would indicate overall soil conditions from April through August over time. We collected 5 (0.5-liter) subsamples of soil from each soil sampling area. We collected the first subsample from the geographic center of the sampling area and subsequent subsamples at 100 m distance in each of the 4 cardinal compass directions. We brushed away the humus and collected the top 15 cm of soil in a 0.5-liter receptacle, then combined the 5 subsamples to create 1 (2.5-liter) sample from each soil sampling area.

We delivered soil samples to Spectron Labs in Phoenix, where minerals, pH, total dissolved solids and organic matter were measured with the Wakely-Black method, where soil samples are digested in acid prior to being read for organics via spectrophotometry. Levels of Magnesium (Mg), Ammonium (NH_{4+}), Potassium (K), Phosphorus (P), Calcium (Ca), Iron (Fe), Manganese (Mn), Sodium (Na), Chloride (Cl), Zinc (Zn), Sulfates (SO_4), Copper (Cu), and Selenium (Se) were measured after digestion in acid with an atomic absorption spectrophotometer (Perkin Elmer 2380, Perkin Elmer Life and Analytical Sciences, Wellesley, MA). Organics such as Nitrates (NO_3) and Phosphorus (P) were measured calorimetrically on an ultra violet-visible light spectrophotometer (Odyssey DR 2500, Hach Instruments, Loveland, Colorado). We averaged the mineral and organic matter levels (ppm) from the 4 samples within each study site to estimate soil characteristics of the study site.

Statistical Analysis

First, we compared soil mineral levels from soil samples averaged across all study sites to the published range recommended for domestic sheep diets (Puls 1995). Then, we graphically displayed data using scatterplots of soil characteristics at each site against fawn recruitment estimates to illustrate potential relationships and identify outliers. To determine effects of soil characteristics on fawn recruitment, we regressed the 10-year average of annual fawn-to-doe ratios (1995-2004) on each individual soil variable. We constructed a Pearson correlation matrix to identify relationships among soil characteristics across all study sites. We realized that we performed multiple tests of variables with a potential lack of independence, and the experiment-wise error rate could have been high. However, because this study was the first attempt to relate soil characteristics to pronghorn population parameters, we accepted Type I errors as preferable to Type II errors. Therefore, in order to minimize the potential for Type II errors, we chose not to apply Bonferroni corrections to α levels. We considered relationships to be statistically significant if $P \leq 0.10$ (Zar 1984).

Next, we used backward-entry stepwise linear regression to develop models to predict pronghorn fawn recruitment based on combinations of soil characteristics (SPSS 5.0 New York, NY). We set the significance level at $\alpha = 0.05$ for model entry and 0.10 for removal. We developed models using independent soil variables; when soil variables were correlated, we selected only those that explained more variation in fawn recruitment based on univariate analysis. We calculated a modified Akaike's Information Criterion (AIC_c) to describe the parsimony of each model (Burnham and Anderson 1992).

Results

Average Fe, Mn, Zn, and Cu were the only mineral levels from soil samples that were below the published range recommended for domestic sheep diets at every site (Table 1; Puls 1995). Most other average soil mineral levels were considerably higher than the published range recommended for domestic sheep diets (Table 1). Average level of K in the soil was the only component significantly correlated with average fawn recruitment across all 8 sites (Table 2). Upon first examination, percent organic matter in the soil was not significantly correlated with average fawn recruitment ($r^2 = 0.066$). When we investigated the scatter plot comparing percent organic matter in the soil to average fawn recruitment, we noticed that Sites 5 and 6 were likely outliers that affected the significance and regression coefficient by a factor of 10 (Figure 2). When we removed Sites 5 and 6, average level of K in the soil was no longer significantly correlated with average fawn recruitment, while Zn and percent organic matter were significantly correlated with average fawn recruitment (Table 3).

Table 1. Range and mean mineral levels in soil samples collected at 8 different pronghorn habitat sites across Arizona (2003), and adequate recommended mineral levels for domestic sheep diets (Puls 1995).

Variable	Range (ppm)	Mean (ppm)	Recommended (ppm)
Chloride	31.50 – 92.80	64.06	0.25
Phosphorus	18.40 – 35.65	24.73	0.25 – 0.50
Potassium	41.85 – 81.78	58.45	0.80 – 2.00
Sodium	14.53 – 33.20	21.40	0.40 – 0.70
Calcium	310.8 – 1251.5	646.14	0.36 – 1.40
Magnesium	39.53 – 80.25	68.48	0.20 – 0.30
Iron	20.80 – 25.75	**22.89**[1]	100 – 280
Manganese	0.55 – 15.23	**5.53**	40 – 100
Zinc	0.10 – 2.03	**0.54**	50 – 100
Copper	0.25 – 0.58	**0.40**	5.0 – 10.0
Selenium	1.53 – 3.25	2.35	0.40 – 1.0

[1] Bold indicates levels are outside recommended dietary range for domestic sheep

We selected percent organic matter, levels of NH_{4+}, K, Fe, Zn, and SO_4 in the soil for entry into the linear regression modeling process. We developed 6 linear regression models to predict pronghorn fawn recruitment across all 8 sites, based on combinations of soil characteristics (Table 4). The model including only K level (ppm) in the soil was the most parsimonious (Figure 3). Adding variables additional to K improved r^2 values only slightly and resulted in a loss of significance, while increasing the complexity of the model.

Table 2. Regression coefficients for soil components as related to average pronghorn fawn recruitment (fawns:100 does; 1995-2004) at 8 sites in Arizona, 2003.

Variable	r^2	SE	*P*
pH	0.078	0.10621	0.504
Total dissolved solids	0.000	0.11059	0.997
Percent organic matter	0.066	0.10689	0.539
Nitrate	0.039	0.10839	0.637
Ammonium	0.103	0.10475	0.438
Sulfate	0.245	0.09607	0.212
Chloride	0.009	0.11012	0.827
Phosphorus	0.015	0.10979	0.776
Potassium	**0.495**[1]	0.07861	0.052
Sodium	0.011	0.11000	0.807
Calcium	0.035	0.10866	0.658
Magnesium	0.074	0.10640	0.513
Iron	0.223	0.09746	0.237
Manganese	0.023	0.10930	0.719
Zinc	0.058	0.10735	0.566
Copper	0.205	0.09863	0.260
Selenium	0.040	0.10838	0.636

[1] Bold indicates significant correlation ($P \leq 0.05$)

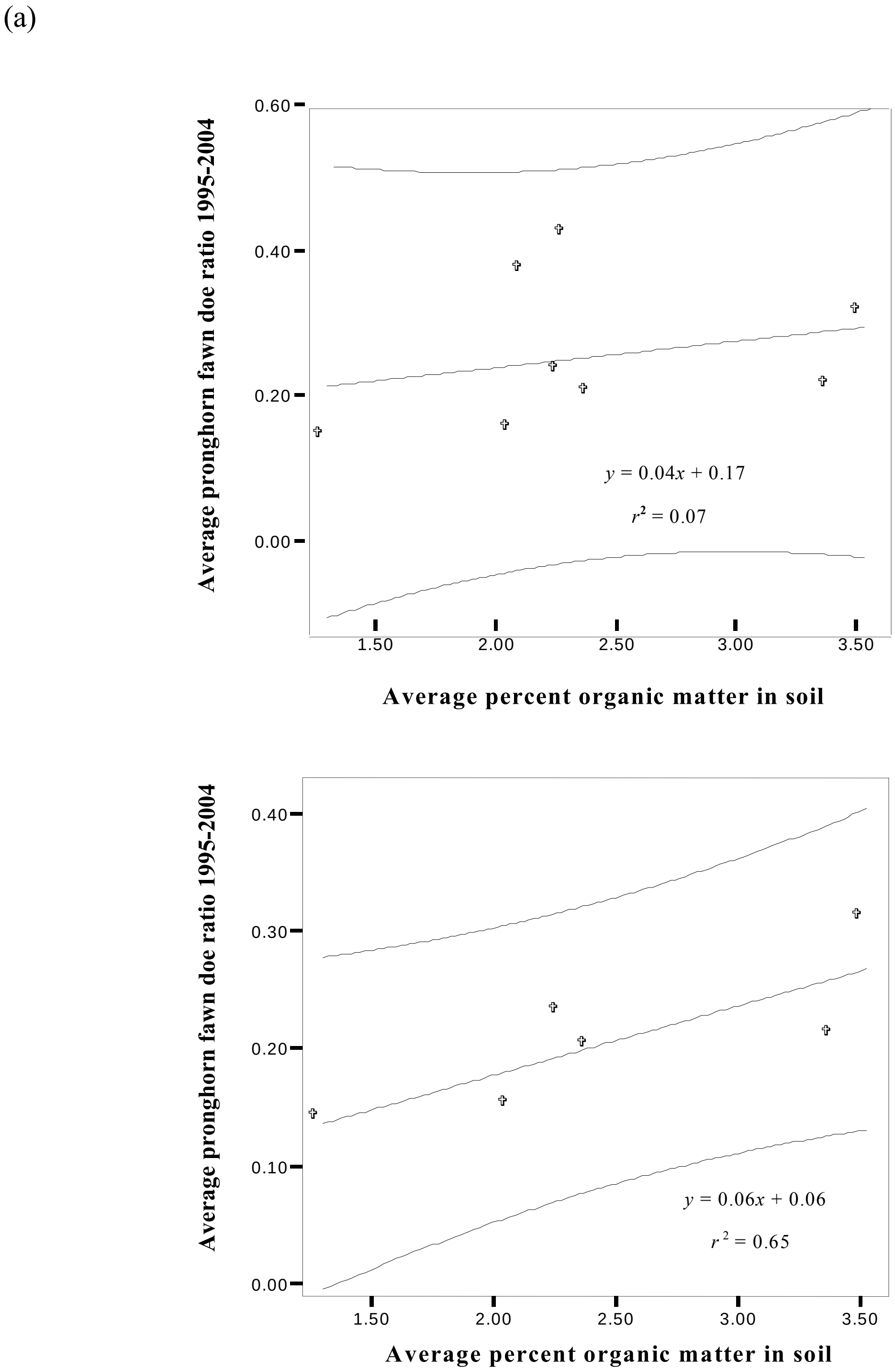

Figure 2. Relationship of percent organic matter in soil samples to average annual (1995-2004) pronghorn fawn recruitment estimates (fawns:100 does) for (*a*) 8 sites and (*b*) 6 sites excluding Sites #5 and #6 (where intensive predator control was regularly practiced), Arizona.

Discussion

Mineral levels in forage are directly related to mineral levels available in the soil, which varies across geological areas dictated by the underlying bedrock (Kubota et al. 1967, Reilly 1996). Augustine et al. (2003) found that large herbivores selectively graze sites according to levels of nutrients in the soil as reflected in forage plants. Mineral levels in the soil, therefore, should largely dictate minerals available to pronghorn. However, across most of our study sites, pronghorn as well as cattle, used mineral blocks commonly provided for livestock. While it is unknown whether these isolated resources could affect the entire local pronghorn population, it is a confounding influence that could not be discounted. While we found few significant correlations between average pronghorn fawn recruitment estimates and individual soil components, we were able to reveal some interesting relationships.

We found levels of most soil minerals were much higher than recommended for domestic sheep diets (Table 1), while others were deficient or adequate. However, the relationship between levels of particular minerals in the soil and those available in forage plants can be complex. For instance, plants found in clay soils often contain higher levels of Se than plants in sand because clays retain Se better, thereby providing more Se to plants (Gissel-Nielsen 1976). However, levels of other minerals, such as P, N, and S, pH, and amount of organic matter in soil also influence uptake of Se by plants (Gissel-Nielsen 1976). Forage plants from several sites in Arizona contain lower than adequate levels of Se recommended for domestic livestock, and it is likely that other minerals, such as Cu and Zn, are below adequate levels as well (Frederick 1997).

Effects of Se deficiencies have been suggested and documented in many free-ranging ungulates, including pronghorn. Kubota et al. (1967) found that white muscle disease or muscular dystrophy in livestock was correlated with sites having low Se in plants and underlying parent soil material. Flueck (1994) measured the effect of Se on reproduction of black-tailed deer (*Odocoileus hemionus columbianus*) in California and found that Se supplementation increased fawn production from 32 fawns per 100 does to 83 fawns per 100 does. Se deficiency has been reported in pronghorn from Idaho, and the deficiency coincided with decreased fawn recruitment and clinical signs of "weak calf syndrome" in newborn fawns (Stoszek et al. 1980). Dunbar et al. (1999) found that adult pronghorn from a site with chronically low fawn recruitment had a mean liver Se concentration below the minimum adequate level for domestic ruminants. Heffelfinger et al. (1999) found that 73% (73/100) of liver samples from pronghorn collected across Arizona were below the 0.25 ppm minimum adequate level reported for domestic goats, cattle, and sheep (Puls 1995).

Table 3. Regression coefficients for soil components significantly ($\alpha \leq 0.10$) related to average pronghorn fawn recruitment (fawns:100 does; 1995-2004) at 6 sites (Excluding Sites #5 and #6 where intensive predator control was practiced) in Arizona, 2003.

Variable	r^2	SE	*P*
Percent organic matter	0.650	0.04069	0.053
Zinc	0.593	0.04389	0.073

Copper deficiency has also been documented in many free-ranging ungulates including pronghorn (Robbins 1993, Heffelfinger et al. 1999). McCafferty (1990) suggested that Cu deficiency predisposes domestic sheep to *Chlamydia* sp. infection, which can cause reproductive problems. Heffelfinger et al. (1999) analyzed liver tissue and serum samples from 100 pronghorn around the state for Cu concentration and found that 73% had levels below the lower limit recommended for domestic ruminants. In 1992, *Chlamydia* sp. was identified from cervical and preputial samples in approximately 80 % of 37 pronghorn captured in Arizona (Dr. O. Alcumbrac, White Mountain Animal Hospital, personal communication). In addition, serum Cu levels were below the adequate range for domestic livestock.

Table 4. Modified Akaike's Selection Criterion (AIC_c) ranking of linear regression models correlating soil components with average annual fawn recruitment (fawns:100 does; 1995-2004) at 8 sites in Arizona, 2003.

Model	r^2	Standard error of the estimate	Significance[a]	$-2\ \log_e \int$	AIC_c	Delta AIC_c
1	0.495	0.07861	0.052	0.107	2.773	.00
2	0.637	0.07296	0.079	0.165	6.565	-3.79
3	0.822	0.05722	0.056	0.115	12.115	-9.34
4	0.831	0.06438	0.157	0.342	21.675	-18.90
5	0.835	0.07791	0.364	0.905	40.905	-38.13
6	0.835	0.11017	0.683	2.298	98.298	-95.52

1. $Z = 0.006\ K^{b} - 0.12$
2. $Z = 0.007\ K^{b} + 0.054\ POM^{c} - 0.284$
3. $Z = 0.006\ K^{b} + 0.079\ POM^{c} - 0.029\ SO_4^{d} + 0.083$
4. $Z = 0.005\ K^{b} + 0.072\ POM^{c} - 0.030\ SO_4^{d} + 0.018Zn^{e} + 0.103$
5. $Z = 0.006\ K^{b} + 0.079\ POM^{c} - 0.032\ SO_4^{d} + 0.017Zn^{e} – 0.005\ Fe^{f} + 0.218$
6. $Z = 0.006\ K^{b} +0.077\ POM^{c} - 0.031\ SO_4^{d} + 0.019Zn^{e} – 0.005\ Fe^{f} - 0.002\ NH_{4+}{}^{g} +0.20$

[a] Degrees of freedom were equal to number of variables in the model.
[b] Average level (ppm) of Potassium.
[c] Average percent organic matter.
[d] Average level of (ppm) Sulfates.
[e] Average level of (ppm) Zinc.
[f] Average level of (ppm) Iron.
[g] Average level of (ppm) Ammonium.

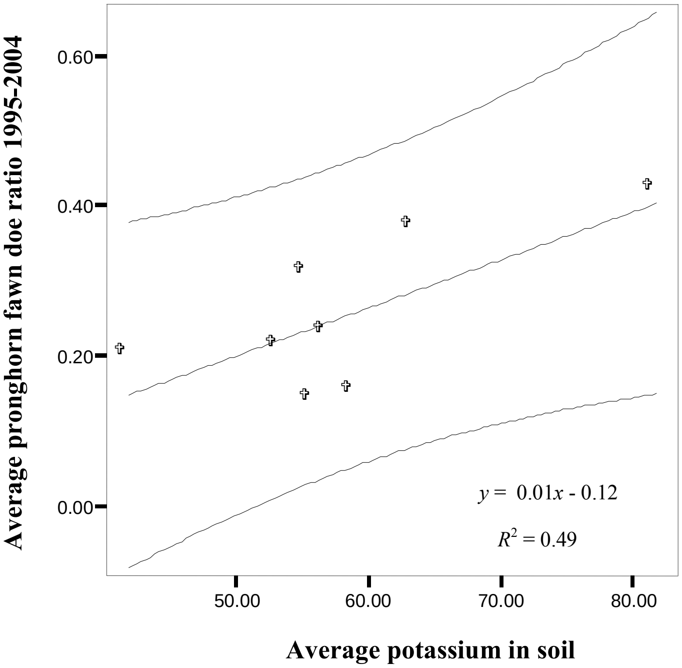

Figure 3. Relationship of Potassium (ppm) in soil samples to average annual (1995-2004) pronghorn fawn recruitment estimates (fawns:100 does) at 8 sites in Arizona, 2003 "Data are from Model 1 in Table 4."

Although data regarding mineral status and requirements for pronghorn are lacking in Arizona, it seems likely that pronghorn have levels of Cu and Se below those seen in healthy domestic animals. Given that Cu and Se deficiencies can cause clinical illness and influence reproductive capabilities in domestic animals in Arizona (Robbins 1993, Bradley et al. 1997, Frederick 1997), it is possible that these mineral deficiencies may affect reproduction in Arizona's pronghorn populations. However, we found no significant relationship between Cu or Se levels in the soil and our long-term pronghorn fawn recruitment estimates (Table 2). Small sample size may have affected our results; however, if Cu and Se deficiencies are affecting pronghorn health and populations in Arizona, they do not play a significant role in explaining differences in fawn recruitment estimates.

We found that K levels in the soil were positively correlated with fawn recruitment (Table 2). Potassium levels in the diet are correlated with weight gain in domestic sheep lambs (National Research Council 1985). If a similar relationship exists in pronghorn, the correlation to fawn recruitment could be explained by fetal and fawn development. Reduced K levels in the soil could result in K deficient diets and consequently reduced weight gain among fawns. Smaller pronghorn fawns could be more susceptible to mortality from starvation, disease, and predation (Von Gunten 1978).

When we investigated the scatter plot comparing percent organic matter in the soil to average fawn recruitment, we considered Sites 5 and 6 as likely outliers. These study sites had fawn recruitment estimates much higher than most of the other sites, and were in areas where intensive predator control was practiced over most of the last decade. Reduction of predator numbers during the fawning period can increase pronghorn fawn survival (Neff and Woolsey 1980), which could have masked effects of soil conditions on fawn recruitment estimates. When we removed these 2 study sites we found that percent organic matter in the soil was positively correlated with fawn recruitment. Soil organic matter increases the productivity of grassland ecosystems by improving soil drainage, aeration, water-holding capacity, pH, and compaction. It also supplies essential nutrients and provides a carbon and energy source for soil microbes (Brady 1974). In grazed areas, livestock removes some of the plant biomass that provides soil organic matter, and over time this could result in an incremental reduction in available organic matter (Johnson et al. 1971). Augustine et al. (2003) found that intensive grazing of herbivores caused a net loss of N in areas with nutrient-poor soils. Furthermore, percent organic matter in the soil could affect availability of other important minerals in forage plants (Frederick 1997). Thus, organic matter in the soil could affect forage quality as well as quantity, which would subsequently affect pronghorn fawn recruitment.

When we removed the likely outliers, we also found that levels of Zn in the soil were positively correlated with fawn recruitment. Dairy cattle fed diets supplemented with Zn were found to have increased lactation and improved udder health over those fed Zn deficient diets (Tomlinson et al. 2002). One of the most profound effects of zinc deficient diets on domestic sheep is weakening of reproductive functions (National Research Council 1985). These relationships, if present in pronghorn, could easily explain a positive correlation between levels of Zn in the soil and fawn recruitment.

This study was a preliminary attempt at relating soil components and conditions to pronghorn fawn recruitment, and as such, we caution readers about strict interpretation of our results. With our small sample size, exploratory study design, and potential lack of independence, significance of the relationships we observed should be viewed with skepticism. Results we obtained could be entirely spurious relationships within the data set and not representative of the natural processes studied. However, our results demonstrate some interesting correlations and we believe further investigation of soil chemistry is warranted. Future studies should include greater efforts to estimate the range of soil conditions available within sites as well as sampling more sites in order to increase the power of statistical inferences.

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Effects of Diet Habits on Pronghorn Recruitment in Arizona

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***Abstract**:* Several studies have implied that diet composition and quality are important to pronghorn (*Antilocapra americana*) population densities and recruitment (Beale and Smith 1970, Koerth et al. 1984). However, a relationship between pronghorn fawn recruitment and diet habits in Arizona has not been established. We investigated diet habits during late spring/summer across 8 pronghorn habitat sites in Arizona, representing different levels of pronghorn population density and fawn recruitment. We estimated forage class composition from fresh pronghorn fecal samples collected during gestation and lactation seasons, and measured fecal 2,6-diaminopimelic acid (DAPA) concentrations (mg/g). We regressed diet composition and quality estimates against fawn:female (fawn:doe) ratios, estimated from standard annual aerial surveys, to determine relationships between diet habits and fawn recruitment. Although estimates of dietary plant species richness were positively correlated with pronghorn fawn:doe ratios ($r^2 = 0.40$, $P = 0.09$), seasonal DAPA concentrations were negatively correlated with pronghorn fawn:doe ratios ($r^2 = 0.22$, $P = 0.03$, $r^2 = 0.32$, $P = 0.01$) for the gestation and lactation seasons, respectively. The statewide approach we employed would have only detected effects that were consistently significant across a varied landscape. The relationship between dietary richness and fawn recruitment supports the contention that forage diversity is important to fawn recruitment, while the counterintuitive results relative to DAPA concentration illustrate the need for further research.

Proceedings Pronghorn Workshop 22: 83-95

***Key Words**: Antilocapra americana,* Arizona, DAPA ,diet, pronghorn.

Pronghorn, being ruminants, are able to utilize a vast array of forage to obtain nourishment because gastrointestinal microbes are able to easily convert forage into usable

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nutrients (Wallach and Hoff 1982). Energy and protein requirements for adult ruminants vary with reproductive cycle, and late gestation and lactation require the highest protein and energy intakes for females (Nelson and Leege 1982). Energy requirements and food intake increase from 17 to 32 % in pregnant mammals, whereas energy expenditure increases from 65 to 215 % in lactating females (Robbins 1983). During pregnancy, protein requirements increase 3 times over requirements for maintenance (Nelson and Leege 1982).

Protein content in the overall diets of Texas pronghorn diet varied from 9.8 % in winter to 11.4 % in spring (Koerth et al. 1984). Koerth et al. (1984) compared this to predicted requirements for deer and concluded that year-round diets would meet pronghorn requirements for maintenance. Given that pronghorn does are in the third trimester of pregnancy in spring, it is unknown if 11.4 % protein would meet requirements of pregnant or lactating does, and Koerth et al. (1984) hypothesized that lack of adequate nutrition during spring could contribute to low fawn production.

Over the last 15 years, pronghorn have declined throughout most areas in Arizona. In 1987, the statewide population of pronghorn was estimated at 12,000 individuals, but declined to less than 8,000 by 2000 (Arizona Game and Fish Department [AZGFD] 2001). AZGFD (2001) indicated low fawn recruitment has been a major contributor to the pronghorn decline, and Neff (1986) considered it the most important management issue for pronghorn in Arizona. Lee et al. (1998) identified forage availability and quality as factors potentially influencing fawn recruitment.

Given the variable nature of precipitation in Arizona and that nutrient content varies in plants with season (Van Soest 1994), inadequate quality or quantity of forage during the spring and summer could contribute to poor fawn recruitment in Arizona. Diet diversity may be linked to nutritional quality of available forage; rangelands lacking high-quality forage require animals to forage more indiscriminately (Heller 1980). Although studies have found that forage diversity can affect pronghorn population densities and habitat selection (Beale and Smith 1970), the impact of diet habits on pronghorn recruitment in Arizona has not been investigated. We estimated diet composition and quality across several areas of pronghorn habitat in Arizona during the spring/summer gestation and lactation seasons. We then related diet composition and quality estimates to fawn recruitment estimates to determine if pronghorn in sites with better access to high-quality forage had higher fawn recruitment.

Study Area

We conducted this study at 8 sites in 5 grassland regions in Arizona based on pronghorn fawn recruitment estimates in the areas (Figure 1). Sites 1 & 2 encompassed approximately 423 and 432 km^2, respectively, in northeastern Arizona in the White Mountain Grassland Wildlife Area, 7 km west of Springerville (34° 11’ N, 109° 18’ W) at an elevation of 2,070 m.

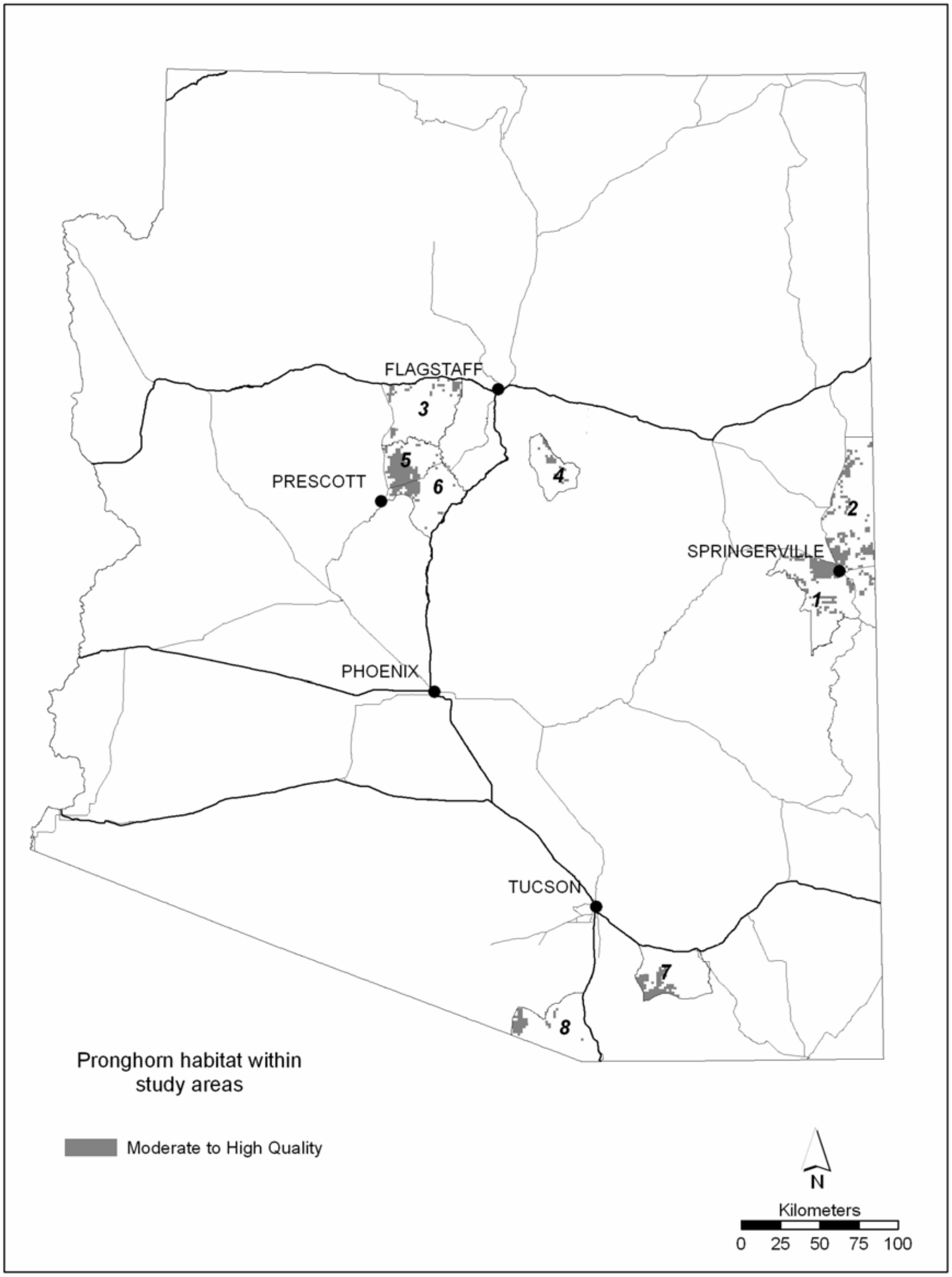

Figure 1. Arizona study sites showing pronghorn habitat quality where estimates of pronghorn fawn:doe ratios and diet habits were collected, 2002 -2004.

4 sites were located in north-central Arizona; Site 3 encompassed approximately 128 km^2 in Garland Prairie, 7.2 km south of Parks (35° 12' N, 111° 57' W) at an elevation of 2,072 m; Site 4 encompassed approximately 86 km^2 on Anderson Mesa, 11 km east of Mormon Lake (34° 58' N, 111° 22' W) at an elevation of 2,194 m; Site 5 encompassed approximately 344 km^2 in Lonesome Valley 15 km east of Prescott (34° 44' N, 112° 18' W) at an elevation of 1,550 m; and Site 6 encompassed approximately 159 km^2 in the Fain Ranch area, 5 km east of Prescott Valley (34° 37' N, 112° 15' W) at an elevation of 1,550 m.

The remaining 2 sites were located in southeastern Arizona; Empire Ranch (Site 7), 8.2 km east of Greaterville (31° 46' N, 110° 139' W), encompassed approximately 215 km^2 at an elevation of 1,462 m, and the Buenos Aires National Wildlife Refuge (Site 8), 97 km southwest of Tucson (31° 33' N, 111° 29' W), encompassed approximately 128 km^2 at an elevation of 1,096 m.

Predominant vegetative communities in the northeastern study sites (1 and 2) were Great Basin grasslands with sections of Petran montane conifer forest and Great Basin conifer woodland (Brown 1994). Temperatures ranged from below zero in the winter to 18°C in summer, with mean annual temperature of 8°C, and precipitation of 30.0 cm (NOAA 2003). Despite similarities in climate, habitat quality for the 2 northeastern study sites varied dramatically (Ockenfels et al. 1996), and in the past decade the mean pronghorn fawn:female (fawn:doe) ratio was greater in Site 1 (25.9 fawns/100 does) than in Site 2 (15.7 fawns/100 does).

Predominant vegetative communities in north-central study sites (3-6) were Great Basin grasslands, with some patches of Great Basin conifer woodland (Brown 1994) that were more abundant at Anderson Mesa than other sites. Temperatures ranged from below zero in the winter to 18°C in summer with an annual average of 9°C and an annual average precipitation of 55.0 cm. Habitat quality for the 4 north-central study sites varied substantially (Ockenfels et al. 1996), and in the past decade the mean pronghorn fawn:doe ratio was 37.1 (fawns/100 does) at Garland Prairie, 11.7 at Anderson Mesa, 37.7 at Lonesome Valley, and 41.8 at Fain Ranch.

Predominant vegetative communities in southeastern study sites (7 and 8) were semidesert grasslands, with some remnants of Sonoran savannah grassland in Buenos Aires (Brown 1994). Temperatures ranged from 9°C in the winter to 26°C in summer, and the mean annual temperature was 18°C in both sites. Mean precipitation is greater in Empire Ranch (50.0 cm) than in Buenos Aires (44.0 cm). Habitat quality also varied substantially between southeastern study sites (Ockenfels et al. 1996), and in the past decade the mean pronghorn fawn:doe ratio was greater in Empire Ranch (23.2 fawns/100 females) than in Buenos Aires (12.9 fawns/100 females).

Methods

Field data collection. We estimated annual pronghorn recruitment in each study site by calculating fawn/doe ratios (number of fawns:100 does) using data collected during standard fixed wing, aerial herd composition surveys conducted each Autumn by the Arizona Game and Fish Department.

We collected fecal samples for diet analysis during 2-3 week of gestation and lactation seasons estimated for each site. We estimated average parturition dates using elevation and latitude according to Ticer et al. (2000), and information from observations of field personnel. Gestation time seasons were estimated by backdating ½ trimester from average parturition dates, assuming an average gestation of 252 days (O'Gara 1978). Beginnings of the lactation time seasons were determined by adding 20-25 days to the estimated end of the parturition dates.

We located pronghorn groups and observed them with a spotting scope until the majority of the individuals had defecated, and then collected individual pellet groups. Each season we collected 15-20 individual fecal pellet groups/site. We pooled 5 pellet groups from each study site for each season to create 3-4 composite samples for diet analysis. We froze fecal samples until laboratory analyses were performed.

Table 1. Average diet composition by forage class and diversity estimates for gestation and lactation season pronghorn diets at 4-6 sites in Arizona, 2002 - 2004.

Site stat.	Season	Forb %	Grass %	Shrub %	Forb richness	Grass richness	Shrub richness	Species richness
1	Gestation	83	11	0	29	4	2	38
	Lactation	75	3	1	49	5	2	67
2	Gestation	88	6	3	23	4	2	32
	Lactation	84	3	4	34	3	2	44
3	Gestation	66	14	20	41	7	10	58
	Lactation	52	11	35	39	7	10	56
4	Gestation	74	7	16	55	7	10	71
	Lactation	68	11	18	45	7	10	62
5	Gestation	68	7	22	26	6	8	41
	Lactation	65	4	26	24	5	10	40
6	Gestation	77	3	20	28	6	10	44
	Lactation	66	6	22	21	6	9	37
F^a	Gestation	1.09	0.74	0.67	1.59	0.47	1.49	2.27
	Lactation	0.94	0.69	0.82	2.13	0.94	1.55	**5.39**
P	Gestation	0.46	0.62	0.67	0.31	0.79	0.34	0.19
	Lactation	0.52	0.65	0.58	0.19	0.52	0.30	**0.03**

[a] Difference determined by one-way ANOVA.

Laboratory analysis

We used microhistological analysis to estimate seasonal diet composition, for sites 1-6, for each composite sample according to procedures described by Holt et al. (1992). Since our study sites included 5 different grassland regions with different habitat types and species availability, we categorized plant species according to forage class for analysis. To determine diet composition, we used relative density of each forage class type (grasses, forbs, and shrubs) in fields of a microscope preparation of composite feces (Koerth et al. 1984). We performed microhistological analyses at the 90% (P=0.10) confidence level. We used procedures described by Davitt and Nelson (1984) to calculate fecal 2,6-diaminopimelic acid (DAPA) concentration (mg/g) for each composite fecal sample.

Statistical analysis. We used a Kolmogorov-Smirnov 1-sample test to determine if frequency distributions of each data set were normally distributed (Zar 1999). We graphically displayed data using scatter plots of seasonal diet characteristics at each site against fawn:doe ratios to illustrate potential relationships and identify outliers. To describe diet habits by study site, we averaged seasonal DAPA concentrations, forage class compositions, and species richness. To determine if pronghorn recruitment estimates and diet habits varied more by year than by study site, we used one-way ANOVA for fawn:doe ratios, average annual DAPA concentrations, seasonal percent forage class compositions, and species richness.

To determine affects of diet composition and quality estimates on pronghorn recruitment, we regressed annual fawn:doe ratios on seasonal percent forage class compositions, species richness, and DAPA concentration estimates for all sites. We realized that we performed multiple tests of variables with a potential lack of independence, and the experiment-wise error rate could have been high. However, because this study was the first attempt to relate diet quality and composition to pronghorn population parameters in Arizona, we accepted Type I errors as preferable to Type II errors. Therefore, in order to minimize the potential for Type II errors, we chose not to apply Bonferroni corrections to α levels. We considered all statistical tests to be significant if $\alpha \leq 0.10$ (Zar 1999).

Results

We were only able to analyze diet composition of fecal samples for 6 of the 8 sites and did not complete analysis for all of the years and seasons. We completed diet composition analysis for all seasons for sites 1-2 for 2003, all seasons and years for sites 3-4, and all seasons for sites 5-6, 2003-04. We completed fecal DAPA concentration analysis for all seasons and sites. Pronghorn fawn:doe ratios and average annual DAPA concentrations varied more by year than by study site (F = 0.71, P = 0.66), (F = 0.58, P = 0.76), respectively. Similarly, all seasonal percent forage class compositions and most species richness estimates varied more by year than by study site (Table 1). Total dietary plant species richness varied more by study site than by year (Table 1). None of the seasonal percent forage class composition, or species richness, estimates were related to annual fawn:doe ratios (Table 2). Seasonal DAPA concentration estimates were negatively correlated with annual fawn:doe ratios (r^2 = 0.22, P = 0.03, r^2 = 0.32, P = 0.01) for the gestation and lactation seasons, respectively. (Figure 2).

(*a*)

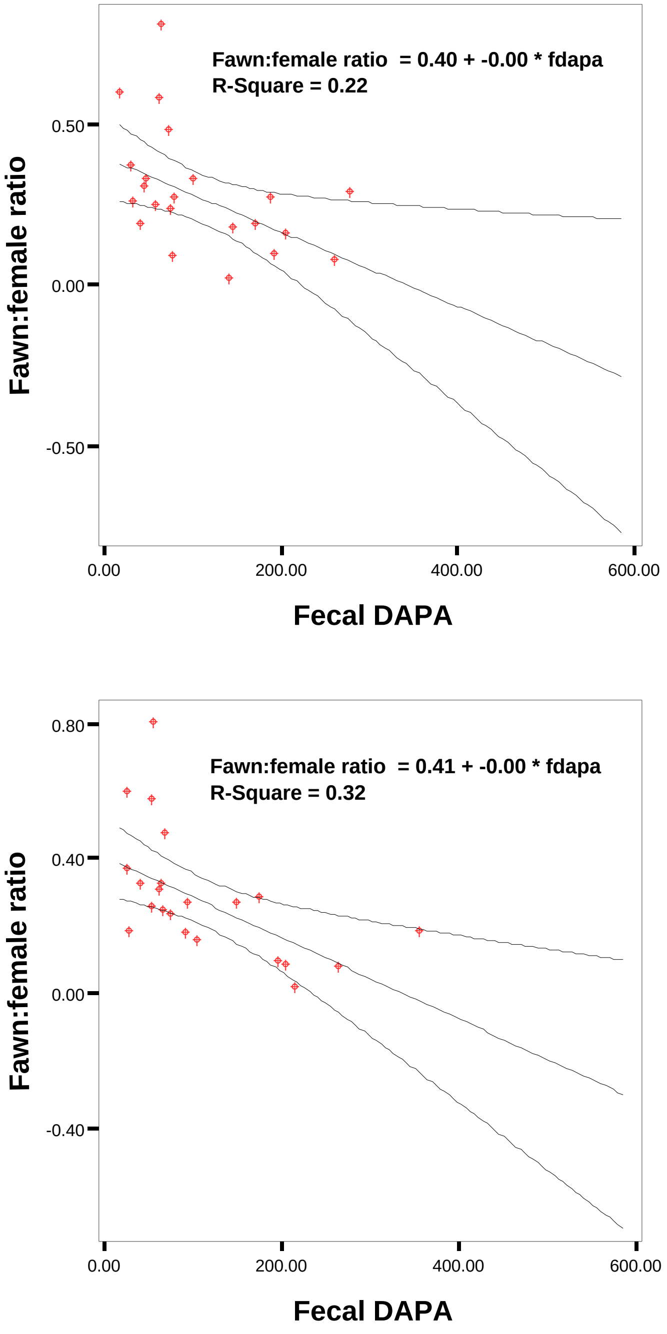

Figure 2. Relationship of gestation (*a*) (r^2 = 0.22, *P* = 0.03) and lactation (*b*) (r^2 = 0.32, *P* = 0.01) season estimates of 2,6 diaminopimelic acid (DAPA) concentrations (mg/g) to annual fawn:doe ratios at 8 sites in Arizona, 2002 - 2004.

Upon first examination, total plant species richness in gestation season diets was not significantly correlated with annual fawn:doe ratios (Table 2). When we investigated the scatter plot comparing total plant species richness in gestation season diets to annual fawn:doe ratios, we noticed that sites 5 and 6 were likely outliers that affected the significance and regression coefficient ($P = 0.09$, $r^2 = 0.40$, Figure. 3). Removing sites 5 and 6 did not affect the significance of correlations between the seasonal percent forage class composition, species richness or DAPA concentration estimates and annual fawn:doe ratios (Table 2).

Discussion

Impacts of diet quality on reproduction of wild ruminants are dependent upon the season (Robbins 1983). Diet quality during gestation can affect fawn development and nutritional demands of females are greatest during lactation. Effects of diet quality on pronghorn populations should be most evident during these critical seasons (Robbins 1983). However, we found few significant relationships between our estimates of diet composition and fawn recruitment. Annual precipitation during the first year of our study was the lowest ever recorded in Arizona (NOAA 2003). Fawn recruitment was extremely low throughout all sites, but seemed to rebound with increased rainfall over subsequent years. Although our fawn recruitment estimates ranged from 0.12-0.79 fawns:female, our attempts to explain this variation using diet composition information was largely unsuccessful.

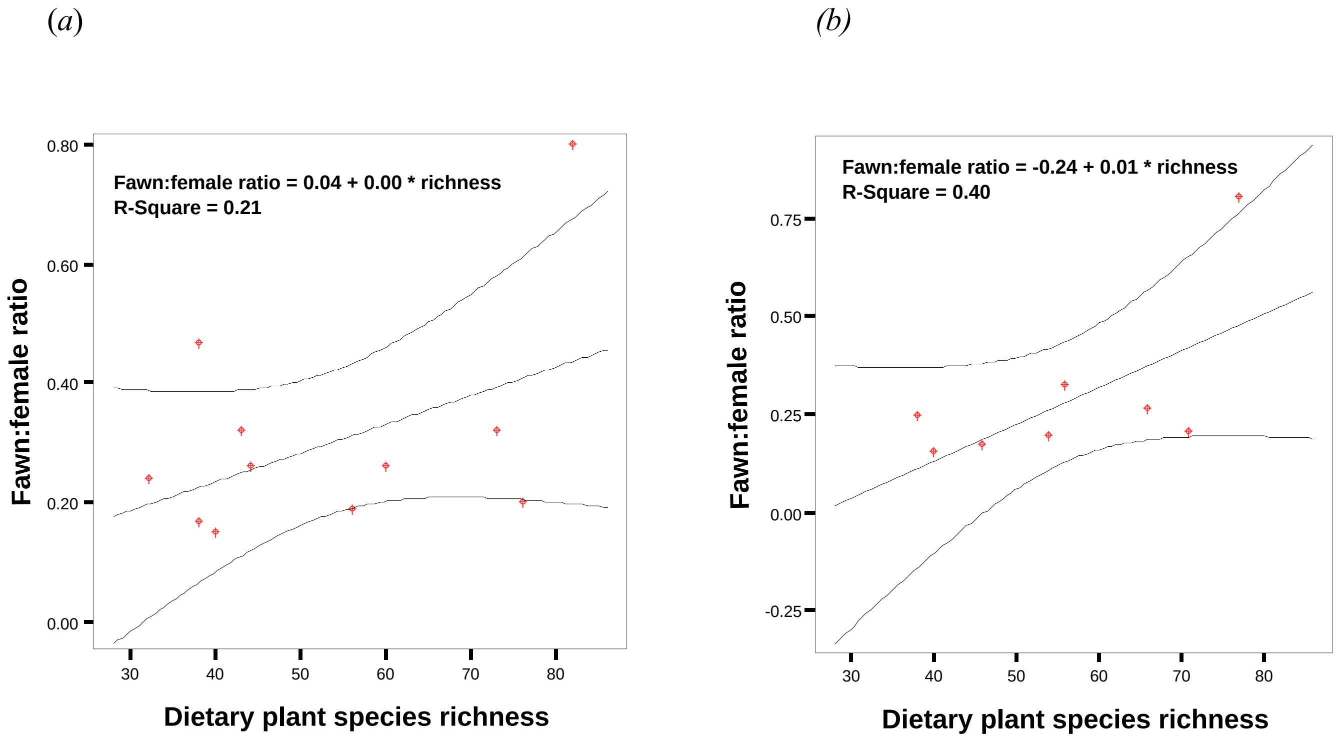

Figure 3. Relationship of plant species richness in gestation season pronghorn diets to annual fawn:doe ratios at 6 sites (*a*) and 4 sites (*b*) in Arizona, 2002 - 2004.

When we investigated the scatter plot relating total dietary plant species richness to average fawn recruitment, we considered sites 5 and 6 as likely outliers. These study sites had fawn recruitment estimates much higher than most of the other sites, and were in areas where intensive predator control was practiced over most of the last decade. Reduction of predator numbers during the fawning period can increase pronghorn fawn survival (Neff and Woolsey 1980, Trainer et al 1983), which could have masked affects of diet habits on fawn recruitment estimates. When we removed these 2 study sites, we found that total dietary plant species richness was positively correlated with fawn recruitment. Increasing diversity of diets could offset affects of low quality forage and may explain the relationship we found. However, it seems this relationship should be consistent among seasons and perhaps stronger during the lactation season, when forage deficiencies in either energy or protein could influence lactating females resulting in inadequate nutrients for proper fawn growth (Koerth et al. 1984). Differences in diet quality could have been present, but not evident in the data we selected to analyze. Diet quality could have been quite different despite similarities in composition. Our results were similar to previous studies relative to forage classes consumed (Yoakum 2004*a*). Pronghorn diets consisted mainly of forbs, which generally contain higher protein concentrations than other vegetation (Stephenson et al. 1985). However, the individual forb species and subsequent protein content available within each site could have differed greatly.

The inverse relationship between DAPA concentrations and fawn recruitment seems to contradict previous research (Osborn and Ginnet 2001). DAPA is a bacterial cell wall amino acid that increases with microbial growth in the rumen (Leslie et al 1989). Low levels of dietary energy inhibit microbial growth and consequently fecal DAPA concentration (Hodgman et al 1996). Fecal DAPA concentration should therefore be an indicator of diet quality. However, Robinson et al. (2001) found that fecal DAPA concentrations did not reflect changes in body weight of captive pronghorn fed a low quality diet. Kucera (1997) thought DAPA was a poor indicator of condition and reproductive performance in mule deer (*Odocoileus hemionus*). Direct measurements of nutritional content of available forage may be more useful in investigating the relationship between diet habits and pronghorn fawn recruitment in Arizona.

Other nutritional deficiencies could have played a role in masking the effects of diet habits on pronghorn fawn recruitment. Dunbar et al. (1999) measured nutritional blood parameters in pronghorn from Hart Mountain National Antelope Refuge in Oregon where the population of pronghorn had decreased 29 % from 1990 to 1995. In 1995, fawn to doe ratio dropped to 1 fawn per 100 does. A mean blood urea nitrogen level for both adult females and fawns were significantly lower than those found in fawns and does from a healthy population in Alberta, and the authors attributed this difference to a low protein diet consumed by pronghorn in Oregon.

Table 2. Regression coefficients for seasonal (Gestation, Lactation) forage class composition and species richness estimates of pronghorn diets as related to fawn:female ratios at 6 sites in Arizona, 2002-2004.

Variable/season	r^2	Standard error of the estimate	*Significance*
Gestation			
Percent forbs in diet	0.030	0.19331	0.609
Percent grass in diet	0.142	0.18180	0.253
Percent shrubs in diet	0.129	0.18317	0.277
Forb species richness	0.181	0.17769	0.193
Grass species richness	0.005	0.19578	0.830
Shrub species richness	0.090	0.18730	0.371
Total species richness	0.000	0.20249	0.966
Lactation			
Percent forbs in diet	0.013	0.20119	0.725
Percent grass in diet	0.017	0.20082	0.690
Percent shrubs in diet	0.000	0.20250	0.983
Forb species richness	0.000	0.20251	0.997
Grass species richness	0.056	0.19674	0.458
Shrub species richness	0.088	0.19343	0.350
Total species richness	0.000	0.20249	0.966

Management Implications

While we found few significant correlations, our data suggests that species diversity is an important component of pronghorn diets relative to fawn recruitment. Confounding factors such as predator numbers (Rothchild et al. 1994), cover (Autenrieth 1984), water availability (Beale and Smith 1970), and other aspects of habitat quality (Yoakum 204*b*) have all been found to influence pronghorn populations and may have influenced our results. Given that energy and protein requirements increase dramatically for ruminants during late gestation and lactation (Nelson and Leege 1982), and that Arizona pronghorn have been shown to have low mineral levels in tissues (Heffelfinger et al. 1999), we believe that determining the protein, energy, and mineral content of pronghorn forage in Arizona would be more useful than fecal indices relative to the effects on fawn recruitment.

This study was a preliminary attempt at relating diet habits of pronghorn and fawn recruitment estimates in Arizona, and as such we caution readers about strict interpretation of our results. With our small sample size, exploratory study design, and potential lack of independence, significance of the relationships we observed should be viewed with skepticism. Results we obtained could be entirely spurious relationships within the data set and not representative of the natural processes studied. However, our results demonstrate some interesting correlations and we believe further investigation is warranted. Future studies should include greater efforts to accurately estimate diet and population parameters as well as sampling more sites over more years in order to increase the power of statistical inferences.

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An Evolutionary History of Pronghorn Habitat and Its Effect on Taxonomic Differentiation

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Abstract: Taxonomic descriptions of pronghorn (*Antilocapra americana*) were based on obsolete criteria and failed to consider the animal's phylogenic history. Pronghorn co-evolved with post-Pliocene savannas under a winter rainfall regime in the Intermountain West. As these habitats became increasingly arid they evolved into grasslands, shrub-steppe, and eventually desertscrub. Climatic variations during Pleistocene time necessitated pronghorn becoming adapted to a great range in temperatures. These adaptations were further honed during the late Pleistocene and early Holocene concomitant with episodic droughts. As a result, pronghorn populations are physiologically and behaviorally adapted to climatic catastrophes. By the time of the differentiation and expansion of the North American deserts 4,000 to 6,000 ybp, pronghorn were found from 20 ° to 53° North Latitude and from just east of the 100th Meridian westward to the Pacific Ocean. This expansive distribution has only recently become fragmented, and with the exception of Lower California, pronghorn populations show little morphological variation. Previous subspecies designations therefore appear unwarranted and in need of revision.

***Key Words**:* pronghorn, *Antilocapra americana,* taxonomy, Pliocene, Pleistocene, Holocene, Intermountain West, climate, subspecies

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Antilocaprids appear to have evolved from a primitive ruminant that arrived in North America from Eurasia during late Eocene or Miocene time more than 20 million years before the present (mybp) as per Kurtén and Anderson (1980) and O'Gara and Janis (2004*a*)**.** Although the modern Family *Antilocapridae* are distinguished largely on the basis of having winter deciduous horn sheaths, other distinctive criteria include horn cores that project directly above over-sized eye sockets, open tear ducts, a lack of lateral toes or dew claws, an unusual brittle and hollow pelage that insulates the animal from extreme temperature changes, and a delicate, characteristic limb bone structure (Valli 2004). The pronghorn's hypsodont teeth are also unusual in that while superficially resembling those of cervids, are more like those of sheep and goats in having crowns that continue down into the alvelous and some permanent teeth erupting after age 4 (Heffelfinger 1997, Rich White, pers. com.).

Philadelphia naturalist George Ord provided the first scientific description of a pronghorn in 1815 after examining "stuffed" specimens of a male and a female at the Philadelphia Academy of Sciences that were collected on the Lewis and Clark expedition (McCabe et al. 2004). It was also Ord (1815) who recognized the unique nature of the animal's horns and gave the pronghorn its scientific name, *Antilocapra americana*—American antelope-goat. Five subspecies or races of pronghorn have since been described:

Antilocapra americana americana (Ord 1815): this, the nominate species and subspecies name, has been assigned to pronghorn not within the distributional ranges assigned to other subspecies.

A. a. mexicana (Merriam 1901): C. Hart Merriam (1901) described this subspecies from a young adult male taken from a series of 11 animals collected in 1899 by E. W. Nelson and E. A. Goldman for the U. S. National Museum in the vicinity of the Sierra en Media, Chihuahua, Mexico. The animals in this series were said to be different from *A. a. americana* by being slightly smaller and paler in pelage, in having a reduced or absent mane, possessing a dorsal streak down the back of the neck, and having more pronounced facial markings than more northern specimens. The skull of the type specimen was described as similar to *A. a. americana*, but with less protruding orbits, more slender nasal bones, thinner auditory bullae, and longer posterior nostrils. The range of *mexicana* was arbitrarily described as originally occurring throughout the deserts and semidesert grasslands of northeastern Mexico, Trans-Pecos Texas, southern New Mexico, southern Arizona, and southern California (Mearns 1907). Later descriptions restricted the range of this species to east of the Santa Cruz River in southern Arizona (see e.g., Hall and Kelson 1959, Hoffmeister 1984).

A. a. peninsularis was described by E. W. Nelson (1912) from a series of 12 specimens collected near what is now the boundary line between Baja California and Baja California Sur. *A. a. peninsularis* was considered to have darker facial markings than *mexicana,* to have darker ear tips than either *mexicana* or *americana*, to possess a more divided rump patch than *americana*, and to have shorter, thicker, and more upright horns than either *mexicana* or *americana*. The horns were said to have warty protrubences below the prong, and the molars heavier than in the other 2 subspecies. Since then, other animals collected in Lower California south of Parallel 31º N have been assigned to this subspecies, primarily on the basis of geography (Figure 1).

A. a. oregona (Bailey 1932): this “Great Basin” race was described on the basis of an adult male collected on Hart Mountain, Oregon, by Vernon Bailey of the U. S. Biological Survey. Bailey, C. H. Merriam’s son-in-law, thought this type specimen could be differentiated from other subspecies of pronghorn by its longer horn length, larger feet, and more varied pelage. Subsequent taxonomists questioned the validity of these characters, and limited this taxon to eastern Washington, Oregon, northeastern California, and extreme northwestern Nevada (Einarsen 1948).

A. a. sonoriensis (Goldman 1945): This, the last race to be described, and is based on a female type specimen collected in 1932 for the U. S. National Museum by Vernon Bailey 65 km north of Rancho Costa Rica in Sonora, Mexico. This animal was said to differ because of its more diminutive size and paler color. Despite none of the more recently collected specimens being nearly so small as the type specimen, all pronghorn in northwestern Sonora, extreme northeastern Baja California, and in southwestern Arizona south of the Gila River have been assigned to this now “endangered” subspecies (Paradiso and Nowak 1971, Wright and deVos 1986).

The small sample sizes used to describe these subspecies, combined with the outmoded methodology of using skull measurements and such plastic descriptive criteria as horn characters and pelage coloration, have caused mammalogists to question the validity and/or distributions of *mexicana*, *oregona*, *and sonoriensis* (e.g., Cockrum1984, Hoffmeister 1984, O’Gara and Janis

Figure 1. Distribution of *Antilocapra americana* and its subspecies according to Hall and Kelson 1959.

2004*a*:25). Pelage characteristics and skull measurements are often highly variable between individuals, and unreliable when it comes to determining subspecific status, which should be based primarily on genetic isolation and local adaptations (Simpson 1945). Most pronghorn populations were more or less connected to other populations prior to 1850, and gene flow presumably occurred between the various "subspecies" (Figure 1).

Moreover, the proposed subspecies make little ecological sense. For example, pronghorn populations formerly occurring in the Sonoran Desert in southeastern California are presently included with the same subspecies occurring in Canada. Conversely, populations assigned to *americana, mexicana, peninsularis*, and *sonoriensis*, can all be found within the boundaries of the Sonoran Desert. All of the pronghorn formerly found in the highly diverse state of California are considered to be *A. a. americana*.

With a few notable exceptions (e.g., in Sonora, Baja California Sur, and extreme southwestern Arizona), most pronghorn populations south of the 38th Parallel were decimated prior to 1940 and have been replaced or augmented with animals from other regions (Yoakum 2004). What had been a moot systematic conundrum became a legal problem with the passage of the Endangered Species Act in 1973—federal legislation that gave the various subspecies of pronghorn a legal status never intended in the original descriptions.

All of the biologists involved in naming pronghorn subspecies were either C. Hart Merriam or his associates. Merriam, who besides being the founder of American mammalogy, was a notorious taxonomic "splitter." He once published a treatise on the grizzly and brown bears of North America in which he sub-divided the grizzly (*Ursus arctos*) into no fewer than 78 species—three of them based on specimens from one mountain range in Arizona (Merriam 1918)! These and similar errors in logic were due to Merriam and his colleagues describing new species on the basis of the color, measurements, and cranial characters of a few "type specimens." Believing that "external pressures" determined individual variation, Merriam considered any significant variation in a specimen as evidence of species differentiation, stating that: "*forms which differ in definite, constant and easily recognized characters should rank as species even if known to intergrade*." Hence regional color phases, and animals with a different skull configuration were considered new species. Merriam did not only consider morphological mutations as individuals possibly leading to species development, he considered each mutation a species (Sterling 1977). As such, his approach contrasted sharply with systematic taxonomists such as Mayr (1942) and Simpson (1961), who determined that 3 characteristic properties were needed to define a species—reproductive isolation, differences in ecological affiliation, and the ability to consistently distinguish morphological differences from other forms.

Because Merriam and his colleagues with the U. S. Biological Survey continued to describe new forms on the basis of "type specimen measurements," mammalogy became a uniquely American "science" with few European biologists accepting their species descriptions. A common response has been to retain American species descriptions but to relegate them to subspecies status. For example, by 1912 Biological Survey personnel had described 2,138 new species and subspecies of mammals, a number later reduced to about 800 species (Sterling 1977). There has nonetheless been no rigorous winnowing of many of the named subspecies including 3 proposed for *Antilocapra americana* (see e.g., Hall and Kelson 1959). It therefore appears that an evaluation of the evolutionary history of this species and it's habitats is warranted. The fossil record strongly suggests that the origins of *Antilocapra americana* were in Western North America, probably in the general area now encompassed by the Intermountain West (Kurtén and Anderson 1980, Heffelfinger et al. 2002, O'Gara and anis 2004*b*). This region, prior to the latter half of the Tertiary Period, about 20 million years before present (mybp) was covered by forests and woodlands, which were occasionally broken up into savannas and parklands (Axelrod 1956, 1958, 1966, 1979*a*, 1979*b*, 1985). Otherwise, the physiognomy of the North American continent looked not too different than it does today; the Great Plains and Great Basin were already in place, and the Rocky Mountains were resuming a general uplifting that had begun during

Oligocene times 25 to 37 mybp (Kurtén and Anderson 1980). This orthographic rising, accompanied by other uplifts to the west, resulted in a developing series of rain shadows that intercepted Pacific storms that increasingly caused a drying of the continent's interior. It was then, that most accounts have North America's grasslands originating (e.g., Dix 1964, Axelrod 1985, Sims 1988).

By the middle Miocene, around 14-15 mybp, *Pliocerus*, the first known antilocaprid, was evolving in North America along with newer, more arid savanna habitats. Two sub-families then evolved, an older *Merycodontinae*, sometimes called pronglets, and the more derivative *Antilocaprinae* or prongbucks. Evolution was relatively rapid, the family attaining its greatest diversity around 7 to 8 mybp when both sub-familes were forced to become increasingly arid-adapted as treeless 'prairies" encroached on the savannas (O'Gara and Janis 2004*b*). Generally, the smaller, 12 to 20 kg pronglets are thought to have favored the more rugged closed habitats, while the larger limbed prongbucks held to the more arid habitats with some species appearing to use caves similar to modern desert bighorn sheep (*Ovis canadensis mexicana*). By 4-5 mybp, only the more arid adapted *Antilocaprinae* survived, the sub-family sharing increasingly open landscapes with horses, camels, and other ungulates.

As the Tertiary's forests continued to retreat, woodlands, savannas, and meadow-like parklands emerged and enlarged throughout the Intermountain West. Here, the climate became not only drier, but also possibly warmer, resulting in an increase in drying winds and a potential for fire—ingredients making these landscapes more conducive to grassland formation and maintenance (Dix 1964). Whatever their causes, savanna-grasslands of sizable extent were present in the Great Basin by about 4 mybp. Vast, open prairies were yet to come, however (Axelrod 1985).

Pliocene Background

The advent of the Pliocene after 5 mybp saw a continued rising of the Sierra Nevada, and a cooler Pacific Ocean (Axelrod 1985). The drying trend in the Intermountain West accelerated even though winter precipitation averages were considerably greater and less variable than today. Winter temperatures in the interior rose, while summers remained cooler than at present with Arcto-Tertiary grasses expanding in the north and summer-growing C-4 grasses becoming increasingly prevalent in the south. Savannas and shrub-steppe captured the valley floors and low plains as the forests retreated from all but the mountains and stream bottoms. By the end of the Pliocene (1.8 mybp), conditions were drier than had heretofore been experienced in the Great Plains and Great Basin (Axelrod 1985). Southward, chaparral, thornscrub, and new "semidesert" grassland began invading valleys and plains in what are now northern Mexico and the American Southwest (Axelrod 1979*a*, *b*; Van Devender 1995; McAuliffee and Van Devender 1998; Figure 2).

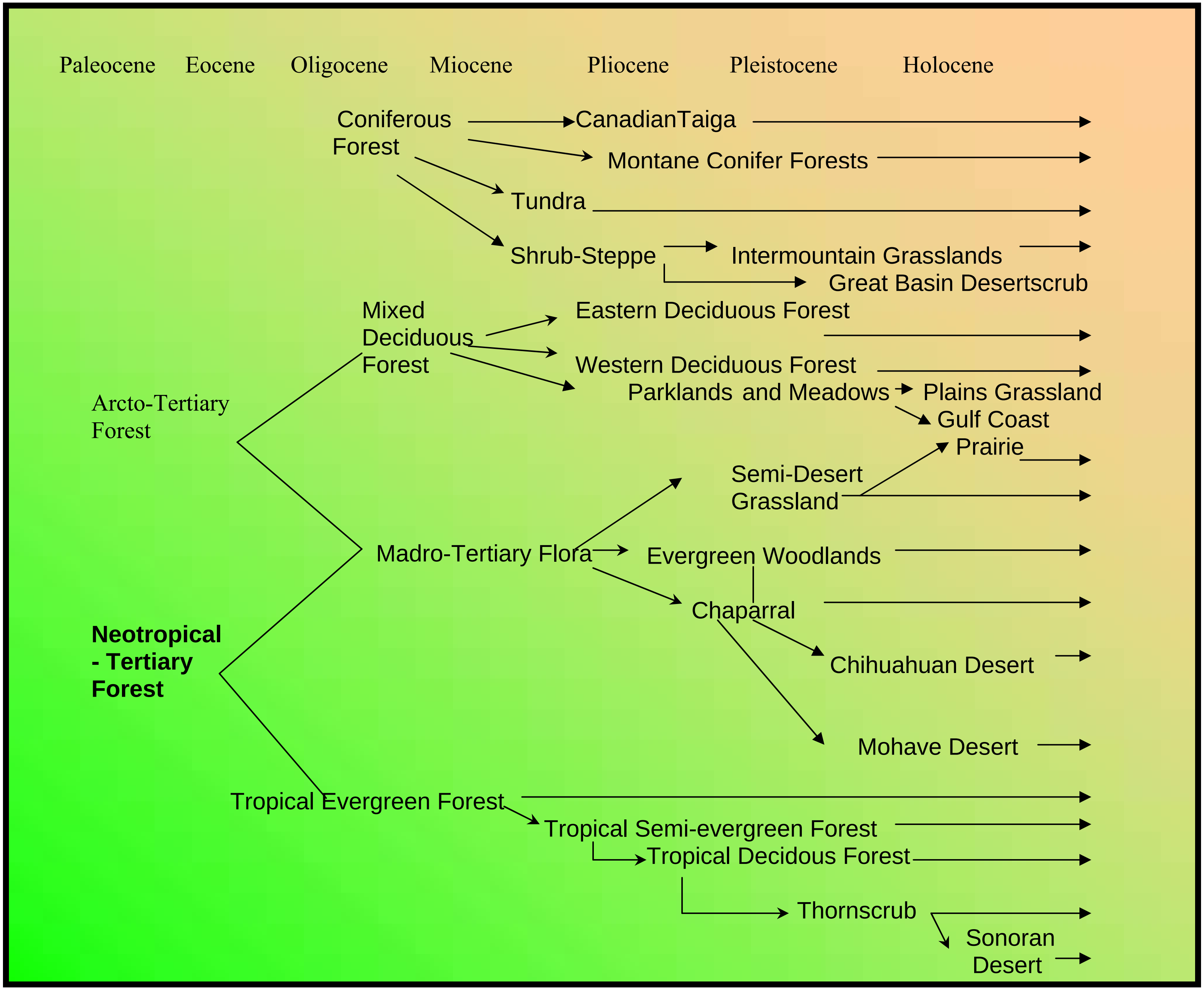

Figure 2. Evolutionary History of North American Biotic Communities

The final years of the Pliocene epoch (3.5 to 1.8 mybp) were a time of evolving mammalian divergence with a large assemblage of large mammals inhabiting western North America. The Antilocaprids were no exception, and no fewer than 10 genera of prongbucks were present ranging in size from the dik-dik (*Madoqua*) sized *Sphenophalos* and *Proantilocapra* to the nearly pronghorn size *Tetrameryx* and/or *Stockoceros* (Skinner 1942*)*. This diverse fauna, formerly composed mostly of browsing ungulates, was now increasingly joined by ruminants with high, hypsodont molars. Adding to this assemblage was the emergence of the land bridge to South America about 3 mybp (Kurtén and Anderson 1980), permitting animals to enter North America from the south to join other mammal species arriving from Asia.

Most fossil floras in western North America after 3 mybp suggest cooler temperatures than now with local glaciers occupying the coldest areas (Axelrod 1979*a*). Although rainfall may have been 500 mm greater than at present on the Pacific coast, the rising Peninsular, Sierra-Nevadan and Rocky Mountain ranges were further interfering with winter precipitation in the interior. By 1-2 mybp, the climate appears to have become increasingly unstable due to rain shadows, cyclonic depressions and changing storm tracks. Winter temperatures became decidedly colder and more severe. Summers, however, may have been warmer than now, with warm season rainfall occurring, particularly in the south (Axelrod 1979*b*). But, more than any other factor, it was an increasing variation in temperature extremes that heralded the coming of the Pleistocene epoch in what was still a generally benign climate for large, open country mammals (Kurtén and Anderson 1980).

Much of the continent remained covered by forest or woodland where newly arrived cervids were evolving in place. Other genera of native North American mammals, including such antilocaprids as *Tetrameryx,* now began to disappear, their place taken by more open country pronghorns including the ancestors of *Antilocapra americana* (Lindsay and Tessman 1974, Kurtén and Anderson 1980, Byers 1997, O'Gara and Janis 2004*b*, Figure 3). By 1.75 to 2.5 mybp, a newer grassland fauna was evolving concomitant with a drier climate, interspecies competition, and accelerating extinctions. Grassland species such as prairie dogs (*Cynomonys*) and grouse (*Pedioecétes*, *Tympanúchus*) appeared (Kurtén and Anderson 1980*),* and it was probably about this time that the various species of grassland sparrows began to evolve, the genus *Ammódramus* differentiating into northern prairie forms with species of *Aimóphila* evolving in the southern savannas.

Between 2 mybp and 75,000 ybp a series of glacial periods occurred, each followed by an interglacial interval of shorter length (Kurtén and Anderson 1980, Grayson 1993, Van Devender 1995). During the glacials, ice sheets covered the northern portions of the continent, while in the south and west a cooler climate prevailed. Winds increased in frequency and velocity with fluctuating temperatures, the intervening inter-glacials being warmer than at present. Both the Rocky Mountain and Sierra Nevada uplifts continued, while the interior basins were subjected to significant loess deposition and drainage alteration. The savannas and "shrub-steppes," populated mostly by Arcto-Tertiary species, alternatively expanded and receded, generally expanding during the warmer, drier interglacials with increased incidences of drought and fire. As conditions fluctuated, *Sphenopholos* evolved into *Antilocapra,* a genus that evolved in turn into the still extant, *A. americana* (O'Gara and Janis 2004*b*).

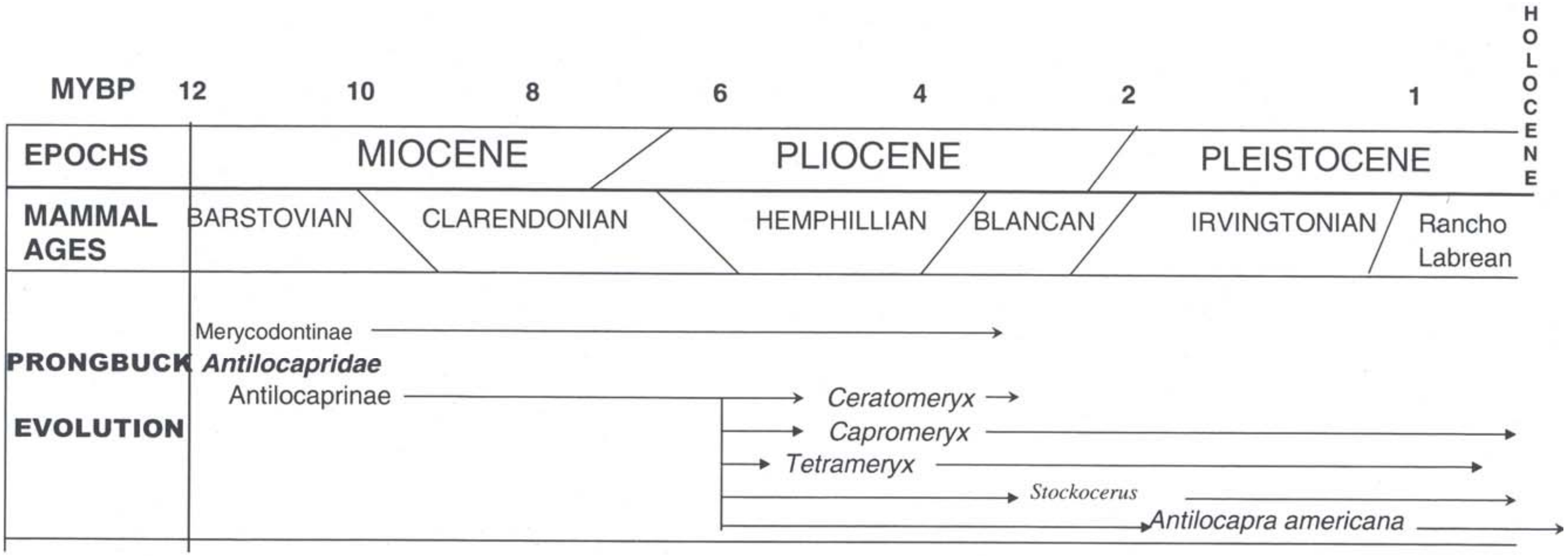

Figure 3: Time line of Late Cenozoic Epochs and Mammalian Ages with Antilocaprine evolution. Information taken from Lindsay and Tessman (1974), Kurten and Anderson (1980), Heffelfinger et al. 2002, and Rich White (pers. comm.)

The Pleistocene: A Time of Adapting and Winnowing

Much of the Great Basin was covered during the early Pleistocene by subalpine forests and tundra, with spruces (*Picea*) and firs (*Abies*) occurring as low as 3,500 feet elevation (Thompson 1990). Temperate montane species such as Utah juniper (*Juniperus osteosperma*) and ponderosa pine (*Pinus ponderosa*) had yet to arrive, and the lower valleys appear to have been primarily clothed in spruce parklands, marshy meadows, or sagebrush (*Artemisia*) steppe with subalpine conifers and shrubs dominating the coarser sites (Nowak et al. 1994; Figure 4). During the interglacials sagebrush and other steppe dominants radiated eastward, westward, and southward, while in the American Southwest, sclerophyllous vegetation expanded northward, westward, and eastward from Mexico (Thompson and Anderson 2000).

What is now western America was inhabited by an array of savanna-inhabiting mammals including several genera of pronghorn, horses, and camels, and the large bison (*Bison priscus*), which first appeared between 1.75 and 0.8 mybp. Then, during the Sangmonian interglacial about 45 thousand years before the present (kybp), many of these ruminants were joined by others from Asia, accelerating large mammal diversity and competition. Some, such as the forest and meadow-dwelling *Mammuthus, Bison,* and *Cervus* had arrived during ice-free periods when such purely grassland species as *Saiga tatarica* were unable to penetrate beyond the Beriengian spruce forests. Ruminants consisted of both browsers and grazers with some of the most successful being the pronghorns, *Tetrameryx* and *Stockocerus* (Kurtén and Anderson 1980. The influx of new arrivals notwithstanding, large mammal diversity now began to decrease due to further climatic shifts and increased competition, the American-derived species being more prone to extinction than their Eurasian counterparts--91% vs. 46% (Kurtén and Anderson 1980). Although grazers went into decline, open country species generally continued to fare well with the antilocaprids being represented by several genera, most of which appear to have been specialized to live in savannas (Heffelfinger et al. 2002). The declines in temperatures in the Great Basin and Rocky Mountains during the glacials forced large herbivores to adopt migratory strategies to cope with attenuated growing seasons, while large mammals in the Intermountain West appear to have evolved a more nomadic feeding strategy (Kurtén 1972, Burkhardt 1996). Some of the smaller prairie mammals, such as prairie dogs and thirteen-lined ground squirrels (*Spermophilis tridecemlineatus*), became common and widespread by adapting a hibernation strategy.

During the most recent or Wisconsin glaciation that lasted from about 45 to11.3 kybp, North America saw significant decreases in growing season temperatures, and although pluvial lake levels may have remained relatively constant, sea levels lowered by about 100 m due to pack ice formation (Van Devender 1995). Then, with the withdrawal of this last great ice sheet beginning ca. 18,000 ybp, sea and lake levels began to rise, mainly due to the spring thawing of snow packs and glaciers. But even though winter temperatures began to warm, summers remained relatively cool. Summer rainfall shifted eastward and southward in the Great Basin and Northern Plains, with rainfall becoming increasingly erratic after about 14,500 kybp (Axelrod 1985). In the northern Great Basin, open conifer woodlands began replacing steppe, savanna, and tundra (Thompson and Anderson 2000). Then, beginning about 14,000 ybp, pluvial lake and ground water levels dropped dramatically indicating a series of massive droughts (Haynes 1991, Betancourt 2004).

Figure 4. Hypothetical landscape of Intermountain Steppe during a Pleistocene Interglacial.

By the end of the Pleistocene ca. 12,000 ybp, *Antilocapra americana* had emerged as a species superbly adapted to temperature extremes as well as arid conditions, having evolved physiological adaptations to prevent both overheating and desiccation (Bromley 1977). Pronghorn do not put on much body fat as its oxidation requires additional use of water—a commodity not always available in the increasingly arid West. Not only did these adaptations allow pronghorn to prosper, the species could now cope with the increasingly erratic conditions that characterized the coming Holocene (Geist and Francis 2001; Figure 5).

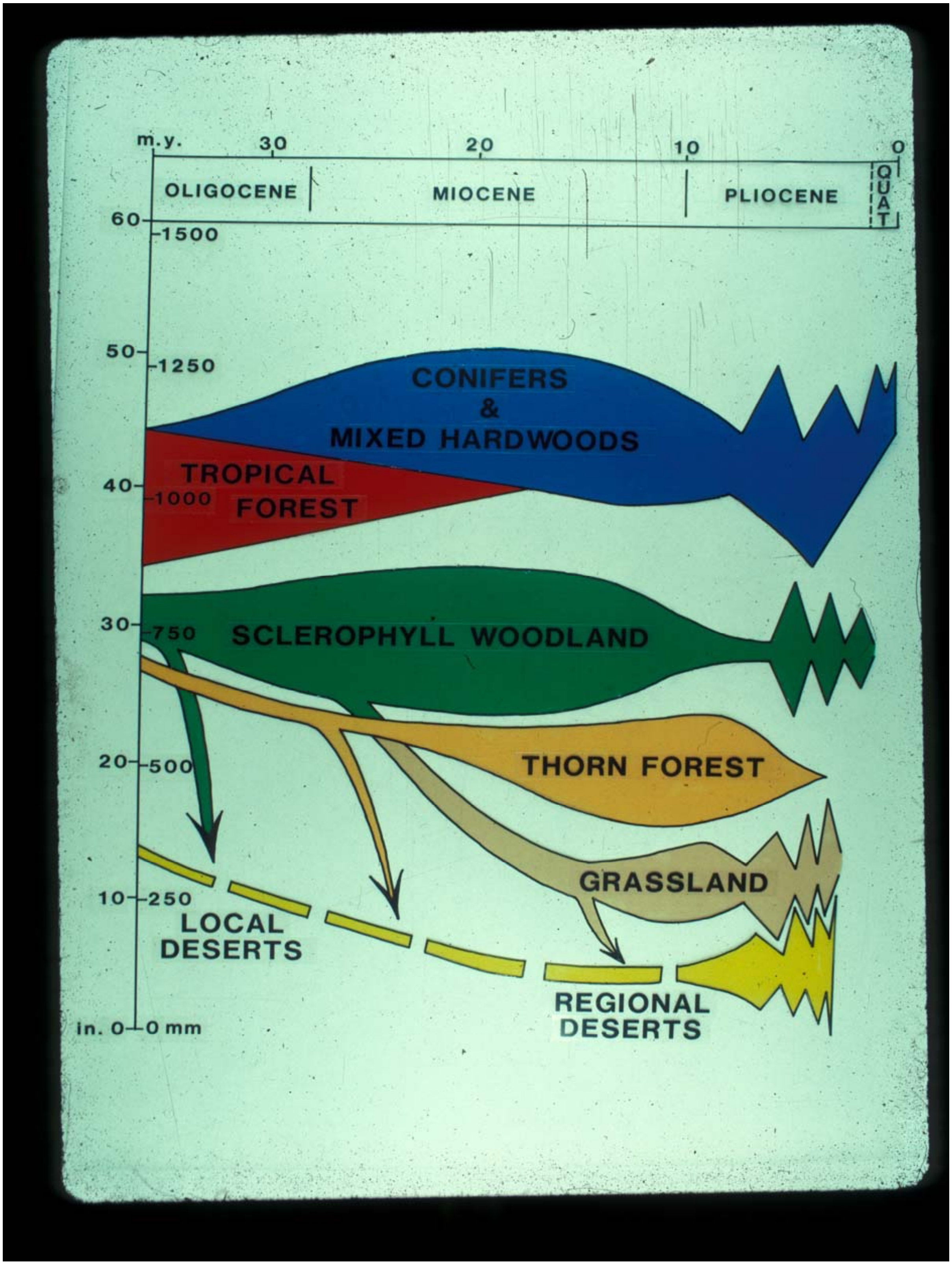

Figure 5. Relative appearance and history of major North American biotic commnities through time as modified from Axelrod (1979).

All in all, the Pleistocene had been a time of great dislocations, but one of plant and animal movement rather than a time of extinctions due to dislocations by new species (Grayson 1991). Although much of the northern prairie region had been locked up under ice during the full glacial, meadow-like grasslands and savannas had generally expanded during the interglacials. In Alaska and northern Canada, forest and muskeg reigned, but further south, new Plains grassland was increasing in size. Here, cool-season (C-3) and warm-season (C-4) grasses alternated in dominance, the former expanding during cold periods when summer rainfall was deficient, the latter shifting northward and westward during warm summer-wet periods (Sims 1988). In the largely glacier-free Intermountain West, vegetation changes around 12-13 kybp were more modest with some plant species remaining essentially in place while others "migrated" attitudinally and/or vertically (Nowak et al. 1994). Several species of small mammals did the same, but some of the larger ones went extinct (Grayson 1993). Still others such as bison were forced to abandon California's C-3 grasslands, where the forb and shrub dependent pronghorn persisted (Stock 1992).

The Holocene: A Time of Honing

Although North America averaged 75 to 100 mm more precipitation between 9 and 11 kybp than at present, and mean temperatures were only 3-4 ºC cooler, some of the winters appear to have been much colder than now with the summers becoming increasingly hotter and drier. The result was a mosaic of extreme climatic conditions and local weather disasters as precipitation amounts and temperature fluctuations became increasingly erratic. Even as winter precipitation continued to dominate the northern and western portions of the continent, periodic droughts increased in frequency and severity. Although the higher mountains were clothed in conifers, sagebrush steppe and juniper savanna once again dominated large areas of the Great Basin and Great Plains as pluvial shorelines lowered, some lakes drying up entirely (Axelrod 1985, Spaulding 1990, Nowak et al.1994, Thompson and Anderson 2000).

Vegetation trends south of the Great Basin at the close of the Wisconsin glaciation are less clear, but the predominant plant cover between 300 and 1700 m elevation in much of what is now Arizona, California, and northern Mexico appears to have been a mixture of woodland and chaparral populated by pinyon pines (*Pinus monophylla*), live oaks (*Quercus* spp.) and junipers (*Juniperus*) (Van Devender 1990, 1995). The climate was milder and wetter than now, with twice the winter rainfall. The summers were cooler, and summer precipitation, while becoming more erratic in the north and west, remained influential in the south (Connin et al. 1998, Betancourt 1990). In Mexico, mixed and subalpine forest communities occupied areas above 2000 m (Bettancourt 1990), while conifer forests, encinal woodlands and chaparral covered extensive tracts of what is now semidesert grassland or desertscrub (Metcalfe et al. 2000). Temperate warm-season grasslands, always localized and restricted to generally level terrain, constituted a major vegetation type in the Central Valley of California and Mexico's Central Plateau.

Some of the large herbivores prominent in fossil deposits after 45,000 ybp including the mammoth (*Mammuthus primigenius*), horse (*Equus conversedens)*, and the camel, *Camelops hesterus*, now began to disappear (Owen-Smith 1987). Only a few of these species were replaced by arrivals crossing over from Eurasia during the interglacials via Berengia. The more recent of these immigrants, including the grizzly bear (*Ursus arctos*), bison (*Bison occidentalis*), and humans (*Homo sapiens*), were savanna-dwellers, which, coupled with earlier arrivals such as the bighorn (*Ovis canadensis*) and elk (*Cervus elaphus*), now began to displace the older, "native" grazers (Martin and Wright 1967). More than two-thirds of North America's ungulates disappeared between 45,000 and 10,000 ybp, including all but one genus of prongbuck, the one we call pronghorn. The formerly widespread *Tetramerex shuleri* was gone by about 37,000 ybp, *Stockoceros onusrosagris* by 11,500 ybp*, and Capromeryx minor* by 11,170 ybp. Despite all 5 of the cervids present during Wisconsinan times surviving, and 5 of the 9 bovids, none of the species of camels, horses and elephants persisted in North America much past 10,000 ybp (Grayson 1991). Of the large (>35 kg) native herbivores adapted to open country, only *Antilocapra americana* survived. All in all, 35 genera of large mammals disappeared (Kurtén and Anderson 1980). Although pronghorn probably retained their unique winter horn sheath growth pattern from pre-Pleistocene times, the insulating characteristics of their hair quite possibly evolved during the Ice Ages to be honed during the Holocene. These, and perhaps physiological and behavioral adaptations allowed *Antilocapra americana* to survive the Pleistocene, whereas its relatives and competitors did not.

That these large mammal extinctions occurred due to climate change is virtually certain (Grayson 1991, Grayson and Meltzer 2002, Tankersly and Redmond 2000). The best climatic explanation appears to be the winter droughts that began in the Intermountain West about 14,000 ybp and continued on to the megadrought described by Haynes (1991) for southeastern Arizona around 11,000 ybp (10,700-11,190). Such droughts, punctuated by episodes of extremely low temperatures, not only triggered plant die-offs, expansive fires, and widespread insect outbreaks, they resulted in years in which nutritious vegetation was totally lacking and the reproductive success of large herbivores would have been almost nil. Given the intense competition and predation then existing, it is no wonder that so many open country herbivores, including all of the antilocaprids save *Antilocapra americana*, disappeared by *ca.* 11,000 ybp (Grayson and Meltzer 2002, Hall and Kelson 1959). It is interesting to note that the pronghorn's only serious surviving competitors were elk in the West and bison in the East, and that both of these animals were primarily gramivores. Hence, pronghorn experienced no serious competition during the Holocene until the advent of Western Man and his livestock.

Only a few large grassland mammals remained to be hunted by Man, who arrived in western North America about 11,500 ybp (Frison 2004). Of these, only bison, mammoths, and mastodons persisted, and then only where summer-growing grasses still thrived. Connin et al. (1998) found that late Pleistocene mammal teeth from such species as *Bison* and *Mammuthus* indicated a strong preference for consuming summer growing C-4 grasses, and both these grasses and their consumers had become increasingly restricted to east of longitude 114º W and south of latitude 35º N prior to perishing in the "Clovis megadrought" that took place ca. 11,000 ybp (Haynes 1991). *Antilocapra americana*, on the other hand, exhibited the lowest C-4 values, feeding primarily on C-3 plants at all sites tested (Connin et al. 1998). This is also in contrast to such extinct forms as *Stockocerus onusrosagris*, which appears to have primarily fed on C-4 grasses (Rivals and Semperson 2006).

Pronghorn had not only become superbly adapted to extremes of heat and cold, but also to drought, exhibiting the same adaptations to these extremes as they do today. Unlike *Bison occidentalis*, which was going through a reduction in size, pronghorn cranial material was essentially the same in Folsom Age (10,800 ybp) specimens as is the case today (G. Frison, *pers. com*.). This is interesting in that the pronghorn's congener, *Capromyrex* had also diminished in size prior to becoming extinct during Folsom time, suggesting that adaptations to small habitats may have led to a dead end (Figure 6). Perhaps the pronghorn's retention of body size, coupled with its cursorial abilities, was not so much an adaptation to escape predators, as to cover distance and expand into new ranges during times of climatic stress.

Figure 6: Progression in size of Caromeryx from Rancholabrean times through late Pleistocene.

By ca. 9,000 ybp, modern rainfall and seasonal drought patterns were largely established (Thompson et al. 1993). Of the 3 air masses determining western North America's climate—a cold, dry air mass centered in the northwest; a warm, moist air mass in the Gulf of Mexico, and an intense but erratic Pacific air mass--the latter was the more important for the stronger the "westerlies," the more extensive the drought. Given these emerging fore-summer drought patterns, North America's deserts and grasslands began to assume their defining characters based on temperature minima and regional drought patterns (Betancourt et al. 1990, Betancourt 2004). Only in the cold Intermountain West and northern Great Plains was winter precipitation reliable enough to maintain a semblance of the conifer-savanna and sagebrush shrub-steppe habitats that had formerly defined so much of the West.

Eastward, in the continent's midsection, a bi-seasonal rainfall pattern and an influx of C-4 grasses from the south characterized a shifting region of prairie grassland, while to the south and southeast, summer precipitation patterns favored tall grass and coastal prairies composed of both Arcto-Tertiary and Madro-Tertiary grasses (Figure 7). In the American Southwest and northern Mexico, a scantier bi-seasonal rainfall pattern, coupled with increasingly warmer winters, resulted in the replacement of most of the C-3 grass dominated grasslands by a semidesert grassland savanna. Here, the higher elevations were occupied by fire-maintained savannas of C-4 bunch-grasses punctuated by *Juniperus* spp. and the recently arrived *Pinus ponderosa* and *P. monophylla*. Meanwhile, temperate grasslands, dominated by winter rainfall and characterized by spring-responding grasses and forbs, were assuming control of California's valleys (Sims 1988). Having attained the status of a "sweepstakes" winner in its ancestral shrub steppe and conifer savanna habitats in the Intermountain West, pronghorn could now also occupy newer open country environments as long as winter precipitation provided spring forb growth and nutritious browse plants (Jensen et al. 2004, Figure. 8).

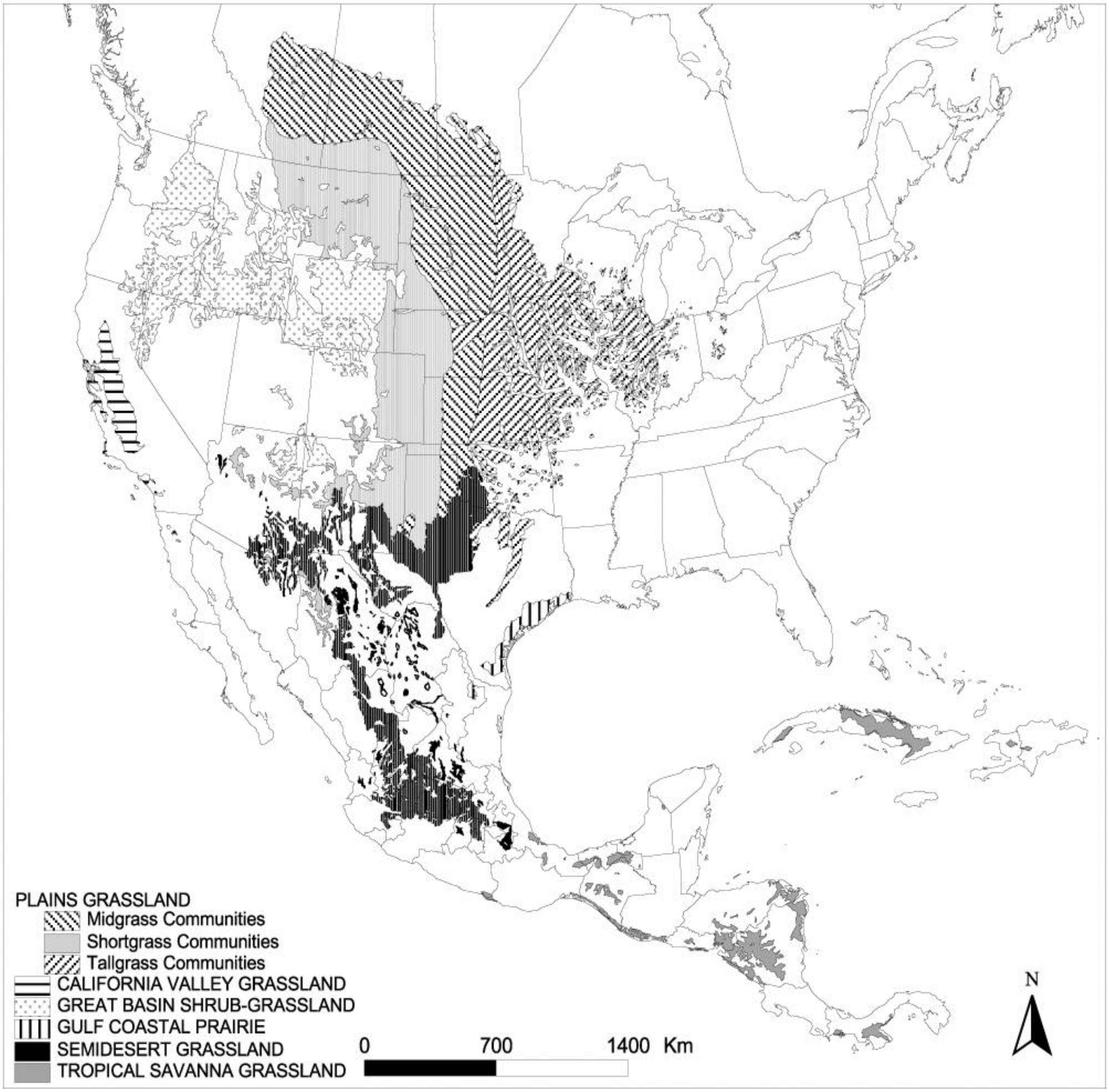

Figure 7. Grasslands of North America, ca. 1850.

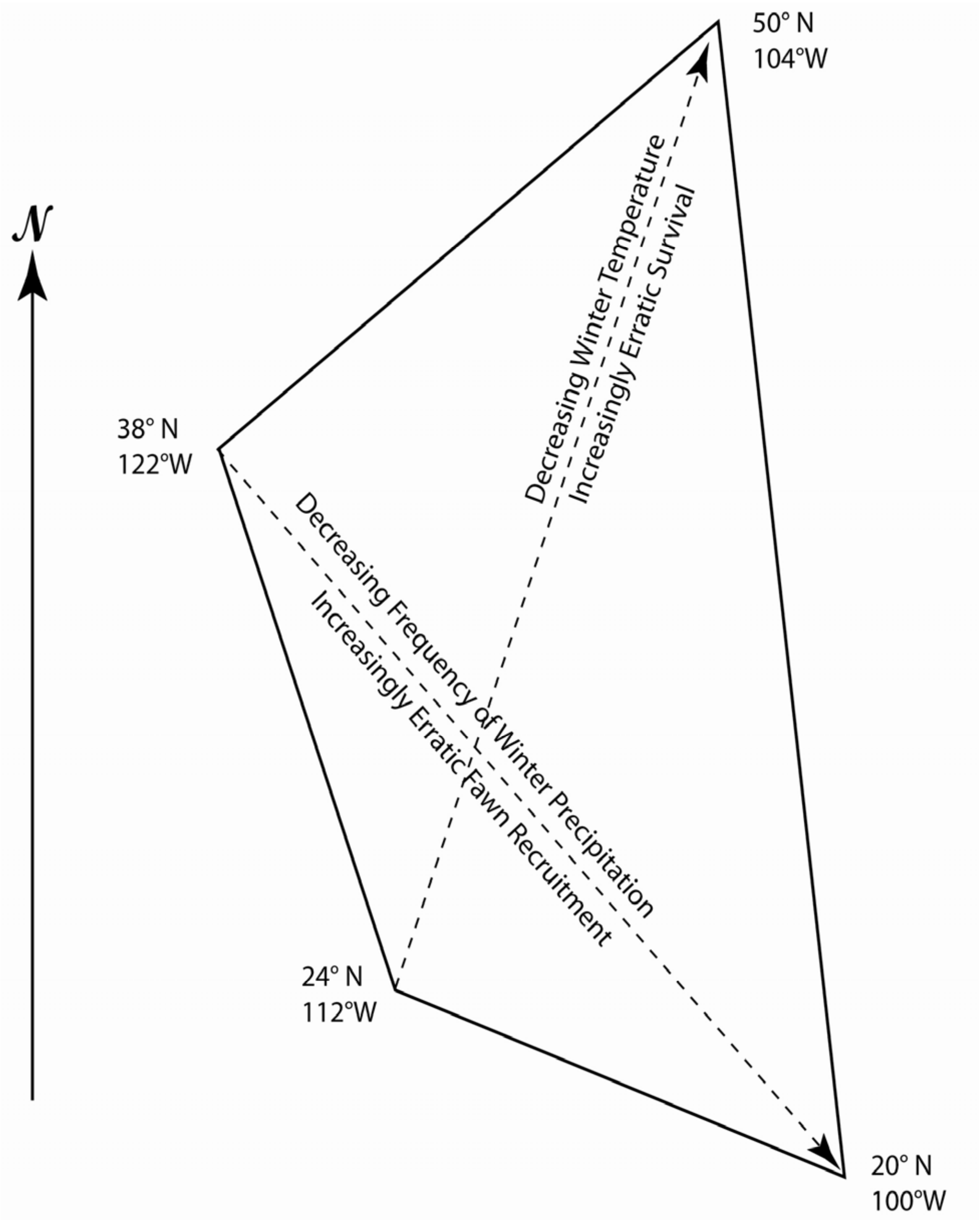

Figure 8. Schematic of evolutionary pressures on *Antilocapra americana*.

Summer temperatures rose continued to rise after 8,000 ybp and are thought to have been warmer than even today's (Axelrod 1979). Rainfall amounts continued to decline in the continent's western interior where summer precipitation became increasingly erratic, opening up much of the remaining woodland to invasion by open savannas and shrub-steppe (Van Devender 1990, Metcalfe et al. 2000). Even greater climatic oscillations occurred during the Altithermal, a hot, dry period between 4,500 and 7,000 ybp, a period characterized by nearly total winter precipitation failure accompanied by searing droughts and winds (Antevs 1955).

By 4,000 ybp such arid-adapted plants as *Juniperus osteosperma* and *Ephedra viridis* were declining below 1300 m in the Great Basin (Nowak et al. 1994), and the few large herbivores present had to vacate much of their former range and occupy new habitats elsewhere. Bison continued a retreat from California, the Great Basin, and the "Southwest" that continued on through to historic times, while some *Cervus elaphus* populations moved southward into the highlands of what is now Arizona and New Mexico (Carrera and Ballard 2003). The pronghorn, being a C-3 feeder was better equipped to survive these climatic catastrophes, not only in California, but anywhere in the West that still received reliable winter precipitation. Only in such extremely arid sites as Death Valley and the Gran Desierto did pronghorn totally disappear.

Although summer precipitation in the Southwest may have increased after 4,500 ybp, winter rainfall amounts were often erratic, and lower elevations were invaded by an increasing array of cacti along with such shrubby desert trees as catclaw (*Acacia constricta*) and mesquite (*Prosopis* spp.). Coastal grasslands competed with coastalscrub, while in the interior Southwest, only the level, more favorable sites, were occupied by a "semidesert grassland" consisting of a mixture of Plains grasses and xeric-adapted shrubs and succulents. To the southeast, in northern Mexico, semidesert grasslands increasingly gave way in turn to Chihuahuan desertscrub, while in present-day Sonora and southwest Arizona, cacti and small trees such as foothill paloverde (*Cercidium microphyllum)* prospered in what would become the Sonoran Desert (Van Devender et al. 1990).

Periodically interrupted by episodes of cooling, a general warming trend prevailed throughout the Holocene. Each cooler (and wetter) episode was followed by another warming trend, the most recent occurring after 1890 (Dix 1964) and during the 1990s. Great fluctuations in temperatures attended these episodes, and the incidences of wind and fire that accompanied them allowed grasslands to spread northward and eastward. The increasing replacement of shrub-steppe and semidesert grassland by desertscrub, notwithstanding, North America's grasslands probably reached their greatest extent sometime between 1600 and 1850 AD when approximately 40% of the continent exclusive of Alaska was an open "prairie" of one type or another (Dix 1964). That North America's grasslands reached their fullest development and extent after the continent's grassland megafauna had been depleted was an accident of evolutionary history, one brought about by the climatic vagaries of the Pleistocene-Holocene transition rather than the fluctuating aridity attendant with the Holocene.

The pronghorn, having survived the climatic "bottlenecks" of both the Pleistocene and Holocene, emerged behaviorally and physiologically adapted to the climatic catastrophes that created the North American deserts. The species matures rapidly, both physically and behaviorally, attaining adulthood before age 2 (Byers 1997, Brown and Mitchell 2006). Females twin during good times and absorb fetuses during bad (O'Gara 1969). The gestation period is longer than in other ruminants of comparable size, and pronghorn fawns are the most precocious North American ungulate (O'Gara 2004*a*, 2004*d*). The physiology of the adults is such that they are able to outrun any and all predators, survive freezing temperatures for days on end, and adjust to conditions of extreme heat and drought. Having little competition from native shrub-steppe and grassland ungulates, pronghorn recently enjoyed a widespread range from Saskatchewan, Canada, to Durango, Mexico, and ranging from sea level to 3350 m – a distribution limited only by declining winter rainfall in the south and east, decreasing temperatures in the north, and unsuitable vegetation in the south and east. So expansive was this widespread distribution that it precluded regional isolation until widespread Western settlement after 1850.

These adaptations are especially manifest in the animal's ability to handle aridity and drought. Pronghorn employ many of the same physiological adaptations described by Grenot (1991) for desert ungulates in Africa and Asia, where drought conditions have been exerting evolutionary pressures for longer time periods (O'Gara 2004*b*, 2004*c*, 2004*d*). Nonetheless, other desert adaptations employed by African ungulates such as the ability to lose >20% of their body weight during drought, obtain moisture through the oxidation of fat, store excess water in the rumen, and shift to feeding at night when humidity levels are high are as yet undocumented in pronghorn—any of which could indicate a shorter exposure to arid conditions in the New World than in the Old.

One result of the pronghorn's adaptations to aridity was the nearly universal occupancy of the Intermountain West's open landscapes, and few if any populations were isolated at the time of Western contact (Hall and Kelson 1959, Yoakum 2004, Jensen et al. 2004). As a consequence, the only statistically significant ($P<0.05$) variations in pronghorn body measurements are a southward cline toward lighter weights and longer horn lengths (Brown et al. 2006;). The only regional variations occurring during the last 4,000 years include adaptations in food habits and gestation season attendant with climatic conditions attendant with the formation of the 4 North American deserts. (See e.g., Murphy 1917, Figure 9).

Lacking regional isolation, pronghorn should exhibit relatively low levels of variation and lack well defined subspecies characteristics as defined by Mayr 1942, Simpson 1945, 1961, and others. This is not only true for body measurements (Brown et al. 2006), pronghorn lack significant variation in pelage coloration and markings—a common subspecies characteristic (Caro 2005).

Pronghorn also exhibit relatively low levels of genetic diversity with animals from the "desert Southwest" being only slightly different than those from more northern states (Lee et al. 1994, Amor 2000). That pronghorn exhibited greater diversity within local populations than between regional "subspecies," also indicates a recent and imperfect differentiation (Rhodes et. al 1998). Furthermore, populations of pronghorn in Arizona descended from populations translocated from Texas, Wyoming and Colorado showed no significant variability in haplotype frequencies, these frequencies only being significantly different in Arizona populations where Montana animals were present (Rhodes et al. 2000). Only minor differences were also noted in populations from extreme southwestern Arizona and Sonora (Hosak et al. 2002, Stephen 2002),

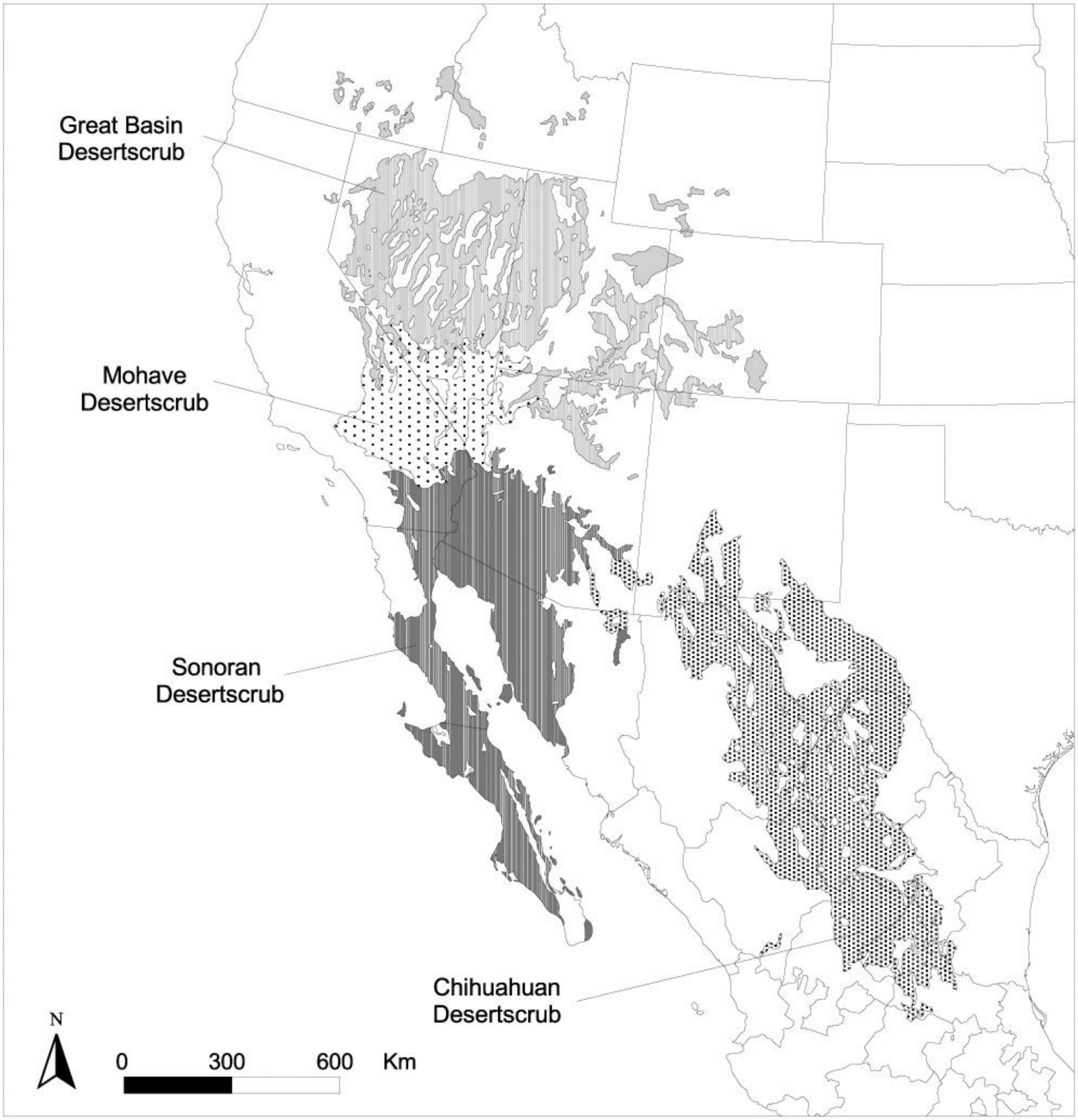

Figure 9. North America's deserts.

suggesting that populations of "Sonoran pronghorn" only separated from other southern populations after the arrival and expansion of Anglo settlement 150 ybp (Wright and deVos 1986).

A lack of subspecies does not negate the value of recognizing ecological guilds exhibiting regional adaptations recently determined through natural selection. One such adaptation is the timing of parturition (Powell 1955). For example, pronghorn in the Sonoran Desert have a prolonged fawn drop that lasts from February into March and April (Murphy 1917, Wright and de Vos 1986, Hervert et al. 2000). The rutting season is similarly synchronized even though it may occur at an unfavorable time from a physiological standpoint (O'Gara 2004*a*, 2004*b*). Postponing ovulation and terminating pregnancies during critical times can be considered behavioral adaptations to regionally arid environments. Pronghorn in some arid areas also appear to exhibit regional variations in size, being smaller in extremely arid areas such as Baja California (Table 1). Pronghorn in the most arid habitats also tend to be found in smaller groups than those on more productive ranges, foraging on cholla cactus (*Opuntia* spp.) and other succulent plants to maintain a water balance (J. Hervert, pers. com.). Indeed, pronghorn populations appear to employ many of the same behavioral strategies employed by gazelles and other arid country ruminants (Taylor 1968, 1969, Nagy 1987, Grenot 1991), these behavioral adjustments evolving more rapidly than physiological adaptations.

Personal experience suggests that translocated pronghorns may take a period of time to adjust their reproductive cycle when moved to areas having different climatic patterns. There are undoubtedly a number of other regional adaptations that influence a translocated animal's chances of success, so that transplant stock should always be selected from populations living in habitats having climates and other characteristics as similar to the release area as practical. But even so, recent investigations into the timing of horn growth as well as breeding and parturition dates indicate "fast track" morphological and behavioral adjustments to climatic variations (Brown and Mitchell 2006. Further evidence of only recent and ongoing adaptations are external measurements from more than 1154 pronghorn from 26 regional populations collected from studies and museum records in areas prior to translocations (Table 1). Arranged by biotic communities, the means of these standard measurements show < 10% difference in all but tail length and weight with most subspecies showing no significant ($P<0.05$) morphological distinctions (Brown et al. 2006). That the largest animals are from Intermountain grassland and the smallest from the Vizcaíno Desert only suggests a decreasing cline in size with diminishing precipitation from the species' origins in the Great Basin southward to the Lower California peninsula.

Cockrum (*in* Arizona Game and Fish Department 1984), along with O'Gara and Janis (2004*c*), noted that the skulls of adult pronghorn show no or very little variation between proposed "subspecies" with more variation within racial distributions than between distributions. There are also relatively small changes in body measurements among populations as manifested in pronghorn body sizes and the lengths of tails, hind feet, and ears, the smallest animals usually being found in the more arid and forage-poor regions of Utah, Chihuahua, Arizona, etc. Moreover, the measurements given by Merriam (1901) for the single male type specimen of the "paler" *A. a. mexicana* fall within the range of males *A. a. americana* collected in Alberta as does the measurements of the type specimen for *A. a. oregona* (Mitchell 1971, O'Gara and Janis

Table 1. Relative sizes of North American pronghorn according to habitat affinity

State or Province	**Biotic Comm.**	**Spp.**	**Total Length (M)**	**Total Length (F)**	**Hind Foot Length (M)**	**Hind Foot Length (F)**	**Male Tail Length**	**Female Tail Length**	**Male Ear Length**	**Female Ear Length**	**Height at Shoulder (M)**	**Height at Shoulder (F)**	**Chest Girth M**	**Chest Girth F**	**Male Weight**	**Female Weight**	**Data sources**
Yellowstone NP	*InterMtn.*	*americana*	1445 (27)	1448 (93)	427 (27)	418 (93)	109 (27)	109 (93)	145 (27)	144 (93)	940 (27)	905 (93)	1032 (14)	987 (93)	59.0 (35)	50.2 (90)	O'Gara 1968
Idaho	*InterMtn.*	*americana*	1402 (18)	1356 (13)	421 (18)	418 (13)	111 (5)	127 (5)	150 (18)	145 (13)	895 (18)	873 (13)			52 (11)		Bodie 1979
Wyoming	*InterMtn.*	*americana*	1403 (18)	1402 (9)	427 (12)	419 (8)	128 (14)	137 (10)	141 (7)	145 (3)	931 (4)	902 (1)				50 (60)	Edwards 1958, BMNH, USNM, MVZ, LACM, MSU
Oregon/Nevada	*InterMtn.*	*americana*	1420(102)	1376 (20)	432 (82)	419 (20)	106 (103)	103 (20)	159 (117)	158 (13)	920 (87)	914 (1)			54.1 (27+)	46.2 (20+)	Einarsen 1948, Mason 1952, USNM,
N.E. California	*InterMtn.*	*americana*	1457 (30)	1415 (3)	448 (27)	416 (3)	112 (254)	85 (3)	163 (362)	141 (3)					51.3 (67)		McLean 1944, MVZ, LACM
No. Arizona	*InterMtn.*	*americana*	1438 (451)	1425 (14)	417 (6)	422 (13)	130 (10)	130 (6)	171 (6)	170 (2)	836 (10)	856 (5)	902 (1)		44.6 (590)	42.4 (8)	AZGFD, Mearns, USNM
Intermountain Average			**1428**	**1404**	**429**	**419**	**116**	**115**	**155**	**151**	**904**	**890**	**967**	**987**	**52.2**	**47.2**	
Mean			**1434 (646)**	**1425 (152)**	**432 (173)**	**418 (150)**	**111 (414)**	**111 (137)**	**161 (538)**	**146 (127)**	**915 (146)**	**899 (113)**	**1023 (15)**	**987 (93)**	**46.3 (730)**	**49.3 (178)**	
Alberta	*Plains Gra.*	*americana*	1416 (16)	1406 (9)	405 (15)	397 (9)	105 (15)	97 (8)	143 (15)	142 (9)	875 (11)	860 (9)			54 (35)	48 (40)	Mitchell 1971
Montana	*Plains Gra.*	*americana*	1338 (36)	1359 (12)	376 (36)	366 (12)	135 (36)	127 (12)	152 (36)	150 (12)	874 (36)	831 (12)					Buck 1947
North Dakota	*Plains Gra.*	*americana*	1320 (1)		400 (1)		110 (1)										Bailey 1931
Nebraska	*Plains Gra.*	*americana*													55.3 (1001)	44.1 (604)	Menzel, K. 1980
Colorado	*Plains Gra.*	*americana*	1399 (68)	1438 (78)	421 (46)	416 (35)	116 (45)	118 (36)	144 (45)	149 (35)	895 (58)	893 (53)			47.7 (21)	45 (40)	Hoover et al.1959, Bear et al. 1973, Firchow 1986)
New Mexico	*Plains Gra.*	*americana*		1330 (1)		400 (1)		120 (1)		140 (1)							USNM
Plains Average			**1368**	**1383**	**401**	**395**	**117**	**116**	**146**	**145**	**881**	**861**			**52.3**	**45.7**	
Mean			**1382 (121)**	**1425 (100)**	**402 (98)**	**402 (57)**	**121 (97)**	**117 (57)**	**147 (96)**	**148 (57)**	**886 (105)**	**879 (74)**			**55.1 (1057)**	**44.3 (684)**	
W. Utah	*GB Desert*	*americana*	1285 (7)		417 (7)						885 (7)		920 (7)		50.1 (8)		Smith and Beale 1980
Nevada	*GB Desert*	*americana*	1371 (16)	1366 (13)	422 (16)	415 (13)	95 (16)	101 (13)	160 (10)	168 (8)					54.8 (7)	48.3 (6)	USNM, MVZ
Great Basin Des.	**Average**		**1328**	**1366**	**420**	**415**	**95**	**101**	**160**	**168**	**885**		**920**		**52.5**	**48.3**	
	Mean		**1345 (23)**	**1366 (13)**	**420 (23)**	**415 (13)**	**95 (16)**	**101 (13)**	**160 (10)**	**168 (8)**	**885 (7)**		**920 (7)**		**52.3 (15)**	**48.3 (6)**	
San Joaq, V. CA.	*CAV Grass*	*americana*		1400 (1)		444 (1)		120 (1)		185 (1)						45.4 (1)	
S.E. California	*Moj. Des.*	*americana*	1421 (1)	1500 (1)	445 (1)	440 (1)	105 (1)	130 (1)	155 (1)	155 (1)	1010 (1)	910 (1)					
S. California Average			**1421**	**1450**	**445**	**442**	**105**	**125**	**155**	**170**	**1010**	**910**				**45.4**	MVZ, FMNH, Carr 1971
	Mean		**1421(1)**	**1450 (2)**	**445 (1)**	**442 (2)**	**105 (1)**	**125 (2)**	**155 (1)**	**170 (2)**	**1010 (1)**	**910 (1)**				**45.4 (1)**	
W. Texas	*Semidgras*	*mexicana*	1365 (2)		415 (1)		115 (2)		140 (2)								TTU
New Mexico	*Semidgras*	*mexicana*	1350 (14)	1297 (12)	390 (14)	393 (11)	122 (14)	138 (9)	156 (13)	148 (12)	930 (13)		928 (14)		53.1 (13)	35.0 (1)	Mearns 1907, UNM, D. Brown
S.W. Texas	*Semidgras*	*mexicana*	1346 (1)	1346 (1)	394 (1)	394 (1)	64 (1)	64 (1)	152 (1)	150 (1)	922 (1)	876 (1)			43.0 (114)	40.0 (128)	
Chihuahua	*Semidgras*	*mexicana*	1372 (4)	1350 (1)	415 (3)	405 (1)	139 (4)	145 (1)	171 (3)	180 (1)	831 (1)		898 (3)	890 (1)	49.8 (4)*	49.0 (1)	
Coahuila	*Semidgras*	*mexicana*	1421 (8)	1350 (3)	421 (8)	413 (3)	109 (8)	117 (3)	152 (8)	144 (3)							
Chihuahuan Average			**1371**	**1336**	**407**	**401**	**110**	**116**	**154**	**156**	**894**	**876**	**913**	**890**	**48.6**	**41.3**	Mearns 1907, MSB, Buechner 1950, Mearns 1907
	Mean		**1374 (29)**	**1312 (17)**	**403 (27)**	**398 (16)**	**118 (29)**	**129 (14)**	**155 (27)**	**149 (17)**	**923 (15)**	**876 (1)**	**923 (17)**	**890 (1)**	**44.2 (131)**	**40 (130)**	Merriam 1901, FMNH
CA/AZ Border	*Son. Des.*	*americana*	1384 (1)		419 (1)		95 (1)		159 (1)				902 (1)		42.2 (1)		Carr 1971
S.W. Arizona	*Son. Des.*	*sonorensis*	1473 (3)	1411 (6)	521 (1)	403 (6)	114 (1)	105 (8)	169 (2)	156 (8)	817 (2)	858 (9)	809 (3)	849 (9)			Wright and DeVos 1985, AGFD 1984,
Sonora	*Son Des*	*sonorensis*	1486 (1)	1382 (4)	457 (1)	425 (4)	95 (1)	104 (4)	162 (2)	153 (4)					34.9 (1)	46.9 (3)	Hervert and Brown pers. files, Goldman 1945
Baja California	*Son Des*	*sonorensis*	1261 (8)	1307 (4)	389 (2)	427 (2)					845 (2)	850 (2)	900 (6)	895 (2)			MVZ, BMNH, USNM, Murphy 1917
Sonoran	**Average**		**1401**	**1379**	**447**	**418**	**101**	**105**	**163**	**155**	**831**	**854**	**870**	**872**	**38.6**	**46.9**	
	Mean		**1337 (13)**	**1373 (14)**	**435 (5)**	**414 (12)**	**101 (3)**	**105 (12)**	**164 (5)**	**155 (12)**	**831 (4)**	**857 (11)**	**873 (10)**	**857 (11)**	**38.6 (2)**	**46.9 (3)**	
Baja Californa S	*Vizcaino*	*peninsular.*	**1319 (15)**	**1295 (8)**	**401 (2)**	**410 (4)**	**84 (7)**	**86 (2)**			**947 (14)**	**936 (9)**	**942 (15)**	**912 (9)**			USNM
Total Average			**1377**	**1373**	**421**	**414**	**104**	**109**	**156**	**158**	**907**	**888**	**922**	**915**	**48.8**	**45.8**	
Total Mean			**1419 (848)**	**1410 (306)**	**420 (329)**	**413 (254)**	**112 (567)**	**113 (237)**	**159 (677)**	**148 (223)**	**905 (292)**	**891 (209)**	**944 (64)**	**968 (114)**	**51.0 (1935)**	**44.7 (1002)**	

*Preliminary data modified from Table 24 in O'Gara and Yoakum 2004 and added to by Carl Mitchell and David Brown

Sample sizes in parenthesis

Museum abbreviations

BMNH	Burke Museum of Natural History
FMNH	Field Museum of Natural History (Chicago)
KU	Kansas University
LACM	Los Angeles County Museum
MSU	Michigan State University
MVZ	Museum of Vertebrate Zoology (Berkeley)
TTU	Texas Tech University
USNM	U. S. National Museum (Smithsonian)
UNM	University of New Mexico

2004*a*). The skull of the female type specimen *of A.a. sonoriensis*, while smaller than the mean for *A. a. americana*, also fell within the range of females collected in Alberta (Mitchell 1971).

Paradiso and Nowak (1971) based their determination to retain *A .a. sonoriensis* as a separate subspecies on the basis of skull measurements from 6 animals collected in Sonora and Arizona. Cockrum (1984:5-9), using the same 6 skulls, disputed this conclusion, however, stating that "such differences do not warrant the application of separate subspecies names." Cockrum then went on to state that all of the specimens that he examined, including the only adult male, were well within the range of the measurements of other "subspecies," and that, "the recognition of *Antilocapra americana sonoriensis* as a separate subspecies is unwarranted at this time." The same may also be said for Nelson (1912), who differentiated 12 specimens of the Sonoran Desert inhabiting "*A. a. peninsularis*" on the basis of color, horn characteristics and heavier molars. Even skeletal characteristics can shift quickly when pronghorn populations in suboptimal habitats are reduced to low numbers (O'Gara and Janis 2004*a*), and horn characteristics and pelage color are extremely plastic criteria for determining subspecies or races.

Subspecies differentiations based on electrophoretic and mtDNA comparisons are ambiguous at best. Most electrophoresis analyses show little genetic diversity between populations (Lee et al. 1989, Stephen 2002, O'Gara and Janis 2004*a*), despite some mtDNA comparisons showing moderately high levels of differentiation among certain sub-populations of *mexicana* ((Lee (1992, Lee et al. 1994). On the basis of mtDNA, Lee (1992) therefore nonetheless concluded that *A. a. sonoriensis* was not distinct from A. *a.* a*mericana,* and a mtDNA sequence comparison of presumed Sonoran and Mexican pronghorn showed < 1% sequence divergence or essentially no variation among 10 individuals from areas supposedly having both subspecies. A further mtDNA study by Amor (2000), which included 93 individuals of all 5 subspecies, also found little or no subspecies differentiation.

In retrospect, the original descriptions of the 5 "subspecies" of pronghorn were based on faulty criteria involving inadequate sample sizes, a minimum of 15 specimens being needed for any subspecies comparisons (Cockrum 1981). Although previous studies indicate that certain southern populations may differ from northern ones, none of the genetic analyses conducted by Lou (1998), Rhodes et al. (1998), or Amor (2000) showed any discrete differences between the subspecies initially described. It thus appears that pronghorn populations represent a genetic cline, and that the species constituted one general population until 250 ybp.(Pyrah 1987). A more biologically correct designation might be to regard certain southern populations as "desert pronghorn," these animals representing a southern cline of general ancestry—a designation proposed by Monson (1968), and currently used by both biologists and laymen to describe desert bighorn sheep.

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A Comparison of Pronghorn Body Measurements Throughout Western North America

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Abstract: Biologists use mammalian body measurements to make taxonomic, behavioral, and ecological comparisons within and among species. Another application of these comparisons is promulgation of several "rules" to explain intraspecific variation in morphology over broad environmental gradients. We examined body measurements of 223 pronghorn (*Antilocapra americana*) collected from throughout North America to determine whether body measurements varied consistently among biotic communities, ecoregions, and subspecies. We also evaluated variation in pronghorn measurements with annual temperatures (Bergmann's rule), forage productivity as measured by precipitation ("Geist's" rule), and latitude (Allen's rule). Pronghorn showed little sexual dimorphism other than in body weight, and morphological similarities among populations were more apparent than differences. Pronghorn size varied little (P =0.003) with mean annual temperature, and pronghorn from areas receiving greater rainfall were only slightly larger (P = 0.001) than animals in desert areas. Horn size increased slightly (P = 0.0003) from north to south, but did not increase (P = 0.035) with precipitation. Body measurements, however, varied little from north to south (P =0.001) although pronghorn from Arizona and New Mexico had longer ears (P=0.001) than other populations, and pronghorn from the Great Plains had shorter hind feet and longer tails (P 0.0001) than other populations. Analyses of designated "subspecies" revealed few differences, and the species is remarkably monotypic. A possible exception is *A. a. peninsularis*, which tended to be smaller (P = 0.005) than other subspecies. Further investigations into morphological variation among pronghorn populations should examine specific environmental characteristics across spatial and temporal scales and should measure body size using other morphometrics.

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Key Words: *Antilocapra americana,* ecoregion, latitude, morphology, precipitation, pronghorn, sexual dimorphism, temperature.

Morphological variation within a species can provide biologists with a wealth of information. Although recent analyses have focused on molecular techniques, most mammalian species and subspecies originally were described on the basis of morphological characteristics (Feldhamer et al. 2004). Historically, recognition of large-scale patterns of change suggested relationships between an animal's environment and its morphology, which in turn led to the promulgation of ecological "rules." Bergmann's rule recognized the tendency for mammals to increase in size in colder environments (Bergmann 1847), whereas Allen's rule reflected a pattern in which mammals experiencing cold climates tend to have smaller appendages (i.e., ears, tails) than closely related forms in warmer environments (Allen 1877). Similarly, Geist (1998) noted that body size in cervids tends to decrease with declining forage availability. Although biologists have studied these relationships for >100 years, application of these rules remains equivocal and controversial (e.g., Stevenson 1986, Geist 1987, Ashton and Feldman 2003).

As in other mammals, regional variation in pronghorn (*Antilocapra americana*) body measurements have been used as 1 criterion to differentiate subspecies (Merriam 1901, Nelson 1912, Bailey 1932, Goldman 1945), and biologists have long suspected that local variation in pronghorn morphology might depend upon environmental factors (Powell 1953). In a previous paper (Brown and Mitchell 2006), we discussed statewide differences in pronghorn horn size and correlated variation in trophy size to winter temperature. We reasoned that similar comparisons in standard body measurements such as total length, hind foot length, tail length, ear length, and weight might be equally informative and provide insights into regional adaptations and applicability of subspecies designations. Such an exercise also could be used to further evaluate Bergmann's, Allen's, and Geist's rules.

Methods

Tables of pronghorn measurements presented in O'Gara (2004*a*) provided the initial basis for our data search and stimulated us to request additional data. We searched the literature to obtain mammalian measurement data (total length, hind foot length, tail length, ear length, horn length, and weight) for individual pronghorn from the following sources: Elliot (1907), Mearns (1907), Nelson (1912), Murphy (1917), Bailey (1931, 1932), Knipe (1941, 1942, 1944), Goldman (1945), Buck (1947), Einarsen (1948), Büechner (1950), Mason (1952), Carr (1971), Tinker (1978), Menzel (1980), Smith and Beale (1980), Arizona Game and Fish Department (1981), Wright and deVos (1985), Hepworth (2004), and Meeker (2004). In addition, the senior author and his colleagues collected measurements from pronghorn in southern New Mexico (33.18ºN, 107.03ºW) in October 2005, southwestern Arizona (32.4ºN, 112.9ºW) in December 2005, and Sonora, Mexico (31.4ºN, 113.5ºW) in January 2006.

We also contacted museums listed in the Mammal Networked Information System and queried them about availability of pronghorn measurements in their collections. Although a disappointingly small amount of measurement data were available for some larger collections, we obtained useable measurements from Burke Museum of Natural History in Seattle, California Academy of Sciences, Field Museum of Natural History in Chicago, University of Kansas, Los Angeles County Museum, Michigan State University, Museum of Southwestern Biology at the University of New Mexico, Museum of Vertebrate Zoology at the University of California at Berkeley, National Museum of Natural History, Texas Tech University, University of New Mexico, and the U. S. National Museum.

We included only measurements from adult pronghorn collected prior to translocations from other states or countries. However, we used measurements of pronghorn from the National Bison Range (Dow 1952) even though these animals descended from translocated stock because all translocations originated from areas within intermountain grassland (Reichenbacher et al. 1999). These measurements represent the largest database for pronghorn yet gathered.

We gathered data for 223 individual pronghorn ≥2 years old, although we could not obtain every measurement for every animal. We used actual weights when provided and avoided field–dressed weights. We assigned each animal to a biotic community (Reichenbacher et al. 1998) and to an ecoregion (Bailey et al. 1994). Each animal also was assigned to a subspecies based on the original description and map provided in Hall and Kelson (1959). The exception was *A. a. oregona*, which has been replaced by *A. a. americana* (O'Gara and Janis 2004). We obtained mean annual precipitation and mean annual temperature data from the climate station closest to the collection locale having summarized climatic data.

We used *t* tests to compare sexes and analysis of variance (ANOVA) to examine differences in morphology across biotic communities, ecoregions, and subspecies. Linear regression analyses were used to examine relationships between body measurements and mean annual temperature (Bergmann's rule), productivity as indexed by mean annual precipitation (Geist's rule), and latitude (Allen's rule). We analyzed all data in JMP (SAS Institute, 2004), with significance levels of $P \leq 0.05$. When ANOVA results were significant, we ran *post hoc* pairwise comparisons. Due to the large number of statistical tests conducted on the same dataset, we also used sequential Bonferroni corrections for multiple comparisons (Rice 1989).

Results

We initially compared measurements and weights of 150 male and 73 female pronghorn collected from 44 locations within 8 biotic communities and 11 ecoregions ranging from Alberta southward to Coahuila, and westward from western Nebraska to Baja California Sur. Males and females did not differ in any standard measurements ($P \geq 0.23$, Figure. 1a). Female lengths averaged only 0.01% shorter than males, and male hindfoot lengths were within 2% of those for females. Males, however, weighed significantly more than females ($t = -4.88$, df = 32, $P \leq 0.0001$; Figure. 1b). Thus, in subsequent analyses, we combined males and females except when comparing body weights.

Comparisons of body measurements across biotic communities showed a range of values (Table 1). Pronghorn did not differ in total length across communities ($P = 0.05$, NS after sequential Bonferroni correction). However, they differed in tail length ($F = 22.4$, df = 3, 51, $P < 0.0001$), hind foot length ($F = 49.9$, df = 4, 33, $P < 0.0001$), ear length ($F = 16.0$, df = 4, 133, $P < 0.0001$, male horn length ($F = 18.3$, df = 4, 16, $P < 0.0001$), and male weights ($F = 147.2$, df = 2, 27, $P < 0.0001$). Although mean lengths of animals in different biotic communities fell within 10% of each other, other measurements varied more widely. Pronghorn from Chihuahuan Semidesert and Plains Grassland had longer tails than animals from Sonoran Desertscrub or Great Basin Shrub Steppe communities. Pronghorn from Plains Grassland also had shorter hindfoot lengths, smaller horns, and weighed less than animals from other communities. Although sample sizes were small, pronghorn from Intermountain Grassland on the Coconino Plateau had longer ears than animals from other areas, which did not differ in this respect (Table 1).

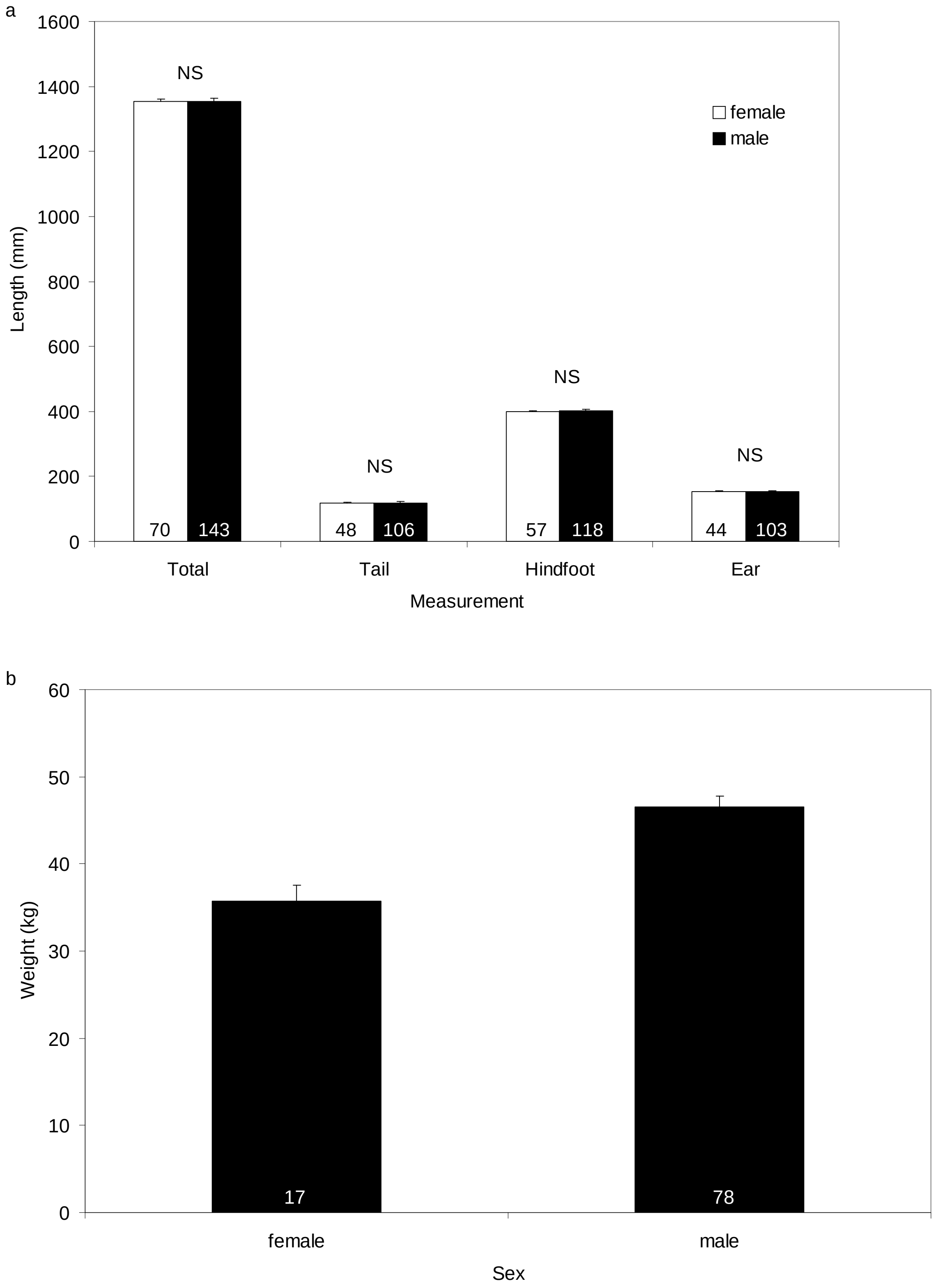

Figure 1. Mean (+ SE) (a) morphological measurements (mm) and (b) body weight (kg) of male and female pronghorns collected throughout western North America between 1890 and 2006. Sample size is indicated at the base of each bar. NS = not significant (*P* > 0.05).

Analyses based on ecoregions varied somewhat from those based on biotic communities (Table 2). Pronghorn differed in total length ($F = 4.81$, df = 6, 36, $P = 0.001$), tail length ($F = 27.7$, df = 4, 42, $P < 0.0001$), hind foot length ($F = 34.5$, df = 6, 34, $P < 0.0001$), ear length ($F = 51.1$, df = 5, 17, $P < 0.0001$, male horn length ($F = 14.1$, df = 4, 20, $P < 0.0001$), and male weights ($F = 45.1$, df = 3, 25, $P < 0.0001$). Pronghorn from the Middle Rocky Mountains were longer than those in the Great Basin (Table 2). Animals from the Northern Great Plains Steppe had longer tails, shorter hindfoot lengths, and weighed less than those from other ecoregions. Pronghorn from the Arizona-New Mexico Mountains had the longest ears, whereas those from the Middle Rocky Mountains had the shortest ears (Table 2).

In our test of Bergmann's rule, we found no relationship between body length and either latitude or temperature ($P = 0.05$). Male weights declined as latitude increased ($r^2 = 0.16$, $P = 0.0003$; Figure. 2), however, the opposite of what is predicted.

In our test of Geist's rule, using mean annual precipitation as an index to plant productivity (Sneva and Hyder 1962), we found that pronghorn were significantly longer in areas receiving more precipitation ($P = 0.0001$, Figure. 3). Precipitation, however, only explained 12% of variation in the data.

Per Allen's rule, hind foot and male horn lengths increased at lower latitudes, although relationships were weak (hindfoot: $r^2 = 0.08$, $P = 0.0003$; horn: $r^2 = 0.15$, $P = 0.0003$; Figure. 4a). Ear lengths did not vary ($r^2 = 0.039$, $P = 0.0189$, NS after sequential Bonferroni corrections). In contrast to Allen's Rule, tail length weakly decreased with increasing temperatures ($r^2 = 0.09$, $P = 0.0002$; Figure. 4b), but the relationship did not hold true for latitude ($P = 0.03$, NS after sequential Bonferroni correction). No other variables varied significantly with temperature ($P > 0.003$, NS after sequential Bonferroni corrections).

Finally, we analyzed body measurements across 4 subspecies. Only tail length differed significantly among subspecies ($F = 16.8$, df = 2, 51, $P < 0.0001$, Table 3). Sonoran pronghorn had significantly shorter tails than *A. a. americana* or *A. a. mexicana*, which did not differ significantly from each other. Specimens of *A. a. peninsularis* tended to be shorter than other subspecies, but differences were not statistically significant ($P = 0.05$, NS after sequential Bonferroni correction; Table 3).

Discussion

We conducted these analyses on data collected by many people, over more than a century, and across 3 countries. Therefore, we cannot account for accuracy or precision of original measurements or for any errors made in transcription from field notes to other databases. In addition, despite the relatively large overall database, sample sizes for some locations were small.

Not all significant relationships we found are biologically meaningful. Most pronghorn measurements varied within populations as much as between populations, and mean measurements appeared similar across time and space, and between sexes. Weights were the most variable measurements, probably due to variations in stomach contents, and changes in seasonal and sex-related physiology such as pregnancy, lactation, and rutting behavior.

Table 1. Body measurements (mm) and weight (kg) of male and female pronghorn in different biotic communities (as defined in Reichenbacher et al. 1998) for western North America, 1890-2006. Horn length and weight are included for males only.

Biotic community	Total length			Tail length			Hindfoot length			Ear length			Horn length			Weight		
	n	*x*	SE	*n*	*x*	SE	*n*	*x*	SE	*n*	*x*	SE	*n*	*x*	SE	*n*	*x*	SE
Sonoran Desertscrub	23	1,349.1	21.6	14	98.7A[a]	4.0	12	417.3AB	11.5	13	157.4A	2.4	5	293.2BC	32.1	---		
Great Basin Shrub-steppe	46	1,368.5	13.2	36	108.0A	3.2	44	424.6A	2.2	31	149.8A	1.8	25	316.5B	8.3	28	56.5A	1.3
Chihuahuan Semidesert	44	1,355.1	12.2	39	120.7B	4.4	40	402.0B	4.0	40	155.1A	1.6	14	376.7A	8.5	11	53.2A	1.2
Plains Grassland	51	1,348.8	6.6	51	131.5B	2.2	52	375.8C	2.7	51	148.8A	1.8	36	280.2C	10.0	36	36.3B	0.59
Coconino Plateau	8	1,419.4	21.8	---			8	422.6AB	4.9	3	197.7B	2.7	---			---		
Vizcaino Desert	23	1,325.7	20.4	---			---			---			---			---		

[a] Means within columns with different letters are significantly different ($P < 0.001$)

Table 2. Body measurements (mm) and weight (kg) of pronghorn males and females in different ecoregions (as defined in Bailey et al. 1994) across western North America, 1890-2006. Horn length and weight are included for males only.

Ecoregion	Total length			Tail length			Hindfoot length			Ear length			Horn length			Weight		
	n	*x*	SE	*n*	*x*	SE	*n*	*x*	SE	*n*	*x*	SE	*n*	*x*	SE	*n*	*x*	SE
Middle Rocky Mountains	12	1,440.9AB[a]	28.7	11	101.5A	3.7	12	419.1AB	5.5	7	138.9A	3.0	4	341.3A	5.6	9	56.2A	2.9
Arizona-New Mexico Mountains	8	1,419.4A	21.8	---			8	422.6AB	4.9	3	197.7C	2.7	---			---		
Chihuahuan Desert	44	1,355.1BC	12.2	39	120.7B	4.4	40	402.0B	4.0	40	155.1B	1.6	14	376.7A	8.5	11	53.2A	1.2
Columbia Plateau	24	1,353.9BC	14.7	22	104.4A	1.6	22	430.1A	2.3	24	153.0B	1.6	21	311.8B	9.5	19	56.6A	1.4
Northern Great Plains Steppe	51	1,347.5BC	6.1	51	133.1C	2.5	52	376.5C	2.9	48	149.5AB	1.8	36	280.2B	10.0	35	36.0B	0.53
Sonoran Desert	46	1,337.4BC	14.8	14	98.7A	4.0	12	417.3AB	11.5	13	157.4B	2.4	6	312.7AB	32.6	---		
Great Basin	7	1,285.4C	20.2	---			7	417.1AB	5.0	---			---			---		

[a] Means within columns with different letters are significantly different ($P < 0.001$).

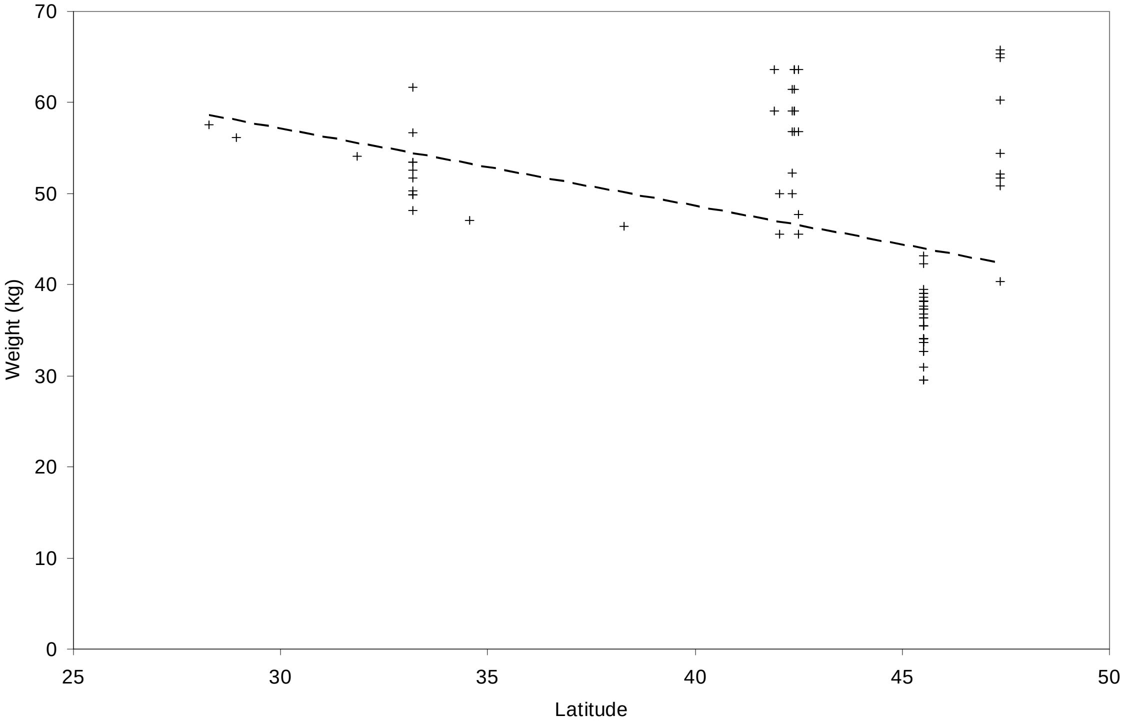

Figure 2. Relationship between male weight (kg, $n = 78$) and latitude for pronghorns collected throughout western North America, 1890-2006.

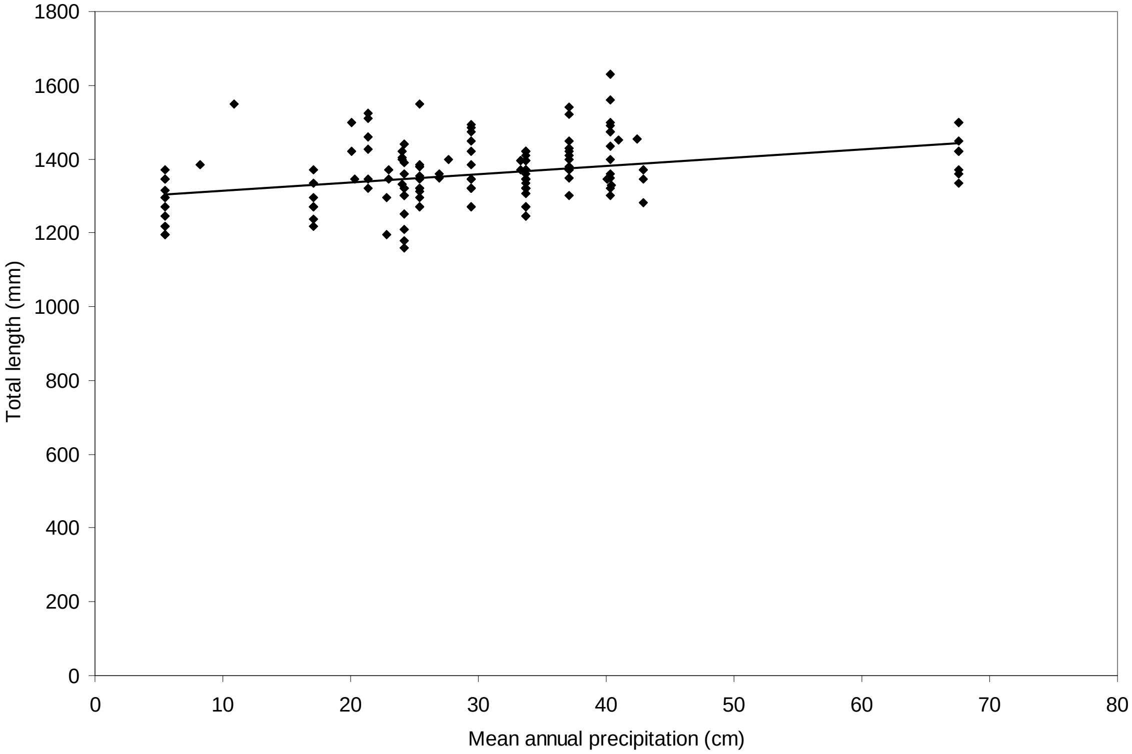

Figure 3. Relationship between total length (mm, $n = 172$) and mean annual precipitation (cm) for male and female pronghorns across western North America, 1890-2006.

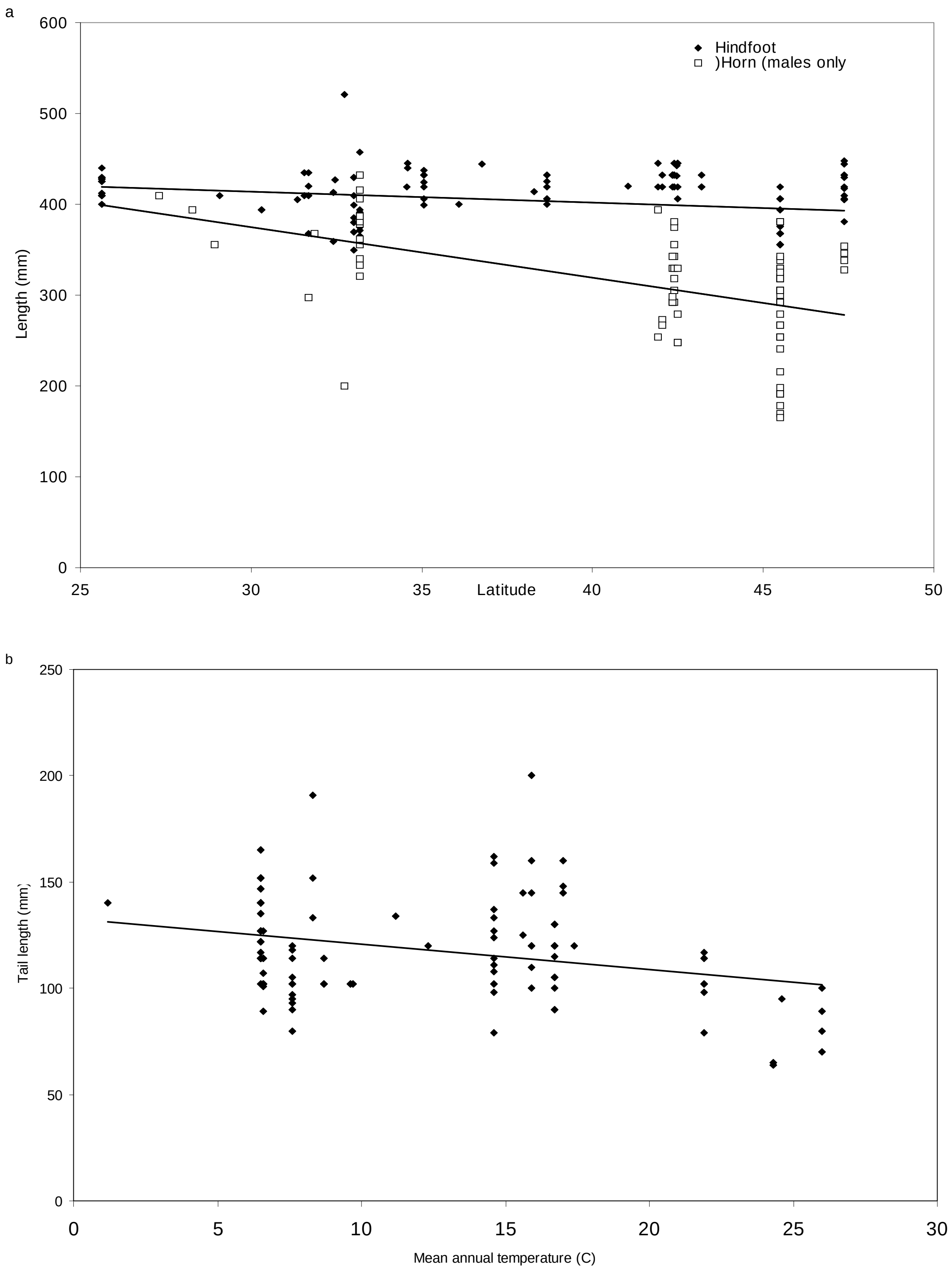

Figure 4. Relationship between length (mm) of (a) hindfoot (*n* = 158) and male horns (*n* = 84) and latitude and (b) tail (*n* = 141) and mean annual temperature (°C) for pronghorns collected throughout western North America, 1890-2006.

Table 3. Standard body measurements (mm) for 4 subspecies of pronghorn males and females collected throughout western North America, 1890-2006.

Subspecies	Total length			Tail length			Hindfoot length			Ear length		
	n	*x*	SE	*n*	*x*	SE	*n*	*x*	SE	*n*	*x*	SE
americana	119	1,369.2	6.9	99	120.9A[a]	2.1	120	402.4	2.7	93	149.5	1.2
sonoriensis	23	1,347.5	22.5	14	99.0B	4.3	12	417.1	12.6	13	157.3	2.6
mexicana	20	1,394.9	13.3	19	115.6A	6.0	18	414.2	4.2	18	161.3	4.4
peninsularis	23	1,325.7	20.4									

[a] Means within columns with different letters are different ($P < 0.001$)

In addition, we were not surprised to find differences in pronghorn from different biotic communities, which are classified by climate and vegetation. Temporal and spatial variation in weather, plant productivity, and subsequent nutrition can have major impacts on physical growth. Thus, pronghorn in desert communities, with lower mean productivity, tended to be slightly smaller than pronghorn from Intermountain Grassland communities.

Analysis by ecoregions also revealed some effects of productivity. We found slight differences among pronghorn populations in the Columbia Plateau, Northern Great Plains Steppe, Great Basin, Middle Rocky Mountains, Arizona-New Mexico Mountains, Chihuahuan Desert, and Sonoran Desert (Table 2).

Pronghorn may be the least variable North American ungulate, with the exception of mountain goats (*Oreamnos americanus*). Male and female mountain goats measurements vary by < 5% (Côté and Festa-Bianchet 2003). Pronghorn populations appear more uniform in size and color than those of bighorn sheep (*Ovis canadensis*, McTaggart-Cowan 1940), elk (*Cervus canadensis*, Murie 1951), mule deer (*Odocoileus hemionus*, Taylor 1956), and white-tailed deer (*O. virginianus*, Taylor 1956).

We found little support for Bergmann's rule in our analysis because we found no significant relationship between body length and latitude. Male weights actually declined with increasing latitude. A better explanation for the slight variation in body lengths is provided by Geist's rule in that pronghorn in wetter, and presumably more productive, habitats had significantly longer body lengths than those in more arid areas. This relationship is weak, however, and better tests examining measurements and productivity at more specific levels are needed.

Horn length was supportive of Allen's rule, because animals at lower latitudes displayed significantly longer horns than that farther north. Although hind foot lengths weakly increased in warmer areas at lower latitudes, ear and tail lengths did not.

Morphologically, pronghorn "subspecies" did not differ significantly from each other. Variation within subspecies was as great as that between subspecies. For example, measurements of Baja California animals within the range of *A. a. sonoriensis* resemble *A. a. peninsularis.* If we compare only Arizona and Sonora examples of *A. a. sonoriensis*, non-peninsular or continental pronghorn are remarkably uniform in size. Such similarity suggests that current subspecies designations, based primarily on morphology, are invalid or inaccurately delineated, particularly because various pronghorn subspecies were named on the basis of very few specimens (Merriam 1901, Nelson 1912, Bailey 1932, Goldman 1945).

Phenotypes are an expression of genetic characteristics, modified by environmental condition, and variance in both genetics and environment may affect phenotypic variance (Bull 1987). Because pronghorn size and extremities do not vary much across the species' range, pronghorn presumably have differentiated very little since Holocene times. These similarities in pronghorn morphology, coupled with universal similarity in pelage markings and color (Brown 2006), suggest a recent separation of populations. According to Allen (1877), the largest animals within a species are located near that species' evolutionary center. If so, morphometrics suggest *Antilocapra americana* evolved in the Intermountain West during Pleistocene times, expanding eastward and southward during Recent times.

We believe additional research on pronghorn body size might provide useful insights into local patterns of growth (e.g., Geist's rule) and changes over time. In addition to standard measurements, we suggest future studies also employ alternate measurements such as head length, incisor arcade, metatarsus:tarsus:femur ratios, and hind limb:body length ratios. Such measurements might not only serve to help identify unique populations, but also provide insights into ongoing regional adaptations.

Management Implications

This exercise and recent genetic studies (O'Gara 2004*b*, Stephen et al. 2005) suggest most pronghorn managers should be concerned more with adaptations of individual animals than with subspecies designations. Most pronghorn conservation efforts should concentrate on habitat rehabilitation and enhancement and should emphasize population rather than subspecies restoration. As such, any translocation stock should be composed of wild-trapped individuals taken from populations adapted as much as possible to conditions similar to the relocation area. Our work indicates populations of *A. a. mexicana*, *sonoriensis*, and *peninsularis* do not differ morphologically from each other or from *A. a. americana*. However, additional genetic work could determine if genetic differences are due to long-term selection or to more recent geographic separation, population bottlenecks, and genetic drift (Stephen et al. 2005).

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Thirty Years of "Pronghorn Management Guides": An Institutional Memory

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Abstract: Three decades ago wildlife managers recognized the need for guides for management of pronghorn populations *(Antilocapra americana)* and pronghorn habitats. Consequently, members of the 1976 Pronghorn Workshop developed the first *Pronghorn Management Guides* published in 1978. Since then, the Guides have been updated 3 times. By fulfilling the objectives of documenting management practices for species and habitats, by providing copies to all pronghorn workers, and periodically updating new ecological findings--management has been better coordinated and enhanced.

These Guides are available in English and Spanish and are used in Canada, Mexico and the United States. Traditional procedures for assembling, producing and distributing Guides are described. Also, recommendations for improving publication quality are provided.

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Key Words: *Antilocapra americana*, institutional memory, pronghorn, Pronghorn Management Guides, Pronghorn Workshop

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The Pronghorn Workshop (PW) has published several editions of *Pronghorn Management Guides* (PMGs) during the last 30 years. These PMGs are a compendium of pronghorn biological data, habitat strategies, and suggested management practices. Information is pertinent for wild free-roaming herds in Canada, Mexico, and the United States. Sufficient copies are printed for distribution to wildlife and land management agencies, conservation and sportsmen organizations, and persons interested in pronghorn ecology and management. These biological/management guides are one of the earliest compendia dedicated to management of a wild ungulate species in North America. The comprehensive book *Pronghorn: Ecology and Management* (O'Gara and Yoakum 2004) contains 3 pages on management guides for pronghorn.

The loss of institutional memory is a characteristic that certain organizations (e.g., government agencies, conservation groups, or specialty workshops) experience over time. Sociologists often refer to this as "generation amnesia." It is the potential loss of historic events, customs or traditions when new employees/attendees rapidly replace persons having years of experience. This characteristic is especially vulnerable for groups such as the Pronghorn Workshop that has rapid attendee turn-over. The objective of this report is to provide an anchor of past procedures and traditions to aid in the future production and distribution of PMGs.

History--Procedures and Results

During the business meeting of the 7th Antelope States Workshop (now the Pronghorn Workshop) conducted in Twin Falls, Idaho, attendees identified the need for coordinating management practices for contiguous herds that do not conform to political boundaries of provinces, states and countries. The influences of various land use practices also was recognized, but it was not clear how agencies could coordinate cooperative efforts for land manipulation practices to benefit pronghorn. Consequently, Workshop delegates appointed committees to draft chapters regarding multi-subject findings and recommendations for management of pronghorn and their habitats. Technical writing procedures were to follow standards adopted by The Wildlife Society. Bob Autenrieth of the Idaho Department of Fish and Game was appointed editor to coordinate and finalize a report that was presented at the 8th Pronghorn Workshop in Jasper, Alberta (Autenrieth 1978). Additional separate copies were printed for those interested in pronghorn management but not receiving copies of the PW proceedings (Autenrieth 1978b).

When the PMGs were originally published in 1978, it was envisioned that with time, new information would become available that would need to be incorporated in revised, updated editions. Subsequently, the PMGs have been updated 3 times. The goal is to update the PMGs every 6 years or so by adding new research findings and conservation practices.

Editions Produced

Editions have been published in 1978, 1992, 1998, and 2006 (Figure. l, Table 1). Originally around 60 pages, each edition has increased in size to the current issue having 160 pages, plus >35 photographs and figure drawings (Table 2). Noteworthy to it's scientific credibility is the expansion from an original 135 literature citations to 352 in 2006. About 1,000 copies are printed for each revision.

Primary use of the Guides is by personnel working for provincial/state and federal wildlife and land management agencies. By identifying management strategies for pronghorn residing in grasslands, shrubsteppes and deserts, pronghorn managers are familiarized with various practices/techniques appropriate for the diverse environmental sites occupied by pronghorn. The Guides also serve as a periodic report on the progress and issues relating to pronghorn management. As such, the Guides are applicable for use as teaching aides in workshops, clinics, and in wildlife management courses at colleges and universities. In addition, data has been used as testimony in litigation cases (Yoakum 2004).

Supplements

Periodically, sufficient new management information becomes available to print supplements. This was accomplished for methods of trapping and translocation by McKenzie (1983) and O'Gara and Yoakum (1984) (Table l). With more frequent printing of editions during the last 15 years, there has been less need for publishing supplements.

Reprints

Two reprints have been published to date: 1978 and 1983 (Table l). This attests to their popularity and management use. They are often cited in management plans and research projects (Yoakum 2004). By being continually revised, they provide up-to-date biological data and management strategies not always available in textbooks.

The third reprint did not indicate that it was a reprint. It condensed the narrative, resulting in 6 less pages. This may result in some confusion when authors in the future cite or refer to page numbers for the differing publications.

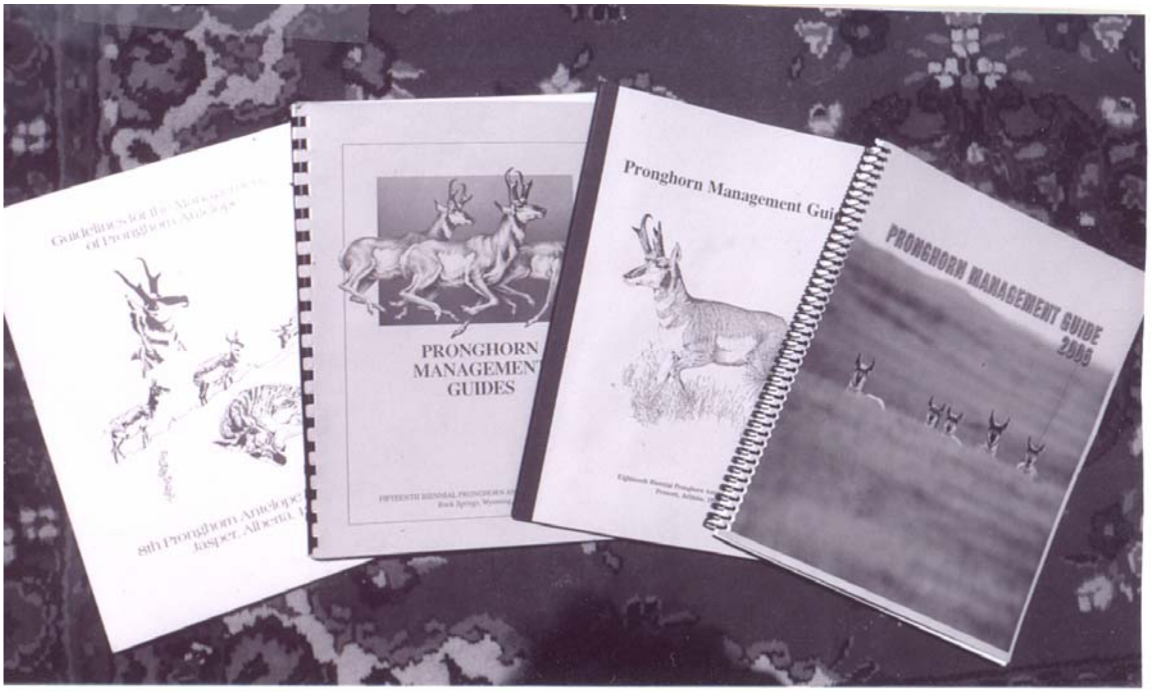

Photo by Jim D. Yoakum

Figure 1. Photograph of all 4 editions of the Pronghorn Management Guides published from 1978 to 2006. From left to right: first, second, third, and 4th edition.

Table l: Summary of editions, reprints and supplements for the Pronghorn Management Guides produced by the Pronghorn Workshop: 1978-2006.

Edition Reprint Supplement	Year Printed	Title	Editors/ Compilers	Pages	Publication Source
First edition	1978	Guidelines for the Management of Pronghorn Antelope	R. E. Autenrieth, editor	59	Pages 472-526 in Pronghorn Workshop Proceedings 1978
First reprint	Same	Same	Same	59	PW and Alberta Fish & Wildlife Division, Calgary, Canada
Second reprint	1983	Same	Same	59	Texas Parks & Wildlife Department, Austin, USA
Supplement	1983	Trapping & Transplanting	J. V. McKenzie, editor	14	Same
Supplement	1984	Additional Capture Methods & Habitat Suitability for Translocation	B. W. O'Gara and J. D. Yoakum, compilers	2	Pages 51 & 52 in Pronghorn Workshop Proceedings 1984
Second edition	1992	Pronghorn Management Guides	B. W. O'Gara and J. D. Yoakum, compilers	101	PW and U.S. Fish & Wildlife, Portland, Oregon, USA
Third edition	1998	Pronghorn Management Guides	R. M. Lee, J. D. Yoakum, B. W. O'Gara, T. M. Pojar, & R. A. Ockenfels, editors	112	PW and Arizona Antelope Foundation, Phoenix, USA
Spanish edition	2002	Guias para el Manejo del Berrendo	Same editors, Translator J. Cancino	142	Centro de Investigaciones Bilologicas del Noreste, La Paz, Baja California Sur, Mexico
4th edition	2006	Pronghorn Management Guides	R. E. Autenrieth, D. E. Brown, J. Cancino, R. M. Lee, B. W. O'Gara, R. A. Ockenfels, T. M. Pojar, & J. D. Yoakum, compilers	158	PW and North Dakota Game & Fish Department, Bismarck, USA
Third reprint	Same	Same	Same	152	PW and North Dakota Game & Fish Department, Bismarck, USA: produced by Texas Cooperative Extension, Amarillo, USA

Table 2. Statistics regarding the Pronghorn Management Guides from 1978 to 2006.

Edition	Editors/ Compilers	Pages	Photos	Figures	References Cited
First (1978)	1	69	0	1	135
Second (1992)	2	101	18	7	219
Third (1998)	5	112	14	7	281
4th (2006)	8	158	38	12	352

Translation

Increased attention has been given to pronghorn management during recent times in the southwestern United States and Mexico. This has prompted the translation of the Guides into Spanish (Cancino 2002)--a major accomplishment and an indication of the need for bilingual wildlife management scientific data (Table 1). Mexico has conducted an intensive 8 year supportive breeding program culminating in the Republic's first translocation of native herds to historic unoccupied habitat (Cancino et al. In Press). This venture is now being conducted with a similar goal for endangered pronghorn in the Sonoran Desert of Arizona (Wilson et al. 2007).

Distribution and Availability of Copies

Unless other arrangements have been made, the host PW agency for the year the PMGs are published is responsible for their distribution. Copies are sent to province/ state wildlife and land management agencies with pronghorn herds as well as organizations involved with pronghorn management and conservation. Single copies are available on request on a first come, first served basis until supplies are exhausted. The current 2006 edition in English is available from the North Dakota Department Game and Fish, 100 North Bismarck Expressway, Bismarck, North Dakota 58501-5059, USA. The 1998 edition is available in Spanish from Dr. Jorge Cancino, Centro de Investigaciones Biologicas del Noreste, Apdo. Postal 128, La Paz, 23000, Baja California Sur, Mexico.

Conclusions and Recommendations for Future Editions

The following production and distribution procedures are recommended to maintain scientific credibility, insure maximum usage and promote efficient distribution.

1. The name *Pronghorn Management Guides* should remain the same unless mandated at a PW business meeting. This facilitates consistency for reference to all editions, literature citations, and library services.
2. Publication funding, usually by state/federal agencies and/or collaborators, might be improved by the PW establishing a permanent publication fund to pay for new editions, thereby freeing the host state from bearing the total costs.
3. As presently constituted in the latest PMG edition (Autenrieth et al. 2006) the PMGs are in a PDF file and copies can be printed or reproduced on a DVD as required. Future editions can therefore be reproduced at such a time as the Workshop deems revisions are needed.
4. Tradition has been that copies are free. This facilitates greater access availability and wide distribution to the many persons working with and/or interested in pronghorn management.

5. The present PW goal of updating editions about every 6 years, is working well, and should be continued. Sufficient new biological data and management procedures occur during this period to warrant updating.
6. Generally, format for technical writing has followed The Wildlife Society standard procedures (Messmer and Morrison 2006). This has worked well and serves to provide scientific credibility. Information in the PMGs stress biological and management principles and practices. Political or personnel agendas are not condoned.
7. Illustrations should consider depicting pronghorn across its North America range, as opposed to emphasizing regions. The PMGs are for all North America and the PMGs should stress this goal.
8. The PW appreciates a representative of Mexico translating the PMGs into Spanish, and encourages continuation of this practice in the future.
9. Because the goal of the PMGs is to provide historic and current biological/management principles and practices--these Guides should remain fluid and dynamic. Continued updating is necessary. Consequently, the PW may deem it appropriate to establish a standing committee to periodically enhance appropriate content and improve technical quality.
10. Agencies or organizations desiring to make quantity reprints of these Management Guides are encouraged to do so; however, it is recommended that they first contact the Pronghorn Workshop for permission and recommendations for publication. Reprinted editions should include (1) name and address of reprinting source, (2) date of reprint, and (3) notation of modification of original edition.

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Evaluating Availability of Pronghorn Fawn Hiding Cover for a Central Arizona Population

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Abstract: Since 1959, the Arizona Game and Fish Department has allowed hunting and conducted management actions including habitat enhancement, predator control, herd augmentations and temporary hunt closures to benefit pronghorn (*Antilocapra americana*) located in Game Management Unit 21 (GMU 21). The GMU 21 population is small and isolated due to habitat fragmentation and highway barriers. Despite management efforts, population trends (survey counts and fawn survival indices) have declined over the past 20 years but trends differ between North and South areas. During the springs of 2002–2004 we evaluated availability of hiding cover for neonate fawns as a potential factor contributing to fawn recruitment trends. Available hiding cover was compared by study area (North vs. South), land ownership, year and grazing pressure (cows year long/sq. mi.). We further evaluated effects of grazing pressure by comparing hiding cover in grazed open pasture sites and ungrazed exclosures. We found more optimum cover in habitat to the south, less optimum on the Prescott National Forest, and a negative effect of grazing pressure. Apart from inter–annual variation in available hiding cover as a result of precipitation patterns, grazing pressure appeared to be the most important factor influencing availability of hiding cover. Most explanatory power of North versus South and ownership was due to lower grazing pressure in pastures to the South versus the North. We suggest that more optimum hiding cover in the South positively influenced fawn recruitment rates, and conversely higher grazing pressures in the North negatively affected available hiding cover and fawn recruitment trends in the North.

Proceedings Pronghorn Antelope Workshop 22: 147-171

Key words: *Antilocapra americana,* Arizona, canopy cover, drought, fawn hiding cover, fawn:doe ratio, forage, grazing pressure, pronghorn, recruitment, visibility, visual obstruction

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Within the past decade pronghorn (*Antilocapra americana*) home ranges, distribution patterns, habitat selection, fawn bedsite selection and mortality factors have been investigated extensively in central Arizona (Knipe 1942; Ockenfels et al. 1996*a*, 1996*b*, 1994; Ockenfels 1994*a*, 1994*b*; Ticer 1997; Ticer and Miller 1994). Ockenfels et al. (1994, 1996*b*) thoroughly described Game Management Unit 21 (GMU 21) pronghorn habitat, selection and distribution, seasonal migrations, movement corridors, and variables that might be contributing negatively to pronghorn use of otherwise suitable habitat. Despite management actions implemented during the past 2 decades designed to benefit pronghorn, habitat quality and management issues continue to affect pronghorn populations in GMU 21 (Ockenfels et al. 1996b, deVos 1999, Ockenfels 1994a and 1994b, Cooper et al. 2003). Primary causes of pronghorn habitat deterioration in GMU 21 are reduced fire frequency, increasing tree and shrub densities, excessive livestock grazing, high fence densities (especially within movement corridors), severe drought and water accessibility.

Annual pronghorn surveys have been conducted since 1959 in GMU 21. The Arizona Game and Fish Department (Department) uses standard, nonrandom survey techniques with fixed–wing aircraft during late July or August (Johnson et al. 1991, Pojar and Guenzel 1999, Rabe et al. 2002,) and counts all groups classifying each animal as buck, doe or fawn. A grid system is flown at approximate 0.5–mile intervals covering all known semidesert grassland habitats for pronghorn in GMU 21. Pronghorn distributions are bounded to the west by the Interstate 17 corridor. Genetic exchange with nearby pronghorn herds within Yavapai and Coconino counties is unlikely due to natural and anthropogenic habitat fragmentation.

Department concerns with pronghorn management in GMU 21 have escalated in the past decade for several key reasons. Research on population statistics for 10 pronghorn populations across Arizona (T. McKinney, unpublished data 2004) suggested only 1 (GMU 21) out of 10 populations had a declining population trend between 1983 and 2002. Survey counts in 2002 reached a 20–yr low (55), third only to counts in 1961 (39) and 1972 (45), despite herd augmentation efforts (Figure 1). Second, buck:doe ratios were below Department species management guidelines 7 out of the past 9 years. Finally, fawn survival indices (fawns /100 does) have declined the past 20–yrs despite 2 above average years of recruitment in 2004 and 2005, and have been below Department guidelines 5 out of the last 10 years.

Beginning May 2002, in conjunction with fawn hiding cover assessments, we initiated monthly aerial surveys to gather data on current habitat distribution and use patterns of pronghorn in the GMU 21. Surveys were consistent with those flown historically for direct comparison. During spring fawning periods (April–May; Ticer et al. 2000), an additional survey was flown to monitor fawn production in the North and South study areas and identify preferred fawning areas. Monthly surveys were discontinued in June 2004 and survey plans revised to continue fixed–wing survey mid–summer (July or August), winter (November –January), and fawning season (April–May) for the next several years.

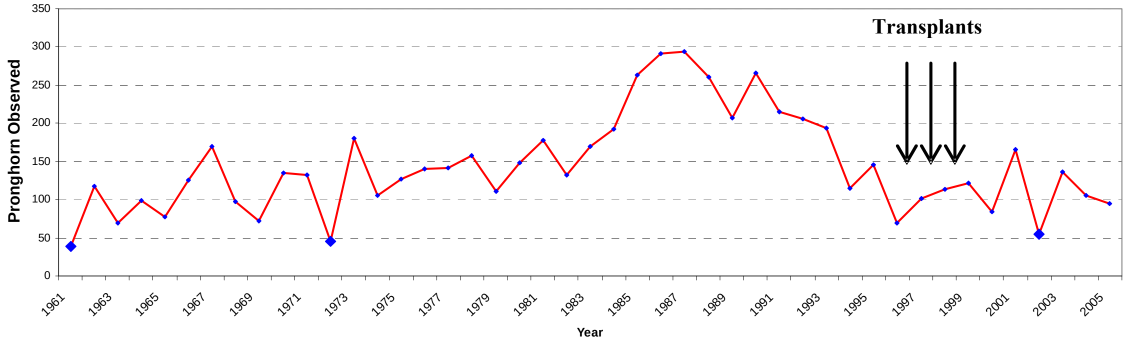

Figure 1: Historic pronghorn survey data for GMU 21 in Arizona. Transplants from Colorado and Utah stock were conducted in 1997 (60 pronghorn), 1998 (137), and 1999 (101). Pronghorn were released in both north and south habitat areas. Annual population surveys were conducted in late summer.

Aerial survey data suggest pronghorns discriminate between habitat in the North and South. Further, there is growing evidence of a disparity in fawn recruitment between the North and South. During spring fawning seasons from 2002–2005 we surveyed a greater number of fawns per 100 does in the South (Figure 2a). Late–summer fawn survival indices (fawn:100 does) met or exceeded the Department's species management guidelines of 30–40 fawns per 100 does, 3 out of 4 years in the South and 1 out of 4 years in the North (Figure 2b). Department biologists believe poor fawn recruitment coupled with high adult mortality are primary reasons for declining pronghorn population trends in GMU 21.

A reasonable amount of research across the West and Southwest has addressed the biology and management of pronghorn. Limiting factors often are of greatest interest, but are always complex due to interactions of variables and often are compounded by the fact that each population has unique sets of environmental and physical circumstances. Although mortality factors such as disease, climatic

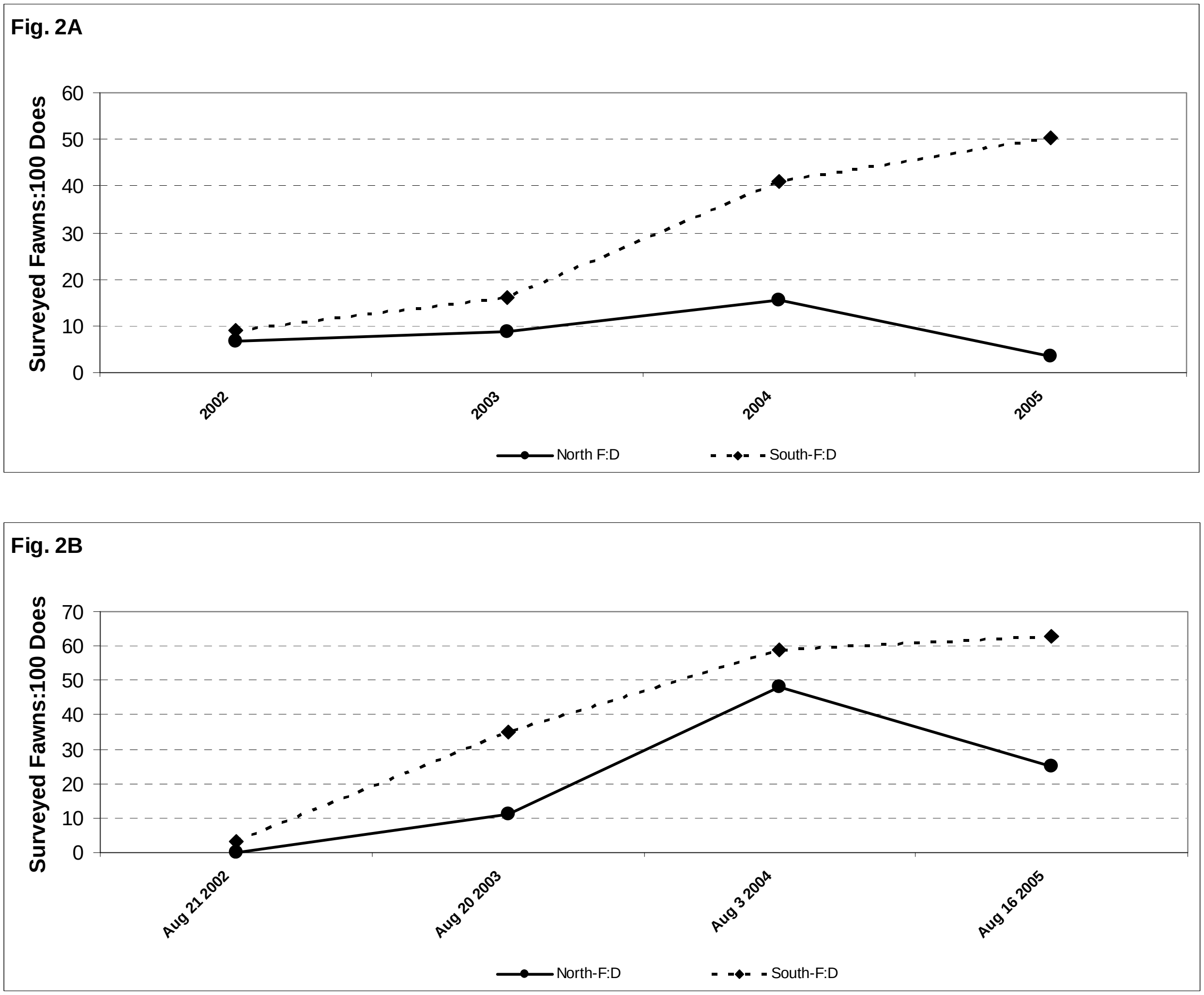

Figure 2. North and South fawn:doe ratios (A) calculated for the spring fawning period (Apr–May) of each survey year (B) late summer fawn survival.

stressors, and predators can periodically reduce populations, researchers commonly agree that habitat quality and availability are critical to maintaining sustainable populations over time (Lee et al. 1998, Autenreith et al. 2006). O'Gara and Yoakum (2004) compiled an exhaustive synthesis of pronghorn research and discussed the concept of density dependence in pronghorn population ecology (O'Gara, 2004a). Research supports the theory that pronghorn population densities are strongly affected by habitat conditions (Yoakum 1978, Kitchen and O'Gara 1982, Hess 1999) regardless of other mortality factors. Vegetative conditions and pronghorn densities ultimately define trends in the population. Researchers have verified 3 key points regarding pronghorn ecology: 1) densities and fawn/doe ratios are highest on diverse and productive rangelands (Aoude and Danvir 2002, Phillips and White 2003); 2) fawn losses are highest during the first 2–3 months after parturition (Neff and Woolsey 1979, Barrett 1984, Gregg et al. 2001, O'Gara and Shaw 2004); and 3) neonate mortality is primarily due to predation. However, land management practices that reduce or eliminate security cover and degrade habitat quality are thought to influence predation (Beale and Smith 1970, 1973; Autenrieth 1982). Pronghorn population–projection model simulations indicated that increases in long–term average mid–summer fawn/doe ratios would affect the likelihood of positive population growth (Phillips and White 2003).

Given the importance of habitat quality and fawn recruitment to population maintenance or growth, management actions should focus efforts on optimization of habitat conditions for fawn production and survival to minimize effects mortality factors have on population trends. A basic requirement for survival of a pronghorn neonate is adequate hiding cover (Neff & Woolsey 1979, McNay 1980, Barrett 1981, Autenrieth 1982, 1984; Alldredge et al. 1991), ultimately influencing fawn recruitment rates. Pronghorn fawns employ a hiding strategy for the first few weeks of their lives and this evolutionary behavior has been documented in all pronghorn neonatal behavioral studies (O'Gara 2004b).

Our primary objectives were to assess availability of hiding cover for neonate fawns during the spring fawning period, and determine if there were differences in available hiding cover between North and South habitat areas in GMU 21. We hypothesized that variations in hiding cover between North and South may influence variations in fawn recruitment between North and South.

Study Area

Approximately 20% of GMU 21 (622 km^2) is contiguous semidesert grassland habitat considered suitable for pronghorn (Ockenfels et al. 1994). Topography includes mesas, rolling hills, flats, drainages and steep canyons. Grasslands are primarily found on basalt origin soil. Woody vegetation occupies drainages, canyons and hillsides. Elevation ranges between 1000–2000 meters (3,280–6,500 ft.). Current pronghorn ranges based on recent aerial surveys encompass approximately 594 km^2 and 7 core areas of suitable habitat (Ockenfels et al. 1996b). Despite development and increasing tree and shrub densities pronghorn continue to move between the North and South using movement corridors.

North and South study areas were delineated based on topography, vegetation, and known pronghorn distribution from long–term aerial survey (1960–present). This delineation is consistent with historical Department reporting of aerial survey data for North and South observations. The North represents 44% of the study area (64,937 acres) and the South represents 56 % (83,279 acres). The 2 areas have very similar topography. The South study area has roughly 8% more terrain with less than 10% slopes. This is consistent with the terrain composition classification within the 1996 landscape–level evaluation model (Ockenfels et al. 1996b) which rated approximately 24% of the terrain that overlaps our South study area as high quality, opposed to 20% for the North study area. Overall, this model rated GMU 21 pronghorn habitat as moderate quality terrain.

Land ownership includes the Bureau of Land Management (BLM, 39.7%), Tonto National Forest (TNF, 10.6%), Prescott National Forest (PNF, 42.3%), and the State Land Department (ASLD, 3.7%). Private in holdings are limited and primarily located within canyons, along many of the creeks (Figure 3). Most of the North study area is PNF lands and most of the South is BLM lands. In 2000, President William J. Clinton issued a Presidential Proclamation for the establishment of the Agua Fria National Monument (AFNM) and it encompasses all BLM lands within GMU 21 pronghorn habitat. Pronghorn were identified as one of many outstanding monument objects to be protected through management and proper care (Presidential Proclamation 7263; Jan. 11, 2000).

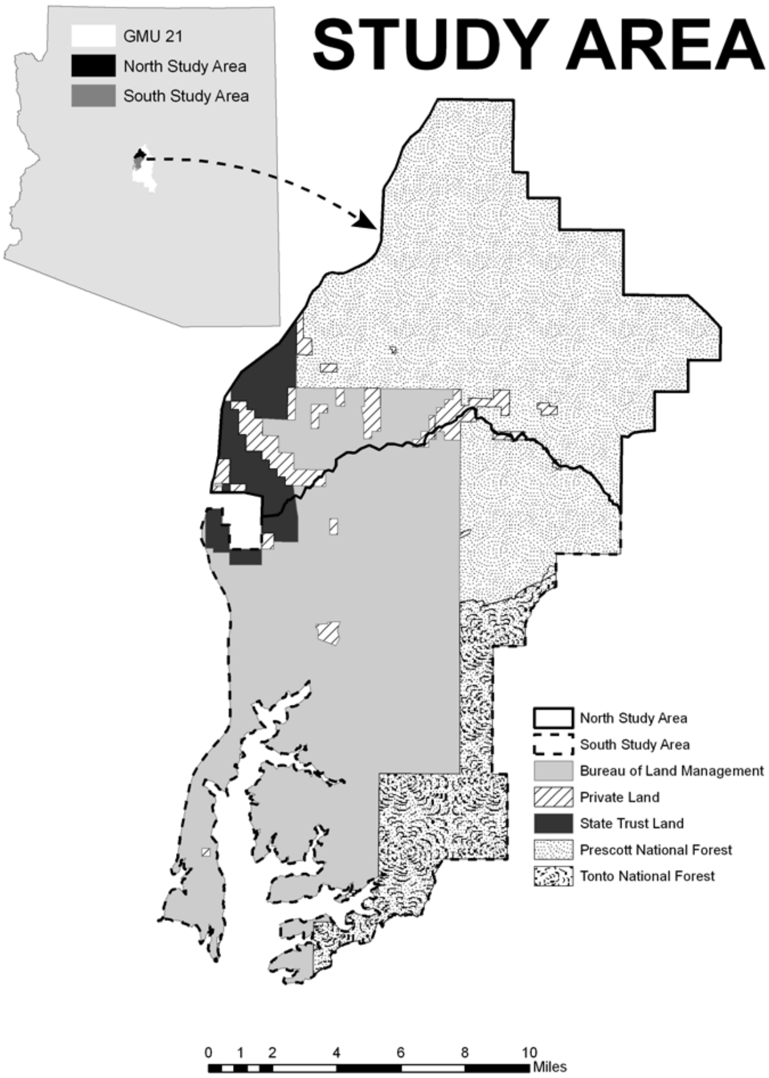

***Figure 3.* Location and ownership of Arizona GMU21.**

The study areas were grazed by livestock year round, managed primarily with deferred rotation strategies for cow–calf operations. One allotment in the North uses a time controlled grazing strategy (Savory 1988). There are 14 allotments that overlap pronghorn distribution. Mean stocking densities (actual use) for 2002–2004 ranged between 48 and 5,561 AUMs (animal unit months) (Table 1). For our analysis we translated AUMs to cows–yr–long per square mile (CYL/mi^2). Using this index, mean stocking densities for the same period ranged between 0.53–17.91 CYL/mi^2.

Precipitation followed a bimodal pattern with peak levels occurring July–September, and again during winter months of December–March. The driest months of the year typically fell between April–June, during the spring fawning season. For the last 54 years, mean annual precipitation was recorded as 38.6 cm and ranged between 74–15 cm. For the same time period temperatures ranged from daily extremes of 46 C to a low of –13 C, with spring season means between 6 C and 23 C (Western Regional Climate Center [WRCC] 2006). Very few days fell below freezing, since 1948 only 56 have been recorded. Annual precipitation increased between study years, reported as 20.6 cm (2002), 35.2 cm (2003), and 51.1 cm (2004). Cumulative drought effects leading into our study period came to an historic low in 2002 with drought indices (Palmer 1965) for our climate division reported as severe to extreme between March 2002 and January 2003. Frequent periods of moderate and severe drought characterize the past decade (National Oceanic & Atmospheric Administration [NOAA] 2006).

Vegetation varied with semidesert grassland dominating mesa tops (U.S. Dept. of Agriculture 1982, Robertson et al. 1997). Mesa tops were interspersed by canyons with riparian deciduous forests along intermittent and perennial streams. Canyon side slopes were dominated by Sonoran desertscrub (Arizona upland division) in lower elevations and interior chaparral and Great Basin conifer (juniper) woodland in higher elevations (Brown 1994). Semidesert grassland on most mesas was dominated by tobosa grass (*Hilaria mutica*) in areas characterized by heavy clay soils. However native and non–native annual grasses and forbs dominated many areas during our study including filaree (*Erodium spp.*), mustards (*Sisymbrium, Brassica*, *Descurainia*, *Chorispora* etc.), borage spp*.,* Indian wheat *(Plantago spp.),* wild barleys (*Hordeum spp.*), red sprangletop (*Leptochloa filiformis*), brome grasses (*Bromus spp.*). Highly preferred perennial forbs were less abundant including Wright's buckwheat (*Eriogonum wrightii*), globe–mallows (*Sphaeralcea spp.*), and sagebrush (*Artemisia spp.*). Dominant trees, shrubs, and cacti included Utah juniper (*Juniperus osterosperma*), redberry juniper (*Juniperus erythrocarpa*), shrub–form mesquite (*Prosopis juliflora*), catclaw (*Acacia greggi*), wait–a–minute bush (*Mimosa biuncifera*), shrub–live oak (*Quercus turbinella*), snakeweed (*Gutierrezia sarothrae*), prickly pear and cholla cacti (*Opuntia spp.*).

Besides pronghorn, endemic game species within the study area included mule deer (*Odocoileus hemionus*), white–tailed deer (*Odocoileus virginianus)*, javelina (*Pecari tajacu*), Gambel's quail (*Lophortyx gambelii*), mourning dove (*Zenaida macroura*), mountain lion (*Lynx concolor*) and black bear (*Ursus americanus*). Occasional observations were made of elk (*Cervus elaphus*) on the fringes of the desert grassland and Pinyon–juniper habitats; however we received no reports of elk using the grasslands. Predator species that commonly occur within the study area include coyote (*Canis latrans*), bobcat (*Lynx rufus*), mountain lion, and golden eagles (*Auila chrysaetos*). Population trends for mule deer and javelina also show declines in the past 2 decades within the study area.

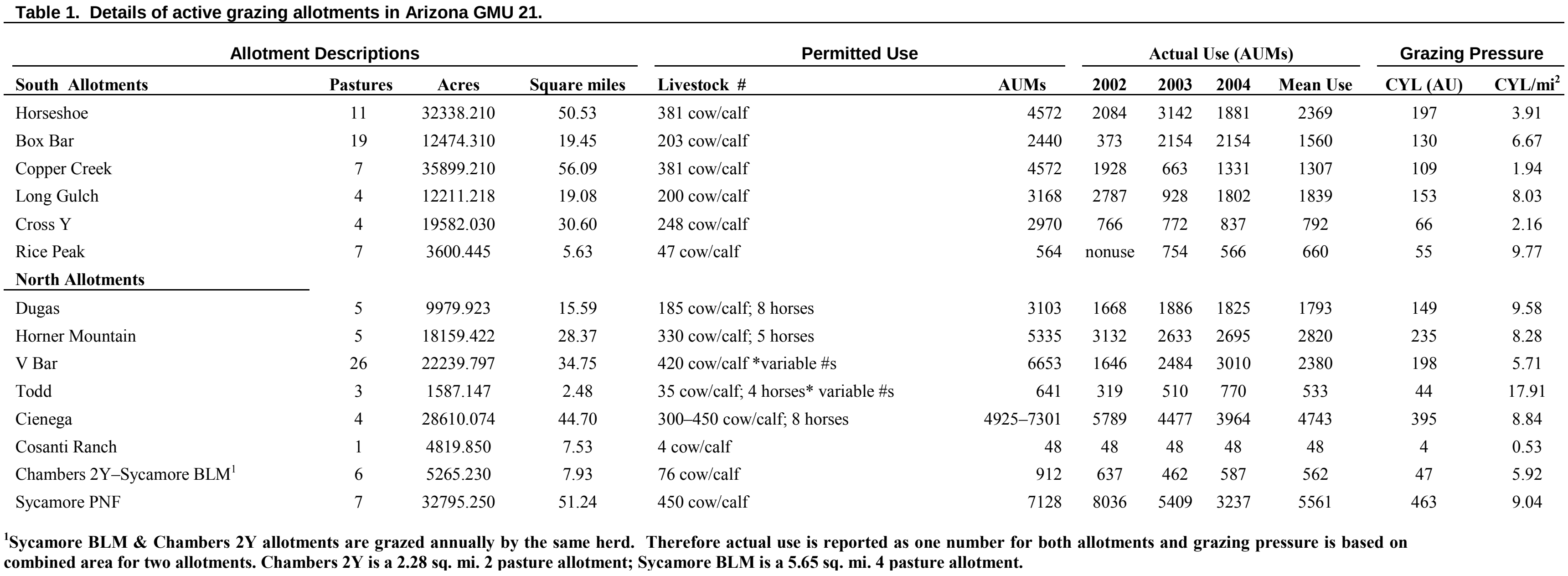

Table 1. Details of active grazing allotments in Arizona GMU 21.

Allotment Descriptions				Permitted Use		Actual Use (AUMs)				Grazing Pressure	
South Allotments	**Pastures**	**Acres**	**Square miles**	**Livestock #**	**AUMs**	**2002**	**2003**	**2004**	**Mean Use**	**CYL (AU)**	**CYL/mi^2**
Horseshoe	11	32338.210	50.53	381 cow/calf	4572	2084	3142	1881	2369	197	3.91
Box Bar	19	12474.310	19.45	203 cow/calf	2440	373	2154	2154	1560	130	6.67
Copper Creek	7	35899.210	56.09	381 cow/calf	4572	1928	663	1331	1307	109	1.94
Long Gulch	4	12211.218	19.08	200 cow/calf	3168	2787	928	1802	1839	153	8.03
Cross Y	4	19582.030	30.60	248 cow/calf	2970	766	772	837	792	66	2.16
Rice Peak	7	3600.445	5.63	47 cow/calf	564	nonuse	754	566	660	55	9.77
North Allotments											
Dugas	5	9979.923	15.59	185 cow/calf; 8 horses	3103	1668	1886	1825	1793	149	9.58
Horner Mountain	5	18159.422	28.37	330 cow/calf; 5 horses	5335	3132	2633	2695	2820	235	8.28
V Bar	26	22239.797	34.75	420 cow/calf *variable #s	6653	1646	2484	3010	2380	198	5.71
Todd	3	1587.147	2.48	35 cow/calf; 4 horses* variable #s	641	319	510	770	533	44	17.91
Cienega	4	28610.074	44.70	300–450 cow/calf; 8 horses	4925–7301	5789	4477	3964	4743	395	8.84
Cosanti Ranch	1	4819.850	7.53	4 cow/calf	48	48	48	48	48	4	0.53
Chambers 2Y–Sycamore BLM[1]	6	5265.230	7.93	76 cow/calf	912	637	462	587	562	47	5.92
Sycamore PNF	7	32795.250	51.24	450 cow/calf	7128	8036	5409	3237	5561	463	9.04

[1] Sycamore BLM & Chambers 2Y allotments are grazed annually by the same herd. Therefore actual use is reported as one number for both allotments and grazing pressure is based on combined area for two allotments. Chambers 2Y is a 2.28 sq. mi. 2 pasture allotment; Sycamore BLM is a 5.65 sq. mi. 4 pasture allotment.

Table 1. Details of active grazing allotments in Arizona GMU 21

Methods

Hiding cover assessment

We assessed fawn hiding cover availability during spring fawning seasons of 2002, 2003, and 2004 in North and South study areas. In central Arizona, researchers have found that pronghorn fawns were most often located <1 km from permanent water sources (Ockenfels et al. 1992, Ticer and Miller 1994) due to the water requirements of the lactating doe and her habitat selection. Therefore we designed our assessment to address the biology of the species. We stratified our evaluation around each of 28 North and 27 South water sources in the core of each study area known to be frequented by pronghorn during the spring fawning period in Unit 21 (Ticer et al., 2000). We used a Geographical Information System (GIS) to generate random UTM coordinates within a 1.5–km buffer zone at each water source to determine sites for data collection. We randomly sampled vegetative structure and estimated canopy cover and visual obstruction at a minimum of 10 random plots for each water source. Random plots located within the high impact areas of livestock waters (typically < 100 m) were not measured and surveyors selected the next random plot on the list. All surveyed random plots were located from 100–1500 m from water sources.

We collected canopy cover data using a modified line–intercept method (Bristow and Ockenfels 2002). We measured vegetation along 4 12.5 m transects centered on the UTM coordinates of the random plots. The orientation of the first of each set of 4 transects was determined randomly and the rest were oriented by increasing 90° from the previous line. This yielded 100 points oriented in 4 directions at 0.5 m intervals. At each point along transects we noted the presence of vegetation within each of 5 height intervals: 0–10 cm, 11–20 cm, 21–30 cm, 31–40 cm, and 41–100 cm. We categorized vegetation as grass, forb, shrub, tree, or cactus. We measured percent cover along the 4 transects as the number of points out of 100 that were covered by vertical projections of vegetation. We calculated percent canopy cover for each height interval, each vegetation type, as well as for "any canopy". We measured live and dead vegetation.

We collected visual obstruction data with a 50 cm by 50 cm visibility board marked at 10 cm intervals placed at the random UTM coordinates of the random plots. An observer viewed the board from a 4 m distance along each canopy cover transect through a 1–inch diameter PVC joint at 1 m height (Bristow and Ockenfels 2002). We measured visual obstruction by vegetation at each height interval as the number of points out of 10 that were obscured by vegetation at each of 5 heights (10 cm, 20 cm, 30 cm, 40 cm, or 50 cm). We averaged measurements from the 4 directions (transects) to quantify % visual obstruction at each random site.

We focused on quantifying the amount of "optimum" hiding cover available. We used canopy cover and visual obstruction measures as response variables and tested the null hypotheses that there were no differences in amounts of optimum hiding cover by study area, land ownership, year and grazing intensity (independent variables). Because canopy cover measurements were recorded as presence or absence within 10 cm height intervals, the 20–30 cm interval becomes the lowest height category with vegetation structure similar to published pronghorn management guidelines (Autenrieth et al. 2006) and research (Ticer & Miller 1994). Preferred habitat is characterized as that with low vegetative structure, averaging 10–18 inches (25–46 cm) and <25 inches (63cm), with 50% or more living ground cover in semidesert grassland habitat (Autenrieth et al. 2006). The *Arizona Statewide Pronghorn Operational Plan* (Arizona Game and Fish Department [AGFD] 2006) defines adequate fawning cover as generally provided by herbaceous vegetation that is >11 inches in height, with little shrub cover. The most relevant research characterized 111 fawn bed sites within our study area (Ticer and Miller 1994). Pronghorn neonate (< 3 weeks) bedsites had a mean total vegetative canopy cover (grass, forbs, shrubs and cacti) of 31.78 %, mean grass height of 29.3 cm, mean forb height of 13.3 cm, and fawns avoided areas with shrub and cacti heights >30 cm. Schuetze (1993) studied seasonal and diurnal habitat selection by pronghorn on Marlow Mesa (30 km^2 within our North study area). One seasonal stratification included the fawning period of April–May. Results indicated that pronghorn selected for areas with greater grass and forb density, and avoided higher shrub and cactus density during the fawning season. Overall, Schuetze (1993) found that pronghorn preferred areas with mean herbaceous (grass and forb) heights of 13–38 cm (25 cm average).

Using these benchmarks we defined "optimum" hiding cover using canopy cover data as the percent vegetation cover (regardless of vegetation type) between 21 and 40 cm, but not reaching the 41–100 cm interval. Given that data were summed by site rather than by point, it was not possible to identify how many points at each site fit this criterion. Instead, we estimated this number at a site by taking the larger of the counts in the 21–30 cm and 31–40 cm intervals and then subtracted the count for the 41–100 cm interval. This is a conservative estimate because we assumed all points with cover between 20 and 40 cm, also had cover between 0 and 20 cm, which was often, but not always the case. Secondly, there were some points where vegetation was found above the 40 cm mark, but not below (e.g., a tree or shrub hanging over the point; D. Warnecke, pers. obs.). This method did produce negative counts for some sites, which were set to zero. However, results did not qualitatively change if we did not subtract the values of the highest category. Finally, we measured live and dead vegetation. Considering these decisions our evaluation likely over estimated the availability of hiding cover.

Using visual obstruction data we defined "optimum" hiding cover as the amount of visual obstruction at the 20, 30, or 40 cm heights, but not reaching 50 cm. Once again, data were summed by site rather than by point, so it was not possible to identify how many points at each site fit this criterion. We estimated this number at a site by taking the larger of the counts at the 20, 30, or 40 cm lines and subtracted the count for the 50 cm line.

Land use (e.g., grazing) and natural phenomena (e.g., fire, drought, insects) can change the make up of grassland communities (McClaran and Van Devender 1995.). We were interested in whether patterns of optimum hiding cover across vegetation types were consistent with patterns found in the dominant vegetation (grasses). We therefore repeated analyses of optimum hiding cover considering only percent grass cover. In order to determine effects of grazing, we also measured vegetation cover and visual obstruction at 36 sites excluded from livestock grazing (within exclosures). We added these 36 observations to the 547 observations used in previous analyses and compared amount of optimum hiding cover in grazed open pastures to ungrazed exclosures.

Grazing pressure was calculated as the number of livestock (horses, cows, sheep) per square mile on an allotment for a one–year period (CYL/sq. mi.). This relative index for grazing intensity was calculated from actual use (animal unit months or AUMs) (Table 1). Land management agencies reported AUMs for the years 2002, 2003, and 2004. We averaged actual use (all livestock classes) for the 3 years and converted AUMs to animal units (AUs or cows year long CYL) and divided by the number of square miles each allotment represents. Effects of grazing on fawn hiding cover (canopy cover) during any given year influences available canopy cover the following year, dependent on the timing of grazing relative to growing season and/or whether timing and amount of winter precipitation initiates early spring growth.

All metrics were in the form of counts (although canopy cover data can be thought of as percentages, given that they are counts out of 100). Counts were generally very small, often zero, with a few sites having much higher counts. These non–negative, right–skewed distributions deviate from the normal distribution at the heart of standard ANOVA and regressions techniques. Instead, counts tend to follow a Poisson or a negative binomial distribution where the variance is equal to the mean or is an increasing function of the mean (Neter et al. 1996, Fox 2002, Dohoo et al. 2003). Several different lines of evidence [rootograms (not shown; Friendly 2000), likelihood ratio $\chi 2$ tests for goodness of fit (Zar 1999, Dohoo et al. 2003), and tests of the added variance component, *theta*, in negative binomial models (Dohoo et al. 2003)] indicated more over–dispersion in data than could be accounted for by a poisson distribution, but which could be fit with a negative binomial. Although the negative binomial distribution was not a perfect fit (e.g., the likelihood ratio for optimum hiding cover data: $\chi 2 = 50.03$, 30 df, $P = 0.012$), it appeared to be a reasonable approximation. Therefore, we used general linear models with a negative binomial error distribution in all regression analyses of optimum hiding cover.

Negative binomial regression works on natural log–transformed data, and Y–axes of the figures and the regression parameters are on the natural log scale. Where appropriate, we back–transformed estimates to the original scale by exponentiating the estimate (raising the estimate to the *e* power) to give estimates of effect sizes (amount that response variable changes with an increase/decrease of predictor variable).

We treated year (2002, 2003, or 2004) as categorical data rather than a continuous because we did not expect a linear trend from year to year. That is, there is no reason to think the effect of the difference between 2002 and 2004 should be twice that of the difference between 2002 and 2003. There was a great deal of year–to–year variation in all measures. Therefore year was included in all models to identify the generally weaker effects of North versus South, ownership, and grazing pressure.

We used Akaike's Information Criteria (AIC) to determine how well statistical models fit data sets (Fox 2002; Dohoo et al. 2003). We were more interested in the *differences* in AIC values for alternative models (ΔAIC), however, because large differences suggest one model better explains the data than another.

Lastly, we excluded certain observations from analyses. This study included a large number of sites on lands owned by BLM, TNF, and PNF measured over 3 years. However, there were also 6 sites on land owned by the State of Arizona and 1 on private land, all surveyed in 2004. These small sample sizes could not support proper analyses and were therefore excluded from the analyses. In order to maintain a consistent data set, these 7 observations were also excluded from models that did not use ownership as a predictor. The same is true of several sites on allotments missing information on grazing pressure. These were either along a fence–line between 2 allotments, or were unassigned. We also excluded one outlier observation (record #435) from TNF in the South during 2002 because it influenced parameter estimates.

We conducted multivariate comparisons to understand differences in the entire suite of vegetation and height categories between the North and South, and between the 3 land managers of

GMU 21. Data consisted of counts of the canopy cover at 5 height intervals (0–10 cm, 11–20 cm, 21–30 cm, 31–40 cm, and 40 cm and above) for each of 5 vegetation types: grasses, forbs, shrubs, cacti, and trees. In order to maintain consistent data among analyses, we again excluded observations from State and Private lands, sites on allotments missing information on grazing pressure, and record #435 from the TNF in the South during 2002. We also excluded record #124, measured in 2002 on the Cienega allotment on PNF land because this observation deviated from multivariate normality.

The multivariate data had 25 response variables (5 height categories for each of 5 vegetation types), too many for clear interpretation of multivariate tests. We used principle components analysis to identify subsets of parameters that explained most of the variation in these variables for use in multivariate hypothesis tests (Everitt 2005). We used standard principal components analysis of the natural log of each of the 25 counts (plus one to avoid zeros) scaled by their standard errors such that each response was on the same scale and centered around zero. Results changed very little when sites within exclosures were excluded. Therefore we used both open grazed pasture and ungrazed exclosure sites in principal components analyses.

We assessed multivariate normality of the log–transformed count data with a plot analogous to univariate normality plots. It involves plotting the generalized distance of the observations from the mean vector of the complete sample against a chi–square distribution with q = 25 degrees of freedom (Everitt 2005). As noted, this plot showed one observation that deviated from multivariate normality (record #124 measured in 2002 on the Cienega allotment in PNF). Removing this observation brought the data set much closer to multivariate normality, therefore we exclude this one observation. While the data do depart somewhat from multivariate normality, multivariate analyses of variance (MANOVAs) are fairly robust to this departure, and the test statistic based on Pillai's trace is robust to most violations (Scheiner 2001; Everitt 2005). We then performed MANOVA on 2 new axes from the principal components analysis of the data organized by height categories. We considered all comparisons significant at $\underline{P} \leq 0.05$.

Results

Deviance goodness of fit tests was significant for all regression models of hiding cover measures relative to independent predictor variables (North–south, ownership, and year). This suggests the negative binomial distribution was not an ideal fit to the distribution of the counts. However, examination of residuals from the models suggested the lack of fit was due to a slight, but consistent over abundance of observations with very large and very small counts, and lack of observations with intermediate counts. Because this lack of fit was consistent across groups and treatments, we feel it did not bias the analyses. This type of lack–of–fit indicates more dispersion within groups than expected. This makes our hypothesis tests more conservative, and it is more difficult to detect a difference between groups if one exists. Because of lack of fit, these models should not be used to *predict* the amount of optimum canopy cover, grass cover, or visual obstruction. They are simply tests of hypothesized differences between variables in GMU21.

Optimum Canopy Cover: Any Type of Vegetation

North versus South: Optimum canopy cover differed between North and South sections of GMU21 ($\beta_{South} = 0.355 \pm 0.104$, parameter ± 1 S.D., *Likelihood–ratio* $\chi^2 = 11.64$, 1 df, $P < 0.001$) and between years ($\beta_{2003} = 0.709 \pm 0.131$, $\beta_{2004} = 1.255 \pm 0.144$; $\chi^2 = 74.39$, 2 df, $P < 0.001$). The interaction between North–South and Year was not significant ($\chi^2 = 3.60$, 2 df, $P = 0.166$). The South had more optimum canopy cover than the North, roughly 1.43 times as much (Figures. 4a and 5a). Compared across years, there was twice as much optimum canopy cover in 2003 as in 2002. In 2004 there was 3.5 times as much as 2002.

Ownership: Optimum canopy cover differed between land ownership ($\beta_{PNF} = -0.354 \pm 0.112$, $\beta_{TNF} = 0.227 \pm 0.177$; $\chi^2 = 17.61$, 2 df, $P < 0.001$), and among years ($\beta_{2003} = 0.718 \pm 0.131$, $\beta_{2004} = 1.263 \pm 0.143$; $\chi^2 = 75.73$, 2 df, $P < 0.001$). The interaction between ownership and year was not significant ($\chi^2 = 4.536$, 4 df, $P = 0.338$). The PNF had less optimum canopy cover than BLM ($z = -3.160$, $P = 0.002$), about 70% as much. While TNF was not different from BLM ($z = 1.282$, $P = 0.200$; Figures 4b and 5b). Differences among years were similar to the model comparing North and South.

Grazing pressure: Grazing negatively effected optimum canopy cover ($\beta_{GrazingPressure} = -0.068 \pm 0.016$; $\chi^2 = 19.59$, 1 df, $P < 0.001$), and the year effect was very similar to that of other models ($\beta_{2003} = 0.711 \pm 0.130$, $\beta_{2004} = 1.230 \pm 0.143$; $\chi^2 = 72.49$, 2 df, $P < 0.001$). With every additional CYL/mi^2, optimum canopy cover decreased on average by 6–7%, or over 3–fold over the whole range of grazing pressures (Figures. 4c and 5c).

Finding the best model:. The single factor (plus year) models (North–South, ownership, and grazing pressure) were roughly similar in terms of explained variation but grazing pressure (plus year) (AIC=3,005) emerged as the best model based on Akaike's Information Criteria compared to the North–South model (AIC=3,013) and ownership model (AIC=3,009).

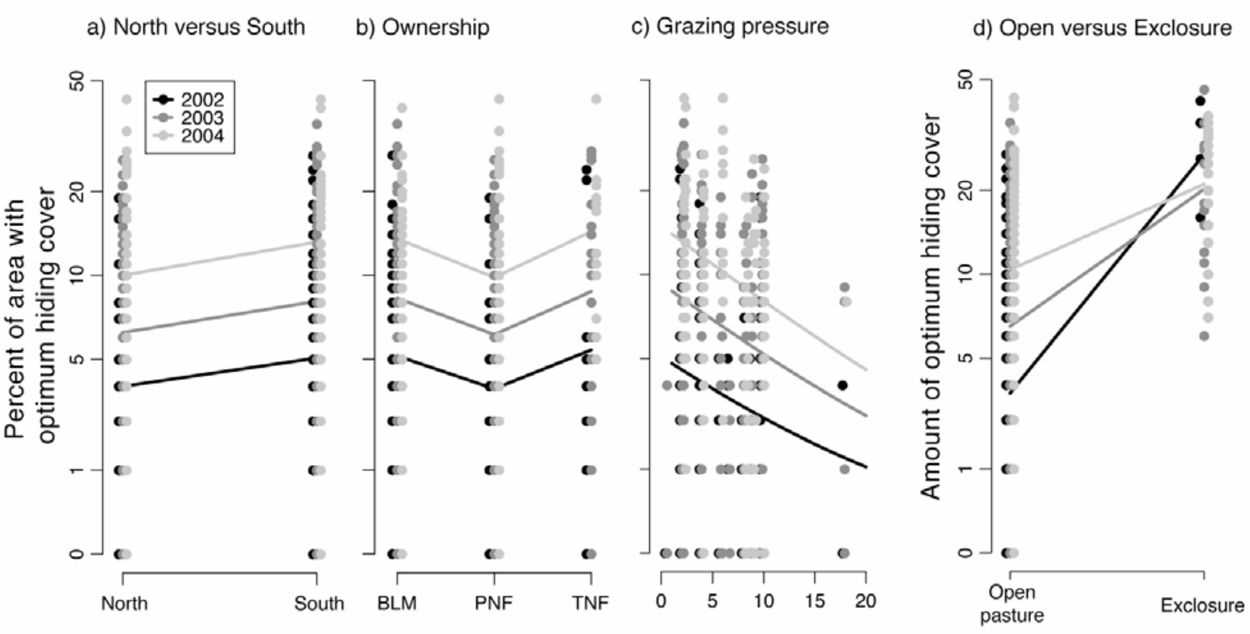

Figure 4. The estimated means (lines) and observed values (dots) for percent of areas with optimum hiding cover according to whether the site was in the North or South (A), land ownership (B), grazing pressure (C), or whether the site was within an exclosure or on open pastures (D). Note: Figure D used a larger dataset focused on open pastures than other models. The key refers to year in all 4 figures.

It appeared much of the explanatory power of North versus South and ownership models was due to differences in grazing pressure (Figure 6). The southern allotments had lower grazing pressure than those in the north (regression weighted by number observations per allotment–with Box Bar and Sycamore PNF pastures excluded because they straddled the North–South line; $\text{Mean}_{\text{South}} = 3.71 \pm 1.47$, $\text{Mean}_{\text{North}} = 8.50 \pm 1.00$, $t = –3.26$, $P = 0.009$). Adding the North versus South factor to the model with grazing pressure (and year) only added noise and increased AIC to 3007, suggesting a less parsimonious regression model. While the grazing pressure parameter was largely unchanged ($\beta_{GrazingPressure}$ increased in magnitude to $–0.071 \pm 0.023$; $\chi^2 = 7.77$, 1 df, $P = 0.005$) the North versus South parameter was not significant ($\chi^2 = 0.02$, 1 df, $P = 0.893$). When ownership was added to the model with grazing pressure (and year), AIC increased to 3,008, ownership was not significant ($\chi^2 = 0.962$, 2 df, $P = 0.618$), and the grazing pressure parameter decreased in magnitude by about 25%, and grazing pressure lost significance ($\chi^2 = 2.86$, 1 df, $P = 0.091$). All of this suggests that outside between–year effects, grazing pressure is the most important factor. However, North and South areas, ownership, and grazing pressure were all confounded with each other and with other extrinsic factors that were not measured or even measurable (e.g., rainfall, fire, exotic plant invasions). This makes it difficult to attribute differences in amount of optimum hiding cover to grazing pressure per se. To really understand how grazing pressure influenced amount of optimum hiding cover would require experimental manipulation. Comparisons between open grazed pastures and exclosures serve as such an experiment.

Exclosures: Note that since exclosure models were fit to slightly different data, AIC values should not be compared to those of previous models. Exclosures effected amount of optimum hiding cover ($\beta_{Exclosure} = 2.250 \pm 0.506$; $\chi^2 = 60.47$, 1 df, $P < 0.001$), and had a between–year effect ($\beta_{2003} = 0.697 \pm 0.127$, $\beta_{2004} = 1.232 \pm 0.140$; $\chi^2 = 68.57$, 2 df, $P < 0.001$). However, there was also an exclosure

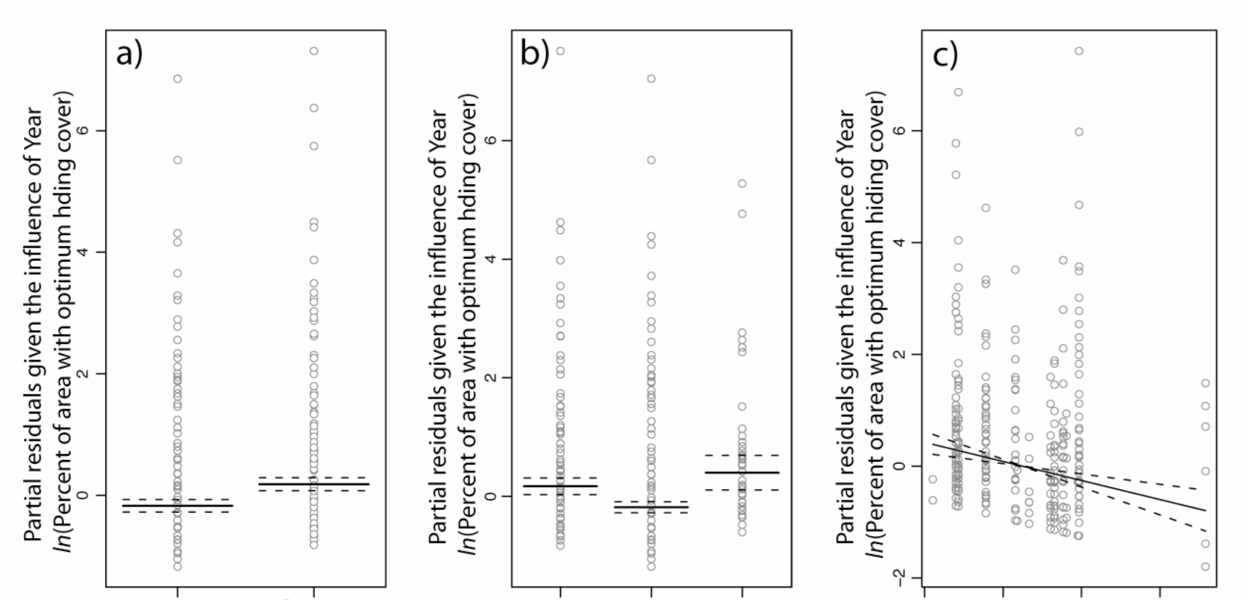

Figure 5. Partial residual plots representing effects of North versus South (A), ownership (B), and grazing pressure (C) after the effect of year has been taken into account. Solid lines are predicted means. Dashed lines are the standard error. Open circles are partial residuals (i.e., residual variation left over after taking year into account).

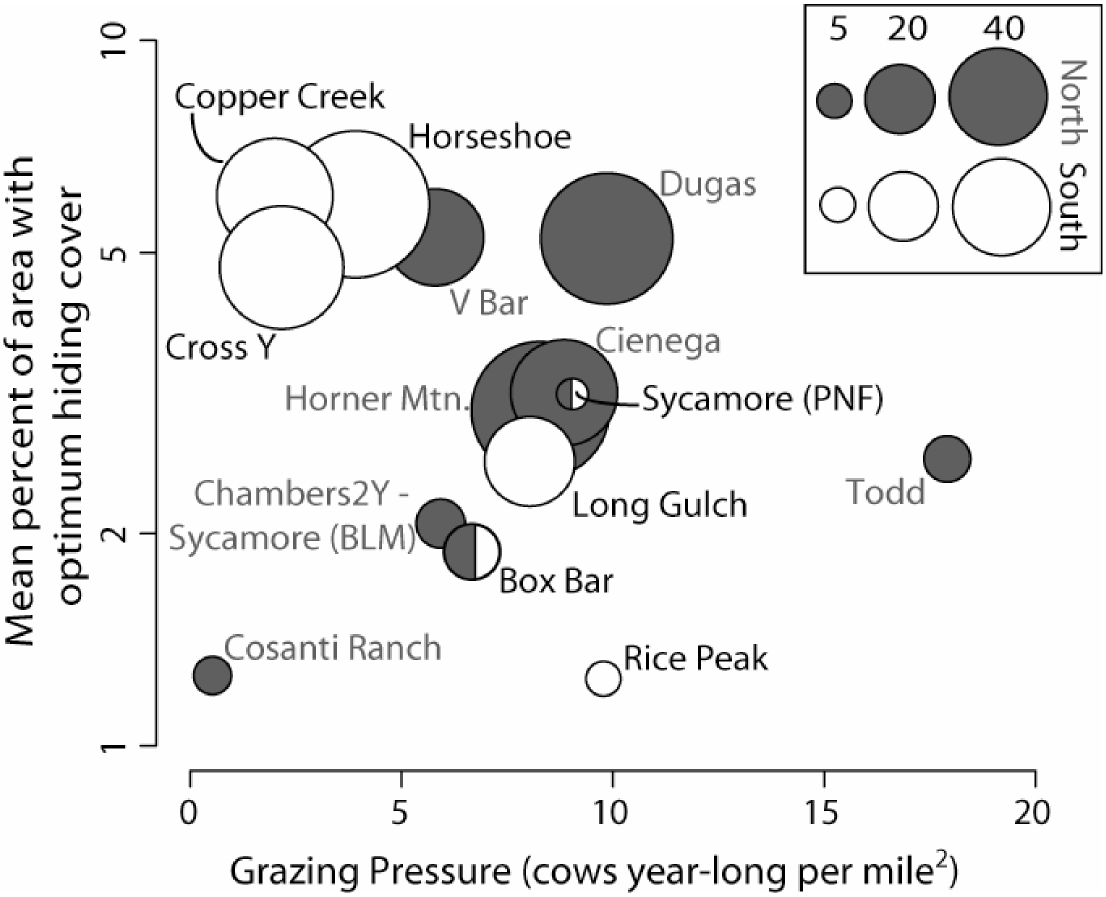

Figure 6: Mean percent of area with optimum hiding cover for each allotment (calculated as the mean of the log of optimum hiding cover plus one) by grazing pressure in the North and South. Area of the circles are proportional to the number of observations in that allotment.

x year interaction ($\beta_{Ex-2003} = -0.999 \pm 0.597$, $\beta_{Ex-2004} = -1.491 \pm 0.577$; $\chi^2 = 7.99$, 2 df, $P = 0.018$). This interaction was largely due to the fact that amount of optimum hiding cover did not differ between years within exclosures ($\chi^2 = 1.28$, 2 df, $P = 0.529$), while it increased with time in open pastures (Figure 4d). In other words, the inter–annual variation that was important in other analyses was not seen when livestock grazing was excluded.

On average, there was always more optimum hiding cover in exclosures than in open pastures. Even when conditions were best in open pastures (2004) they only had about 10% optimum hiding cover while exclosures always had about 20% optimum hiding cover (Figure 4d). Averaging over all 3 years, exclosures had over 3 and a half times more optimum hiding cover than open pastures.

Optimum canopy cover: grasses

Finding the best model: Analyses for amount of optimum grass cover were very similar to analyses for any type of vegetative cover. The final best model based on AIC values included grazing pressure ($\beta_{GrazingPressure} = -0.068 \pm 0.014$; $\chi^2 = 23.45$, 1 df, $P < 0.001$), and a year effect ($\beta_{2003} = 0.908 \pm 0.122$, $\beta_{2004} = 1.504 \pm 0.132$; $\chi^2 = 129.20$, 2 df, $P < 0.001$). With every additional CYL/mi^2, optimum grass cover decreases by 6–7% on average, or over three–fold over the whole range of grazing pressures. Differences in AIC between the best model (AIC = 2,829.9) and those that included ownership (AIC = 2,830.1), North–South (AIC = 2,831.8), or both (AIC = 2,832.1) were minimal and added terms were not significant.

Exclosure:. We directly compared effects of grazing on amount of optimum grass cover by adding observations from exclosures. Results were similar to those for optimum hiding cover overall. There was an effect of exclosure on amount of optimum hiding cover ($\beta_{Exclosure} = 2.430 \pm 0.448$; $\chi^2 = 81.01$, 1 df, $P < 0.001$), and a year effect ($\beta_{2003} = 0.881 \pm 0.120$, $\beta_{2004} = 1.149 \pm 0.130$; $\chi^2 = 118.59$, 2 df, $P < 0.001$). Once again, there was an exclosure x year interaction ($\beta_{Ex\text{–}2003} = –1.20 \pm 0.529$, $\beta_{Ex\text{–}2004} = –1.642 \pm 0.511$; $\chi^2 = 12.56$, 2 df, $P = 0.002$) due to the fact that amount of optimum grass cover did not differ between years within exclosures ($\chi^2 = 1.12$, 2 df, $P = 0.570$), while it increased with time in open pastures. Open pastures averaged about 5% optimum grass cover over the 3 years, whereas exclosures averaged about 19%. Again, even in the best year for open pastures (2004) there was over twice as much optimum grass cover in exclosures as in open pastures (about 19% versus 9%, respectively).

Optimum visual obstruction

Finding the best model: We repeated all regression analyses replacing canopy cover with visual obstruction as the response variable. Results were similar to those for canopy cover. The best model includes grazing pressure ($\beta_{GrazingPressure} = –0.087 \pm 0.017$; $\chi^2 = 25.89$, 1 df, $P < 0.001$), and a year effect ($\beta_{2003} = 0.781 \pm 0.140$, $\beta_{2004} = 1.030 \pm 0.154$; $\chi^2 = 44.43$, 2 df, $P < 0.001$). With every additional CYL/mi^2, amount of optimum visual obstruction decreased by 8–9% on average, or over 4 and a half–fold over the range of grazing pressures. Difference in AIC between the best model (AIC = 3,164.2) and those including ownership (AIC = 3,167.8), North–South (AIC = 3,166.2), or both (AIC = 3,169.5) suggest moderate support for this model. Added terms were not significant.

Exclosures: Exclosures effected amount of optimum visual obstruction ($\beta_{Exclosure} = 1.035 \pm 0.215$; $\chi^2 = 30.75$, 1 df, $P < 0.001$), and there was a year effect ($\beta_{2003} = 0.757 \pm 0.134$, $\beta_{2004} = 0.963 \pm 0.147$; $\chi^2 = 43.69$, 2 df, $P < 0.001$). In this case, the exclosure–by–year interaction was not significant (χ^2 2.47, 2 df, $P = 0.291$) because amount of optimum visual obstruction did not differ between years within exclosures ($\chi^2 = 0.253$, 2 df, $P = 0.881$). Change outside exclosures was not large either, and slopes were not different. The mean amount of optimum visual obstruction was not quite 3 times as great inside the exclosures.

Multivariate comparisons

Principal components of the twenty–five variables: In general, loadings of the first 5 principle components axes grouped by kind of vegetation rather than vegetation height. Counts at each height interval tended to be correlated within a particular vegetation type (Table 2, grey boxes) rather than across vegetation types (Table 2, off diagonals).

Principal components of the 5 height categories: We grouped data by height categories, ignored vegetation type, and examined the principal components. It appeared the first 2 principal components explained most (85%) of the variability in the data (Figure 7a). The new first axis sorted sites according to how much vegetation they had regardless of height interval. The second axis sorted by vegetation height from low to high (Figure 7b).

Table 2– Correlations between log–transformed measurements of 5 different vegetation types at 5 different height intervals for pronghorn fawn hiding cover in Arizona GMU21.

		Grasses					Forbs					Shrubs					Cacti					Trees				
		10	20	30	40	>40	10	20	30	40	>40	10	20	30	40	>40	10	20	30	40	>40	10	20	30	40	>40
Grasses	10	1.00	0.77	0.59	0.46	0.33	–0.14	–0.07	0.01	0.00	–0.10	–0.09	–0.01	0.02	–0.02	–0.04	–0.08	–0.07	0.01	0.02	0.04	–0.03	–0.07	0.01	–0.04	–0.10
	20	0.77	1.00	0.84	0.64	0.44	0.11	0.18	0.16	0.04	–0.10	–0.14	0.00	0.03	–0.02	–0.07	–0.05	–0.02	0.06	0.06	0.08	–0.02	–0.04	0.03	–0.02	–0.03
	30	0.59	0.84	1.00	0.80	0.59	0.18	0.22	0.23	0.10	–0.05	–0.02	0.10	0.14	0.07	0.03	0.01	0.04	0.12	0.12	0.13	0.02	–0.02	0.07	0.02	0.02
	40	0.46	0.64	0.80	1.00	0.71	0.08	0.09	0.12	0.11	–0.02	0.07	0.18	0.22	0.16	0.12	0.02	0.04	0.09	0.10	0.12	0.04	0.02	0.09	0.05	0.07
	>40	0.33	0.44	0.59	0.71	1.00	0.02	0.06	0.08	0.08	0.00	0.10	0.17	0.20	0.13	0.10	0.04	0.09	0.12	0.11	0.14	–0.01	–0.01	0.01	0.01	0.03
Forbs	10	–0.14	0.11	0.18	0.08	0.02	1.00	0.60	0.32	0.16	0.11	–0.05	–0.01	–0.04	–0.04	–0.05	0.00	0.01	0.00	–0.01	–0.01	–0.01	–0.03	–0.02	–0.05	–0.02
	20	–0.07	0.18	0.22	0.09	0.06	0.60	1.00	0.72	0.41	0.25	0.02	0.04	0.03	0.02	–0.03	0.09	0.05	0.04	0.05	0.04	–0.03	–0.02	0.02	–0.07	–0.01
	30	0.01	0.16	0.23	0.12	0.08	0.32	0.72	1.00	0.65	0.39	0.02	0.07	0.06	0.03	–0.02	0.18	0.13	0.11	0.11	0.13	–0.03	–0.03	0.03	–0.02	0.02
	40	0.00	0.04	0.10	0.11	0.08	0.16	0.41	0.65	1.00	0.60	–0.01	0.04	0.05	0.04	–0.01	0.24	0.15	0.15	0.12	0.12	–0.03	–0.03	–0.02	–0.03	–0.02
	>40	–0.10	–0.10	–0.05	–0.02	0.00	0.11	0.25	0.39	0.60	1.00	–0.11	–0.08	–0.07	–0.05	–0.05	0.23	0.13	0.13	0.12	0.09	–0.02	–0.03	–0.02	–0.04	–0.03
Shrubs	10	–0.09	–0.14	–0.02	0.07	0.10	–0.05	0.02	0.02	–0.01	–0.11	1.00	0.82	0.72	0.56	0.53	0.14	0.14	0.16	0.18	0.17	0.08	0.11	0.16	0.13	0.14
	20	–0.01	0.00	0.10	0.18	0.17	–0.01	0.04	0.07	0.04	–0.08	0.82	1.00	0.83	0.68	0.58	0.18	0.20	0.22	0.22	0.21	0.08	0.12	0.14	0.10	0.16
	30	0.02	0.03	0.14	0.22	0.20	–0.04	0.03	0.06	0.05	–0.07	0.72	0.83	1.00	0.80	0.70	0.14	0.15	0.17	0.20	0.20	0.05	0.08	0.10	0.07	0.14
	40	–0.02	–0.02	0.07	0.16	0.13	–0.04	0.02	0.03	0.04	–0.05	0.56	0.68	0.80	1.00	0.80	0.10	0.11	0.12	0.18	0.17	0.12	0.16	0.16	0.14	0.20
	>40	–0.04	–0.07	0.03	0.12	0.10	–0.05	–0.03	–0.02	–0.01	–0.05	0.53	0.58	0.70	0.80	1.00	0.03	0.00	0.06	0.14	0.13	0.14	0.15	0.18	0.16	0.18
Cacti	10	–0.08	–0.05	0.01	0.02	0.04	0.00	0.09	0.18	0.24	0.23	0.14	0.18	0.14	0.10	0.03	1.00	0.78	0.63	0.51	0.50	0.04	0.04	0.09	0.10	0.09
	20	–0.07	–0.02	0.04	0.04	0.09	0.01	0.05	0.13	0.15	0.13	0.14	0.20	0.15	0.11	0.00	0.78	1.00	0.74	0.61	0.57	0.06	0.08	0.09	0.12	0.11
	30	0.01	0.06	0.12	0.09	0.12	0.00	0.04	0.11	0.15	0.13	0.16	0.22	0.17	0.12	0.06	0.63	0.74	1.00	0.81	0.74	0.09	0.05	0.10	0.15	0.13
	40	0.02	0.06	0.12	0.10	0.11	–0.01	0.05	0.11	0.12	0.12	0.18	0.22	0.20	0.18	0.14	0.51	0.61	0.81	1.00	0.82	0.18	0.13	0.13	0.18	0.16
	>40	0.04	0.08	0.13	0.12	0.14	–0.01	0.04	0.13	0.12	0.09	0.17	0.21	0.20	0.17	0.13	0.50	0.57	0.74	0.82	1.00	0.10	0.04	0.12	0.16	0.14
Trees	10	–0.03	–0.02	0.02	0.04	–0.01	–0.01	–0.03	–0.03	–0.03	–0.02	0.08	0.08	0.05	0.12	0.14	0.04	0.06	0.09	0.18	0.10	1.00	0.71	0.60	0.64	0.65
	20	–0.07	–0.04	–0.02	0.02	–0.01	–0.03	–0.02	–0.03	–0.03	–0.03	0.11	0.12	0.08	0.16	0.15	0.04	0.08	0.05	0.13	0.04	0.71	1.00	0.64	0.61	0.72
	30	0.01	0.03	0.07	0.09	0.01	–0.02	0.02	0.03	–0.02	–0.02	0.16	0.14	0.10	0.16	0.18	0.09	0.09	0.10	0.13	0.12	0.60	0.64	1.00	0.74	0.70
	40	–0.04	–0.02	0.02	0.05	0.01	–0.05	–0.07	–0.02	–0.03	–0.04	0.13	0.10	0.07	0.14	0.16	0.10	0.12	0.15	0.18	0.16	0.64	0.61	0.74	1.00	0.78
	>40	–0.10	–0.03	0.02	0.07	0.03	–0.02	–0.01	0.02	–0.02	–0.03	0.14	0.16	0.14	0.20	0.18	0.09	0.11	0.13	0.16	0.14	0.65	0.72	0.70	0.78	1.00

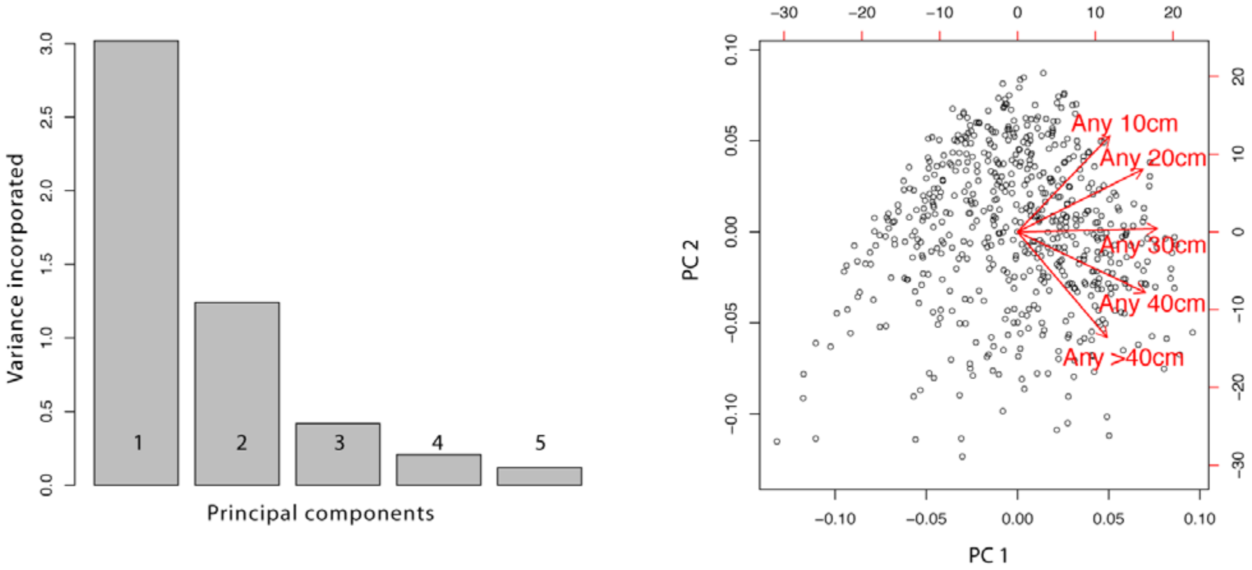

Figure 7: Plots of the principal components derived from 5 new height variables measured as counts of vegetation in each of 5 height intervals regardless of vegetation type .Variance explained by the 5 principle components (A). Data (open circles) and original axes (red arrows) are plotted on the first and second principal components (B).

MANOVAs for the new axes reflecting abundance and height of vegetation (ignoring vegetation type): We performed MANOVA on the first 2 new axes from the principal components analyses organized by height categories. The first axis appeared to represent percent vegetation cover irrespective of height. The second axis indicated whether that cover was concentrated at high or low height intervals. Each main effect was significant: North vs. South (*Pillai's trace* = 0.027, $F_{2,542} = 7.46$, $P < 0.001$), ownership (*Pillai's trace* = 0.046, $F_{10,1078} = 8.99$, $P < 0.001$), grazing pressure (*Pillai's trace* = 0.053, $F_{2,542} = 15.07$, $P < 0.001$), and year (*Pillai's trace* = 0.259, $F_{5,541 \text{ to } 542} = 94.40$ to 94.94, $P < 0.001$). Each factor in the full model with all factors added was also significant (Table 3). Once again apart from year, grazing pressure (open and excluded sites) explained most of the variation. The means of these axes were not meaningful, but they did suggest sites in the North had less (PC1 = –0.31 vs. 0.09) but slightly higher (PC2 = 0.09 vs. –0.17) vegetation than the South. Sites in the TNF (PC1 = 0.46) had more vegetation than those on BLM land (PC1 = –0.02), which had more than those in PNF (PC1 = –0.31). BLM sites have shorter vegetation than those on the other 2 lands (PC2 = –0.25 vs. 0.09, respectively).

Discussion

Measurement and description of security and thermal cover at fawn bedsites has been widely investigated and varies according to biome and specific plant communities (O'Gara and Yoakum 2004). Predation is an important, perhaps chief cause of fawn mortality (Beale and Smith 1973, Neff and Woolsey 1979, Neff et al. 1985, O'Gara et al. 1986, Smith et al. 1986). However it is widely debated whether predation is primary or is a consequence of lack of available fawn hiding cover on some rangelands (Autenrieth 1982). Despite that debate, research has shown that some measure of hiding cover does influence a fawn's ability to conceal itself from predators. Fawns use bedsites with specific microhabitat features (Pyrah 1974, Autenrieth 1984, Alldredge et al. 1991, Rothchild et al. 1994, Canon and Bryant 1997).

Fawn hiding cover assessment indicated more hiding cover was available in the South versus the North during the 3 spring fawning seasons (2002–2004). This result held true for both measures (line intercept and visibility board) and for the dominant vegetation class (grass). We surveyed a greater number of fawns per 100 does in the South (Figure 2a) during the spring fawning seasons from 2002–2005 and late–summer fawn survival indices (fawn:100 does) met or exceeded the Department's species management guidelines of 30–40 fawns per 100 does, 3 out of 4 years in the South. We concluded that more optimum hiding cover in the South may have positively influenced fawn recruitment in the south.

We found annual precipitation levels increased between study years corresponding to greater amounts of optimum hiding cover between years. Regression analyses and multivariate analyses of variance suggest the greatest amount of variation in available hiding cover was explained by effects of inter-annual variation in precipitation. However, inter-annual differences in available hiding cover became insignificant when livestock grazing was removed from the environment, even during extreme drought. We always had more optimum hiding cover at sites excluded from livestock grazing. Even during the year we measured the greatest amount of cover in open sites (2004), we had twice as much optimum cover in the ungrazed sites. Averaging results from all 3 fawning seasons, we measured 3.5 times more optimum cover on sites excluded from livestock grazing. We found that with every additional CYL/mi^2, the percent of optimum cover decreased on average by 6–7%.

Apart from effects of inter-annual variation in precipitation, grazing pressure was the most influential factor affecting available hiding cover. Allotments in the South had significantly lower grazing pressures than North allotments. We concluded that greater amounts of optimum hiding cover in the South might have contributed to higher fawn recruitment rates in the South, despite a long-term population trend that was declining and largely attributable to drought. We also concluded that higher grazing pressures contributed to less optimum hiding cover and might have contributed to lower fawn recruitment rates in the North.

Our multivariate comparisons did not detect differences associated with study areas and ownership, indicating plant communities were similar. However, we found that 85% of the variability was explained by how much vegetation there was (presence or absence) and whether that vegetation was tall or short. While sites in the South had more vegetation, they also had shorter vegetation. This finding is important in that it suggests light levels of grazing pressure can be compatible with maintenance of optimum pronghorn fawn hiding cover if grazing reduces vertical structure within limits, without significantly reducing plant densities over time or during periods of drought.

Table 3. Test statistics for MANOVA with all predictors included and the reduced set of height interval response variables (5 height intervals ignoring the 5 vegetation categories) of pronghorn hiding cover in Arizona GMU21.

	Pillai's Trace	F	$DF_{Numerator}$	$DF_{Denominator}$	P	Percent of explained variance
North–South	0.028	7.696	2	540	< 0.001	6.4%
Ownership	0.019	5.196	2	540	0.006	4.3%
Grazing Pressure	0.048	13.477	2	540	< 0.001	11.3%
Year	0.257	93.395	2	540	< 0.001	78.0%

Increasing evidence suggests that summer and winter droughts are 2 population controls that will likely continue to influence GMU 21 pronghorn population trends. Lack of adequate hiding cover further compounds the potential negative effects of drought on fawn survival. Brown et al. (2006) reported a relationship between mid-summer drought (measured by Palmer Drought Severity Index–PDSI) and observed doe numbers during the same period in 3 southwestern pronghorn populations, including GMU 21. Further, number of fawns per 100 does was correlated with number of does observed the following year. Related findings suggest the influence of midsummer drought on habitat quality impacts carrying capacity and ultimately pronghorn population trends. Additionally, relationships between winter precipitation and late summer fawn survival rates have been tested for several populations in the Southwest, including GMU 21. Brown et al. (2002) found a relationship for GMU 21 and other populations and concluded forb production follows timely and plentiful winter precipitation and might be more important to fawn survival than summer precipitation and grass production on fawn survival rates of following years. A relationship was also found between spring drought and late summer fawn survival rates in GMU 21.

Finally, we recognize that hiding cover and available forage on suitable pronghorn range are 2 limiting factors inextricably related, and both influence fawn recruitment. There is likely a relationship between hiding cover and forage production within our study areas. Although we conclude that hiding cover may be a contributing factor to North and South differences in fawn recruitment, it is very likely that available herbaceous forage and interspecific competition during the spring and early summer also influenced these differences. Diet overlap and competition is more likely where there is low forage productivity, low forage plant diversity, overstocked range conditions, drought, and/or opportunistic grazing responses to seasonal abundance of succulent forage (Hailey et al. 1966, Ellis 1970, Beasom et al. 1982, Stephenson et al. 1985, Neff 1986, Howard et al. 1990, Brown et al. 2002, Brown et al. 2004, Miller and Drake 2006). Experimental treatments on Deseret Ranch, a sagebrush-steppe rangeland in Utah, used fire and plantings (forbs, grasses, shrubs) in conjunction with intermittent grazing and rest to increase habitat carrying capacity and pronghorn production. Aoude and Danvir (2002) reported pronghorn increases after treating as little as 2% of the range per year. Yoakum (2004) reported that removal of livestock grazing from rangelands on the Hart Mountain National Antelope Range (Oregon) in the early 1990’s contributed to a 200% increase in herbaceous forage composition, a 3-fold increase in forb cover, and the highest pronghorn numbers reported since the 1950’s.

Management Implications

Our findings suggest the negative influence of drought on fawn survival and recruitment might be moderated with management actions that improve or maintain habitat quality (cover and forage), and reduce interspecific competition. Further, improved range conditions might moderate potential indirect effects of pronghorn mortality related to lack of alternate prey species (Beale 1986) for predators or predation losses as a result of foraging in suboptimum habitat (Beale and Smith 1970, Anthony 1976). Although predation is a common mortality factor and ecological conditions contribute to the success of predators, habitat quality is believed to influence population trends greater than mortality from predation (Yoakum et al. 2004).

Based on our findings, we suggest long-term implementation of lower livestock stocking densities, not greater than 4–5 CYL/mi^2, and lighter utilization levels to improve pronghorn habitat quality and productivity on semidesert grassland ranges in central Arizona. Lower stocking densities may be appropriate for more arid rangelands. While a recent short-term study on semiarid grasslands in Arizona found no difference in plant community responses to alternative livestock grazing systems (Loeser 2001), numerous studies support the importance of stocking rates and utilization levels over a grazing system (Paulsen and Ares 1962, Valentine 1970, Cook and Child 1971, Van Poolen and Lacey 1979, Pieper and Heitschmidt 1988, Hart et al. 1989, Hughes 1990, York et al. 1994, Holechek et al. 1994). However grazing systems that implement rest are also important (Lyons and Wright 2003) and could improve carrying capacity for wildlife populations (Loomis et al. 1991). Further, a PDSI below -2 could be used as a cut-off value, in conjunction with field assessments, to determine when further actions such as herd reductions or total livestock removal should be taken to reduce interspecific competition. During the first year of our study (2002), PDSI for our climate division ranged from severe (–3) to extreme (–4) between the 2002 spring fawning period and the following winter (January 2003). Between spring of 2003 and 2004, the PDSI indicated moderate drought (–2) or better. We measured increasing amounts of cover between 2003 and 2004. During the springs of 2003 and 2004 we also documented increasing fawn recruitment in the south in conjunction with improved range conditions. Brown et al. (2006) found that July indices more severe than –2.5 resulted in a decline in number of does observed that same month on nearby Anderson Mesa in Arizona. These findings suggest a PDSI of –2 to –3, a range consistent with PDSI reporting and mapping, may be appropriate to use as a threshold for drought management actions.

Finally, wildlife managers should avoid management actions, such as transplants, that increase intraspecific competition within pronghorn ranges that are depleted of cover and/or forage during the aforementioned drought conditions. Wildlife managers should work in coordination with land management agencies to identify pronghorn habitat areas that currently exhibit deteriorated cover and forage conditions and collaborate on habitat management and improvement projects. Project objectives should include improving productivity, species diversity, cover and forage compositions preferred by pronghorn.

Acknowledgments

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Section IV Abstracts

Broad-Scale Landscape Changes Relative to Pronghorn Abundance in West Texas.

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Abstract: Pronghorn (*Antilocapra americana*) populations in Trans-Pecos, Texas have experienced a 70% decline between 1987 and 2001. Although causative factors associated with the declines are unknown, we hypothesize that broad-scale habitat changes (i.e., brush encroachment) may be occurring on historic pronghorn ranges resulting in habitat deterioration and subsequent population declines. Thus, we examined the relationships between pronghorn population demographics (fawn production, buck:doe, density) and habitat changes for the Trans-Pecos district (TP) of Texas from 1977-2004. We obtained imagery (LANDSAT and DOQQs) for the 6 counties in the TP with pronghorn populations during 3 time frames (late 70s, mid-80s, and late 90s) and evaluated habitat change. Using ERDAS Imagine®, habitats were classified as grasslands, shrublands, grass-shrub interface, bare ground, and other. Using change detection functions we evaluated how changes in pronghorn habitats were related to pronghorn demography. Fawn production (range = 305-4,407) and population size (range = 5,061-17,266) showed high variability, whereas buck:doe (range = 1:0.48-1:0.69) remained stable.

Key Words: pronghorn, *Antilocapra americana,* demographic, Trans-Pecos, Texas, population decline, brush encroachment.

Population Productivity and Pronghorn Nutrition During Lactation

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Abstract: Predators, specifically coyotes (*Canis latrans*), are often thought to limit pronghorn (*Antilocapra americana*) populations, yet few studies have investigated the potential role of nutritional constraints. We used fecal nitrogen (FN) and 2,6 diaminopimelic acid (DAPA) to quantify lactation season nutrition for 5 populations in Idaho. We assessed the relationship between these nutritional indices and population productivity with linear regression models evaluated with AICc. Weighted mean FN was the best model explaining 47% of the variation in fawn:doe ratios although the null model was competitive (ΔAICc <3). These results support the hypothesis of summer forage limitation as fawn recruitment appears to be nutritionally limited for some pronghorn populations in Idaho.

Key Words: *Antilocapra americana, Canis latrans*, coyote, lactation, nutrition, Idaho, pronghorn

Comparison of Diet Characteristics of Two Pronghorn Herds in North Central Arizona

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Abstract: We compared the diet characteristics of to 2 pronghorn herds (Anderson Mesa and Garland Prairie) from north central Arizona to see if they might explain differences in fawn recruitment between the 2 herds. Dietary characteristics examined included species composition, forage species diversity, and dominant species during 4 biological periods (late gestation, parturition, lactation, and conception) from April 2002 to August 2004. During each collection period, a minimum of 16 separate pellet groups were collected and combined to form 4 replicates per sampling period by year by herd location. We determined pronghorn diet composition and plant species diversity using microhistological analysis. The statistical design of our study was a completely random 4-factor factorial with years, herd location, biological season, and forage class/species as factors. The Garland Prairie herd had significantly higher forage species diversity across all years and seasons. In 2002 and 2004, the Garland Prairie herd had higher amounts of forbs and lower amounts of shrubs than the Anderson Mesa herd. There was little difference in the diet composition in 2003. Across the 3 years Garland Prairie pronghorn consumed an average of 8.5 % grass, 74.5 % forbs and 17 % shrubs, while Anderson Mesa pronghorn consumed 12.2 % grass, 53.4 % forbs, and 30 % shrubs. The greater species diversity and higher amounts of forb and lower amounts of grass and shrub in the Garland Prairie diets may explain the higher fawn recruitment in this herd than the Anderson Mesa herd.

Key Words: pronghorn, *Antilocapra americana,* diet, fawn recruitment, Anderson Mesa, Garland Prairie, Arizona.

Petroleum Development and Pronghorn: Where Are the Break Points?

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Abstract: The extraction of resources for energy development is a complex issue, especially in the western USA. Nowhere are the issues more visible than in the Upper Green River Basin of western Wyoming. To date there have been limited efforts to understand the nature of pronghorn (*Antilocapra americana*) use of wintering ranges and impacts of natural gas development on shifts in winter habitat use. One goal of this project is to understand how fragmentation effects winter habitat use by pronghorn. Specifically, we are examining whether a threshold level of fragmentation that leads to site abandonment by pronghorn exists, and if so the resulting effects on animal health and demography. To understand animal distribution in relation to development, we conducted bi-monthly aerial surveys during winter in which location and group size were noted. Second, we net-gunned 50 adult females and outfitted them with GPS radio-collars. We classified animals as either *control* (n = 25) or *experimental* (n = 25) based upon *a priori* assessments of proximity to areas with energy development. To help understand whether pronghorn movements and distribution are unaffected by the gas field imprint, or if the continued fracturing of suitable habitat reduces pronghorn use, we used satellite imagery from 2002-2005 to create a series of grids that overlapped the Jonah and Mesa Fields and adjoining areas. Different grid sizes (e.g. 500 x 500m, 250m x 250m) for the entire region were used in each of 3 independent analyses. From each grid, we estimated the proportion of area cleared of vegetation (roads included) relative to cell size, and remaining available habitat was then converted into separate individual polygons. The size of each patch was then estimated and assigned an identification value based on its area. Logistics regression suggests that both snow depth and fragment size explain 83% of the variance in detecting pronghorn. We will discuss fragmentation threshold levels for use by pronghorn within or adjacent to gas fields. Pronghorn use of developed gas fields in the Upper Green may not have an optimistic future, although our results are preliminary and we cannot yet fully disentangle effects of habitat fragmentation *per se* from the attendant over-arching footprint of human activity.

Key Words: pronghorn, *Antilocapra americana,* energy development, winter habitat, fragmentation, Wyoming.

Effects of A Species-Level Trophic Cascade on Pronghorn Fawn Survival in Grand Teton National Park

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Abstract: Coyote (*Canis latrans)* predation is frequently cited as an important factor in the mortality of neonatal pronghorn (*Antilocapra americana)*. It has been suggested that the extirpation of gray wolves (*Canis lupus)* contributed to an overall increase in coyote densities and a concomitant rise in predation rates on pronghorn fawns, a process known as trophic cascades. To test this hypothesis I monitored the fates of 108 fawns captured between June 2002-2004 at 3 field sites that were selected to exploit spatial and temporal variation in the distribution and abundance of wolves (i.e., high- density wolf, low-density wolf, wolf-free). All fawns were equipped with expandable, breakaway VHF radio-collars with 4-hour mortality sensors. Fawns were monitored daily for the first 60 days of life and then weekly thereafter until the fall migration. Carcasses were recovered and necropsied to determine causes of mortality. Cause of death was classified as predation, disease, accident/injury, starvation/abandonment, or other. I estimated survival of pronghorn fawns using the known fate model in Program MARK. In addition, I evaluated the relationships between coyote density and fawn survival, wolf density and fawn survival, and coyote density and wolf density using simple linear regression. On the basis of minimum AIC_c, the best model of fawn survival contained parameters for gender, birthweight, and coyote density. Model-averaged survival estimates ranged from a low of $\hat{S} = 0.037$ at the wolf-free site in 2002, to a high of $\hat{S} = 0.432$ at the high-density wolf site in 2004. Based on the top-ranked model, fawn survival was negatively correlated with coyote density and positively correlated with birthweight. Survival of male fawns was slightly lower than for females. The results of the regression analyses indicate that fawn survival is negatively correlated with coyote density ($P = 0.004$) and positively correlated with wolf density ($P = 0.016$), and the relationship between coyote and wolf densities is negative ($P = 0.043$). These results support the hypothesis that indirect effects resulting from the extirpation of wolves may contribute to increased rates of pronghorn fawn predation, and suggest that the reintroduction of wolves may have positive implications for both fawn survival and pronghorn population persistence.

Key Words: pronghorn, *Antilocapra americana,* coyote, *Canis latrans,* wolf, *Canis lupus*, predation

Use of Infrared Thermography to Detect Signs of Diseases in Pronghorn Antelope

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***Abstract**:* Foot and mouth disease (FMD) is an extremely contagious, acute disease of all cloven-footed animals. It is caused by a virus and characterized by fever and vesicular eruption in the mouth and on the feet. We evaluated the use of infrared thermography to detect signs of FMD in experimentally infected pronghorn antelope (*Antilocapra americana*). This is the first experiment to evaluate the susceptibility of pronghorn to FMD virus and to use infrared thermography to detect signs of the disease. Infrared radiation, which is detected by thermal cameras, is emitted by all objects proportional to their temperature. Infrared thermography measures heat emitted from a target surface and displays the information as a pictorial representation. Medical imaging makes use of the fact that heat is one of the cardinal signs of inflammation, so an increase in body surface temperature may indicate inflammation of tissues close to that point. Pronghorn were experimentally inoculated intradermally in the tongue with 10,000 lesion forming units of FMD virus (O1 Manisa strain). Fever, lameness, and early vesicular lesions on the feet were observed 42 hours post-inoculation (p.i.). However, infrared images of the feet detected signs of the disease 22 hours p.i., up to 20 hours before clinical signs were observed. Vesicular lesions that progressed to ulcers were observed on the tongue and at the coronary bands and interdigital clefts of inoculated and exposed pronghorn. Based on this experiment, pronghorn antelope are apparently susceptible to the O1 Manisa strain of FMD virus. At least under experimental conditions, signs of foot and mouth disease can be detected by infrared thermography not only during the time of visual lesions, but up to a day before clinical lesions can be observed by direct observation. Thus, use of this technology may have applications when large numbers of animals need to be screened or when it may be difficult to capture free-ranging pronghorn to evaluate infection with FMD. Use of infrared thermography to detect signs of FMD in pronghorn or any other animal should only be used as a screening tool and not a diagnostic technique. Similar lesions on the mouth and feet of pronghorn as a result of infection of a disease other than FMD could interfere with the diagnostic value of infrared thermography. Because other diseases of pronghorn, including bluetongue and vesicular stomatitis, theoretically could be detected by infrared thermography, they may interfere with evaluation of pronghorn for infection of FMD, therefore further research is needed.

***Key Words**:* pronghorn, *Antilocapra americana,* foot and mouth disease, infrared thermography

Dispersal of Yearling Pronghorns in Western South Dakota

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***Abstract**:* Fifty-seven radio collared pronghorn (*Antilocapra americana*) fawns were captured in western South Dakota during May 2002-2003, of which, 34 were radio-tracked through 15 months of age, by which time all individuals had established a permanent home range. We classified 56% (n = 19) of fawns as dispersers and 44% (n = 15) as residents. Eighty-4 percent (n = 16) of dispersers departed natal home ranges in late October and occupied winter home ranges for 102 to 209 days before dispersing to permanent home ranges during April 2003 and 2004. Dispersal distances from natal ranges to permanent home ranges varied from 6.2 to 267.0 km. Winter home range sizes for all individual pronghorns varied from 39.4 to 509.6 km^2. Permanent home range size for all individuals varied from 15.5 to 166.1 km^2. Mean 95% permanent home range size differed (P = 0.06) between residents (mean = 97.3 ± 15.1 km^2) and dispersers (mean = 48.6 ± 16.0 km^2) but were similar (P = 0.97) among sexes. Mean dispersal distance from natal to permanent home ranges was similar (P = 0.35) for males (mean = 54.2 ± 21.0 km) and females (mean = 26.3 ± 19.9 km). We suggest that dispersal was stimulated, in part, by habitat quality (i.e., patchiness) and pronghorn density. We hypothesize that as habitat patch size decreases, home range sizes and distance traveled during pre-dispersal and dispersal movements by pronghorns increase.

***Key Words**:* pronghorn, *Antilocapra americana,* radio-tracking, dispersal, home range, South Dakota

Long Distance Migration and the Challenges of Protection

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Abstract: The world's long distance migrations are as spectacular as they are threatened. For land mammals, only a few persist and these are jeopardized by agriculture, inadequately-sized reserves, energy development, and a lack of political will to enable robust protection. Among the oldest known, site-specific routes is the 6,000 year old, 600 kilometer long migration of pronghorn from the Upper Green River Basin to Grand Teton National Park in Wyoming. GPS data reveal 3 geographical bottlenecks narrowing to as little as 120 meters through which all members of a population apparently pass. Efforts to conserve this restricted migration route, the longest for a terrestrial mammal between the Arctic and Tierra Del Fuego, concentrate on a 150 km long (one-way) segment averaging less than 1.2 km wide and comprised primarily of public lands. These have yet to be successful although community meetings with diverse stakeholders reflect broad support. Obstacles to protect this narrow ribbon as a corridor fall within the human milieu and include squabbles about why migration needs to be sustained, how best to achieve it, whether legislation is necessary, and if top-down or bottom-up forces are more likely to be successful.

Key Words: pronghorn, *Antilocapra americana,* migration

Two Heads Are Better Than One: A Paired Observer Evaluation of Pronghorn Line Transect Surveys

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Abstract: Distance sampling is used to estimate density for several taxa including pronghorn (*Antilocapra americana*). Line transect surveys produce unbiased estimates of density if key assumptions are met, including all clusters on the line are detected. We conducted aerial line transects for pronghorn in Wyoming and Idaho using independent, paired observers to evaluate the ability of observers to satisfy this assumption. Enumerating groups as both 'detected' and 'missed' enabled evaluation of the data as a sight-resight survey and construction of a logistic regression sightability model. Independent paired observers identified failures to detect all groups within the nearest band; violations were particularly prominent from the rear seat of the aircraft (12 out of 58 groups missed in nearest distance band) contributing to a negative bias in density estimates. Sight-resight and sightability model estimates presented here correct for this bias while improving precision of estimates associated with pronghorn line transect estimates.

Key Words*: Antilocapra americana,* bias, Idaho, line transect, logistic regression, pronghorn, sightability model, Wyoming

A Non-invasive Technique to Weigh Wild Pronghorn: Prospects and Problems

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***Abstract**:* Female body mass is highly correlated with reproductive potential yet few data exist on how human-altered environments affect relationships between female mass and fecundity. Most studies obtain this information in wild ungulate populations through invasive techniques including darting, repeated captures of animals, or culling of study animals. These techniques, while effective, are costly, increase animal stress levels, and are criticized by animal rights advocates. In Wyoming, habitat alteration has been rapid due to an impressive growth in the petroleum industry. Yet other than behavioral measures of avoidance by wildlife, little data exist on changes within animals themselves. Our research on pronghorn and energy development in the Upper Green River Basin strives to measure body mass of wild pronghorn through an incorporated technology of 3 linked components: 1) a Digi-Star scale to record weight with a goal of documenting seasonal change under differing environmental scenarios; 2) an Allflex panel antennae recorder designed to store the radio frequency identification (RFID) number of marked females; and 3) a camera trap to record the radio collar number of the study animal. This system has the advantage of repeatable non-invasive measures of body mass of known individuals under free-roaming conditions considered as both experimental (e.g., industrial development) and control (native sagebrush communities in the absence of development) treatments. This novel approach offers serious advantages for more in-depth monitoring of animal condition but numerous problems must also be resolved for efficient operation. Freeze and thaw regimes during winter, battery function, and animal behavior represent differing levels of challenge. In this first year of a 5 year study, much effort was devoted to selecting and gaining permits for scale placement, testing the data-logging capabilities, and making the scales operable.

***Key Words**:* pronghorn, *Antilocapra americana,* body mass, fecundity, Wyoming

Activity Budgets of Sonoran Pronghorn in a Semi-captive Enclosure

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***Abstract**:* The Sonoran pronghorn (*Antilocapra americana sonoriensis*) is one of the most endangered animals in North America and has been listed as endangered since 1967. Until recently, little was known of basic Sonoran pronghorn life history. While knowledge of a species' behavior is essential to understanding its ecology, these data are difficult to obtain for Sonoran pronghorn because of their endangered status, land-use restrictions, and the large, inaccessible range they occupy. However, with the establishment of a semi-captive breeding facility (260 ha) for Sonoran pronghorn in southern Arizona, it is possible to study their seasonal diurnal activity budgets in a natural environment. We studied the diurnal activity budgets of Sonoran pronghorn from January through November 2005 by instantaneous sampling 6 adults females and recording their behavior (i.e., foraging, bedding, standing, traveling, other) at 2-minute intervals. Annually, pronghorn spent the majority of their time foraging, followed by standing, bedding, and traveling. Pronghorn exhibited seasonal changes in their allocation of time to each behavior diurnally. Climate likely constrained the allocation of time for pronghorn during the spring and summer. However, the constraining factor during the fall was likely forage quantity and quality, as time spent foraging and ruminating increased dramatically during the fall from all other seasons. Information on activity budgets of Sonoran pronghorn will help inform biologists how Sonoran pronghorn are able to cope with the environmental extremes that they face at the edge of the species' range and may be an important tool for the assessment of future reintroduction efforts.

***Key Words**:* activity budget, *Antilocapra americana sonoriensis*, Arizona, behavior, captive breeding, endangered species, Sonoran pronghorn

The Application of the “Supporting Breeding” Concept in the Peninsular Pronghorn Recovery Effort, and Its Validation with Vortex.

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Abstract: The "supportive breeding” concept, defined as “supporting weak wild populations through the release of conspecifics reproduced in captivity”, is being applied in the Peninsular Pronghorn Recovery Plan and was validated by modeling with the computer simulation package VORTEX. Supportive breeding has being applied for several species, from fisheries, forestry, and mammals. VORTEX is designed to simulate small population dynamics and probabilities of persistence under alternative management regimes and fluctuating environmental conditions. Captive management for the peninsular pronghorn started in 1998, with the captive births documented in 2000. Now there are more than 200 animals in captivity. The observed growth rate of this population and that which was obtained from the model agree very well. Three baseline scenarios were developed: the wild population, the captive population, and a “new” population derived from the surplus produced in captivity. Each simulation was repeated 500 over a 50-year timeframe. One of the important results of modeling with VORTEX concerns the impact to the wild population of a “harvest” (capture) of wild fawns to be used as founders for the captive population: the wild population had zero probability of extinction despite these captures (n=16 fawns in 3 years). The model results also demonstrated the importance of initial population size. If this parameter was less than 100 animals, the growth rate became negative (r=-0.037). Survival of fawns was one of the most important demographic factors. A change from 70% to 80% in the fawn mortality results in a negative growth rate (r=-0.103) and a high probability of extinction (P(E)=0.84). Simulation with a “new wild population” generated by the release of a group from the captive population shows positive results because the new population is likely to grow upon establishment. This study suggests that supplementing wild populations will be beneficial. The study also indicates that the risk of extinction can be reduced with "supportive breeding". Captive breeding that avoids adaptation to captive conditions, combined with periodic releases, can be a important factors in minimizing the risk of extinction of the peninsular pronghorn.

Key words: Captive management, modeling, peninsular pronghorn, risk of extinction, supportive breeding.

Movement and Distribution Patterns of Pronghorn in Relation to Roads and Fences in Wyoming

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***Abstract**:* Pronghorn (*Antilocapra americana*) evolved in response to stochastic conditions on the open, western high plains. Survival of the species is dependent on their ability to move in response to fluctuations in food supplies and weather conditions. Using global positioning system (GPS) collars and geographic information systems (GIS), movement and distribution of adult female pronghorn (*n*=72) were studied within a population in southwestern Wyoming. Fences in southwestern Wyoming influenced distribution and movement patterns of pronghorn. Fence density was found to be lower in seasonal home ranges than in the study area. Fence density influenced location of seasonal range with pronghorn choosing those areas within the study area with lowest densities. Fence density was greater within the periphery of home ranges than the remainder of the home range, suggesting home range conformation could be influenced by fences within the outer portion of home ranges. Most (64%, *n*=28) monitored pronghorn were migratory and their migration routes tended to encounter fewer fences than had they traveled randomly in the study area. The presence of fences and, in turn, the type of highway right-of-way fence determined whether roads were included in seasonal ranges and where pronghorn crossed roads within season and during migrations. Seasonal crossings of primary roads within the study area consistently occurred along unfenced sections. These results support limiting fences on pronghorn range and maintaining unfenced sections of highways as movement corridors to reduce the potential for habitat fragmentation through loss of connectivity and allow access to crucial winter range within the study area.

***Key Words**:* pronghorn, *Antilocapra americana*, migration, corridors, connectivity, fences, highways, habitat fragmentation, Wyoming.

Temporal and Spatial Variation in Pronghorn Distribution and Population Dynamics in Alberta

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***Abstract**:* The Grasslands Natural Region of Alberta is considered the most threatened ecosystem in the province. It provides habitat for numerous species of native plants and animals, including 75% of Alberta's 'species at risk'. Among the diversity of prairie wildlife, the pronghorn is the most representative remaining large mammal. The pronghorn is a highly valued resource in Alberta, experiencing high demand as big game species. However, it is sensitive to anthropogenic habitat changes and populations may decrease abruptly during severe winters. The purpose of this study was to examine the key environmental drivers of pronghorn population dynamics in Alberta. Using multi-variate regression, we examined the influences of variation forage productivity, climate, coyote predation, and pronghorn density on pronghorn population dynamics. We also evaluated density distribution in relation to landscape composition. Forage production, driven by moisture availability, presumably linked to doe condition, was a key driver of fawn production, while winter severity had a significant negative effect on population rate of increase. The landscape proportion of native prairie varied widely among Antelope Management Areas and had a profound influence on density distribution ($R^2 = 0.57$, $P < 0.001$). Furthermore, landscape composition influenced density-dependence of doe population rate of increase and fawn production. We developed a generic system dynamics population model representing the key environmental and management factors that influence pronghorn population dynamics in Alberta. The model was based on documented empirical relationships, supplemented with inferences and assumptions from published literature. Key uncertainties were identified and recommendations are offered for enhancing pronghorn management in Alberta.

***Key Words**:* pronghorn, *Antilocapra americana,* Grasslands Natural Region, Alberta, forage productivity, climate, coyote

Section V Panel Discussion

Future Challenges in Pronghorn Management

Dale E. Toweill, Idaho Department of Fish and Game, Boise, ID USA 83707.

Abstract: A panel including David Brown, Fred Lindzey, Richard Ockenfels, and Jim Yoakum was asked to address questions regarding the biggest challenges to pronghorn conservation over the coming 20 years, and the advances in research and management needed to prepare for future challenges. Facilitated by Brad Compton, the panel addressed these and other questions from the audience. Responses focused on pronghorn living space and associated issues including habitat fragmentation, degradation and restoration, and the issue of increasing human understanding of, and support for, pronghorn restoration.

Proceedings Pronghorn Workshop 22: 00-00

Key Words*:* Pronghorn, *Antilocapra americana*, habitat, exotics.

Over the past 2 days we have discussed many topics, from the evolution and habitat requirements of pronghorns to development of new cutting-edge techniques to secure better information more quickly and efficiently than ever before. Now is time to look ahead—to ask those who have spent a major portion of their careers focused on pronghorns to advise the rest of us what they see as the critical issues likely to face us in the coming 2 decades. So, panel, what will be the greatest challenges to pronghorn conservation over the next 20 years?

Ockenfels: The biggest question is still trying to determine how many animals we've got. We have been working on that issue since 1954, and despite advances in transect surveys and other counting methodologies, we still have a long ways to go. Until we can answer that question accurately, we cannot expect to get a good handle on habitat requirements.

Brown: The biggest question is space. Pronghorn populations live at low density and require huge areas of habitat, and habitats are being continually reduced in size by the activities of people building (and fencing) roads, exploring and developing gas and oil reserves, building homes and communities. We need to focus on protecting the habitat that remains—and we must strive to make that habitat better meet the needs of pronghorns by improving habitat quality. We also need to get a better handle on issues that affect pronghorn populations: competition for space and forage, predation, and human disturbance.

Lindzey: My colleagues have already touched on the most critical topics, so I'll reiterate: one of the most severe challenges will be the fragmentation of pronghorn ranges. We need to pay more attention to seasonal ranges and pronghorn movement patterns such as migration, and constantly work to minimize fences and roads that fragment those seasonal habitats. We need to develop, fund, and implement plans to maintain and improve migration corridors.

Yoakum: The major problem facing pronghorns is simply space in which to live. Decreasing habitat is a major factor affecting pronghorn populations throughout the West. The second most important problem is a corollary to this one: the habitat that does remain is deteriorating in quality. And, that deterioration is compounded by increasing human populations occupying and fragmenting pronghorn habitat.

Ockenfels: My colleagues are absolutely correct in their focus on pronghorn habitat. Although I identified many issues in the notes I prepared for this panel—issues that included improvements in habitat measurement to determine status and trend, fragmentation due to roads and highways, methods for pronghorn reintroduction to previously-occupied habitats, competition for food and space with other ungulates and impacts on nutrition, the role of exotic plants and animals in the landscape—the key is move beyond habitat fragmentation to habitat restoration. How can we restore what remains of pronghorn habitat? Particularly in grasslands and juniper-pine forests: how do we restore productivity to the landscape?

Is there opportunity to provide a better focus to research? What advances will be necessary to address these challenges?

Ockenfels: Clearly, we need to improve our ability to measure habitat so that we can better assess status, trend, and future condition of the landscape and the plants on which pronghorns depend. We must devise better ways to reconnect pronghorn habitat to counteract the effects of habitat fragmentation, and then we must work to restore pronghorn populations. We need a better understanding of the link between nutrition and productivity. Migration corridors must be first identified, and then protected from development of roads and ranchettes. We need better ways of estimating mortality rates and population size. And we need to work on new technology development, such as using video and infrared sensing to reduce the need for human presence and cost when conducting population surveys.

Brown: We need a better understanding of pronghorn ecology, and especially competition with livestock. We have avoided addressing some of these issues for political reasons and because we have had the luxury of viable pronghorn populations, but with increasing fragmentation and degradation of habitats, we can no longer avoid such questions.

Lindzey: If habitat fragmentation continues, we need to know how to better move pronghorns and how to use structural devices such as overpasses or underpasses to re-link pronghorn habitats.

Yoakum: The focus needs to be on protecting and restoring pronghorn habitats for 200 years, not just 20. The long-range focus must be on habitat quality. We need better information on how to improve habitat. The insidious loss of habitat quality is poorly documented, and without documentation, it is difficult to identify causes and provide management strategies for habitat restoration. The Pronghorn Workshop should provide field trips that focus on the condition of pronghorn habitat in different ecosystems, and develop methodologies for rating (and improving) habitat quality.

Brown: And we need to address the concept of habitat conversion. I agree with Jim [Yoakum] whole-heartedly—we need a new focus on *improving* pronghorn habitat.

What are your thoughts on noxious weeds and other exotic species?

Brown: New exotic plant invasions on pronghorn range are a problem, and it seems like we face a new invasion almost every year. We haven't solved this problem, but the bright spot is that we haven't lost any native species yet. We will probably need to learn to live with—and manage around—new species, and they're not all plants! Livestock, horses, burros, even elk in some areas can all compete with pronghorns for habitat and food, and we need to learn ways to manage with them as components of the pronghorn habitat.

Yoakum: We now even have exotic antelope (oryx) on pronghorn range, although their feeding habits are quite different and potential for competition is minimal. As for exotic plants, there are many in the West such as the ubiquitous cheatgrass. The problem with cheatgrass is really a 'barb' problem—the plant itself is nutritious and is used by pronghorn in the spring. Other exotic plants are forbs, including alfalfa, which of course is highly nutritious, highly succulent, and highly preferred by pronghorns. I am not against all exotics, rather, I am pro-pronghorn. I know of no exotic plants poisonous to pronghorn—as opposed to domestic livestock. *Halogeton* is preferred by pronghorns, although it is anathema to domestic livestock.

Ockenfels: When we talk about exotics species in the West, we cannot overlook the top 3. In increasing order of abundance, they are: corn, wheat, and humans. In the big picture, cheatgrass is not a problem; conversion of pronghorn habitat to wheat is a problem. Conversion of pronghorn habitat to agriculture is a huge problem.

Do humans care enough to protect habitat to keep pronghorn populations viable?

Brown: Not enough people care. People care only when they are informed and educated, and most ranchers and others in the West are now more tolerant of pronghorns and the animals are more appreciated than a few decades ago. There are currently discussions about trying to reintroduce pronghorns into Washington state. We need to try to put pronghorns wherever suitable habitat remains.

How can we make people need pronghorns?

Brown: People do not *need* pronghorns, they have to *want* them, whether for good venison or simply because they find the animals interesting.

Ockenfels: Mammal watching is hard to do, and had to promote. Pronghorns, however, provide excellent opportunities for wildlife viewing, and we have emphasized that kind of opportunity in our Arizona viewing guide. We need to involve educators, to show them that we have the tools, that we know and can teach the concepts, so that we can really *show* people what pronghorns are and how they live … by dots on a map, a video clip … to make understanding about the values of pronghorns come easier.

Given the highly specialized physiology of pronghorns, is there opportunity to promote the species for medical research?

Ockenfels: Perhaps. I have never thought of that.

The song "Home on the Range" is known by nearly every elementary student; can we promote that to make students more aware of pronghorns?

Brown: I don't know about that, but there have been 4 or 5 recently-published books about pronghorns—evidence of increasing awareness and education.

Yoakum: I have been called to consult with Yellowstone National Park, to help managers figure out how to increase pronghorn herds. People can easily see pronghorns because they are diurnal, active when most visitors come to the park. I'm also aware of a ranch in southern California wanting to restore pronghorns for wildlife viewing in an area where pronghorns have been gone for over 100 years. The barrier is habitat change over the past century due to agricultural practices and over-grazing. We need to restore the habitat—restore it, and pronghorns can return.

Given that habitat fragmentation is the big problem, how do we move from documenting loss to restoring habitat?

Lindzey: Fences must come down. Many fences in Wyoming, originally built to control domestic livestock, are no longer needed and should be removed. There are many opportunities to remove fences from both public and private lands, and this kind of action would be extremely beneficial to pronghorns.

Brown: We have been terribly wasteful of pronghorn habitat: think of Denver Airport. Look at all the fenced railway lines across the land. We must do more to make the public aware that we can reclaim pronghorn habitat simply by removing fences, and then transplant pronghorns if necessary to restore pronghorn populations.

Ockenfels: In Arizona we have gone from having no contact with the Arizona Department of Transportation to almost daily contact, helping plan transportation corridors twenty years in the future. We are now planning improvements for wildlife along human transportation corridors that haven't yet been built, and we are trying to design future projects to benefit multiple species of wildlife as well as humans. We won't stop building highways, but we can—and must—design them better.

How can we get away from the "wildlife-friendly" designation for 4-strand barbed wire fences in favor of 3-strand or 2-strand fences—or better yet, no fences at all?

Brown: We all need to develop projects to remove fences and educate landowners. We need an active pronghorn friendly organization to raise funds and spear-head habitat projects for pronghorns, much like the Rocky Mountain Elk Foundation has done for elk.

Ockenfels: I can't even win that battle internally, within my wildlife management agency. It seems someone always changes the plans back to meet minimum standards. We do need to change our message to make it clear that having *no* fence is preferable to a wildlife-friendly fence.

Yoakum: The term "wildlife friendly" was developed to differentiate among fences—a matter of degree. Within the last decade hundreds or thousands of miles of public land fences have been constructed, and many *not* wildlife friendly. Fences are now being removed by conservation organizations, which is a tremendous improvement although it does make control of domestic livestock more difficult on both public and private lands.

Brown: The Pronghorn Guide shows several different fence designs, allowing agencies to choose. There are tremendous discrepancies among private landowners.

Ockenfels: The process of reading the landscape and fitting the fence to the need is critical. One need not design the entire fence to a single standard, but should modify the design to fit the landscape.

Brown: One of the things we need is a better means of communicating with ranchers and landowners. Wildlife interests must speak up to help people identify the purpose and need of the fence, and to consider the impacts on wildlife as well livestock.

Section VI Contributed Posters

Pronghorn as a Focal Species for Conservation Planning in the Northern Great Plains

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***Abstract**:* Economic imperatives continue to alter the landscape of the Northern Great Plains. Historically, landscape change was associated with the conversion of native grassland to crop production. Although new tillage continues at a lower rate today, other economic pressures are incrementally reducing the capacity of native landscapes to support biodiversity by continuing to alter the composition, configuration and ecological functions of prairie ecosystems. Lack of large-scale areas where biodiversity is the primary management objective may explain why 74% of 39 species classified as grassland obligates with distributions centered in the Northern Great Plains are listed as imperiled by federal, state, and provincial governments. Since it is impractical to monitor or impossible to measure all species' responses to landscape change, it is useful to select a subset of focal species that can represent the spatial compositional and functional requirements of others. The pronghorn is a relatively ubiquitous obligate grassland species that may seem a poor indicator for the ecosystem, because it is common. However, preliminary research in Alberta indicates that pronghorn distribution and demography are sensitive to landscape composition and change. Across 22 years of survey data, Ln [density] was directly related to the proportion of native prairie remaining in Antelope Management Areas ($R^2 = 0.57$, $P < 0.001$). GPS telemetry revealed long distance migration (>100 km) did not occur among pronghorn captured during winter in cultivated landscapes, but was common in pronghorn captured in mixed and native prairie winter ranges. The maximum displacement distance of an individual pronghorn from winter to fawning range was 445 km, the longest recorded unidirectional seasonal movement recorded for a land mammal south of the tundra. Marked pronghorn moved across state/provincial and international boundaries. Landscape configuration

and anthropogenic features appeared to influence migration occurrence and pathway selection. Demography was sensitive to climate, including growing season precipitation and winter severity. Furthermore, the pronghorn is a charismatic species that is highly valued as a game animal and its status is routinely monitored by wildlife agencies. We suggest that although common, the biological and socioeconomic attributes of pronghorn noted here make it a priority species to include with others as an indicator for cooperative landscape-scale conservation planning in the transboundary region of Montana, Alberta and Saskatchewan. We refer to this area as the Northern Sage Steppe.

22nd Biennial Pronghorn Workshop
May 16-19, 2006
Idaho Falls, Idaho

Section VI Business Meeting Agenda and Minutes

May 18, 2006

- Role Call/Identification of Voting Members
- Revised *"Field Guide to Pronghorn Management"* Update – David Brown
- *Hall of Fame* Update – David Brown
- Workshop Proceedings – Dale Toweill
- Next Meeting Location – Brad Compton
- Workshop Funds – Brad Compton
- State Status Report Database – Bruce Ackerman
- Other Items - All

CALL TO ORDER

Brad Compton called the meeting to order at 12:15 PM. The meeting was held during a hosted lunch and most of the workshop registrants attended.

ROLL CALL/IDENTIFICATION OF VOTING MEMBERS

Agencies: Alberta – Kim Morton; Arizona – Richard Ockenfels; Baja CS – Jorge Cancino; Idaho – Brad Compton; Kansas – Matt Peek; Nebraska – Richard Nelson; North Dakota – Bill Jensen; Oregon – Don Whittaker; Saskatchewan – Al Arsenault; South Dakota – Andy Lindbloom; Texas – Duane Lucia; Utah – Adam Bronson; Wyoming – Bill Rudd; Bureau of Land Management – John Augsburger; United States Geological Survey – Robert Claver; United States Fish & Wildlife Service – Mike Foster; Natural Resources Conservation Service – Cindy Zachmeier;

Universities: Arizona State University – Dave Brown; University of Idaho – John Byers; University of Calgary – Shannon Gavin; Sul Ross University – Louis Harveson; South Dakota State University – Chris Jacques; University of Wyoming – Fred Lindzey.

FIELD GUIDE TO PRONHORN MANAGEMENT UPDATE

David Brown reported the *"Pronghorn Management Guide 2006"* is completed and is being distributed at this workshop. Dave expressed appreciation for all the people who assisted with the revision.

HALL OF FAME UPDATE

David Brown reported on progress being made to develop criteria for inclusion into the Pronghorn Hall of Fame. David submitted a draft (Appendix) of the philosophy behind, and criteria for, inclusion into the Pronghorn Hall of Fame. Brad Compton suggested a minor amendment. Don Whittaker made a motion to accept the criteria with amendment. Richard Ockenfels seconded the motion. The motion carried unanimously. **Action: David Brown will lead a committee effort to begin soliciting nominations and identifying individuals for inclusion into the Pronghorn Hall of Fame.**

WORKSHOP PROCEEDINGS

Dale Toweill outlined the process and timelines for publishing the proceedings for the 22nd Pronghorn Workshop. Several papers were still outstanding and Dale set a deadline of July 18 for authors to submit their papers. Several authors indicated they would only be publishing abstracts. Dale also solicited volunteers to review papers. Volunteering to review were Don Whittaker, Brad Compton, Carl Mitchell, Bill Miller, Bruce Ackerman, Craig McLaughlin, Tom Pojar, Tom Keegan, and Jorge Cancino.

NEXT MEETING LOCATION

Brad Compton solicited nominations to host the next workshop. Paul Jones offered Alberta. New Mexico had expressed interest via e-mail, but nobody was present at the workshop to formally make an offer. **Action: Alberta will host the 23rd Pronghorn Workshop. Dates and place will be announced at a future time.**

WORKSHOP FUNDS

Brad Compton discussed his experience with establishing a checking account and soliciting seed funding for the workshop. This workshop did not accept credit or debit cards because of banking limitations and state law. Brad also mentioned he had been in contact with Larry Kruckenburg, WAFWA Secretary, who offered to establish a WAFWA account for future pronghorn workshop funds. WAFWA would establish a dedicated Pronghorn Workshop account and allow hosting agencies to borrow against the account for seed money. Another advantage is a WAFWA sponsored account would allow hosting agencies to accept credit and debit cards for registration. Brad made a motion to transfer all left-over funds from the 22nd Pronghorn Workshop to WAFWA to establish a Pronghorn Workshop account. Bill Miller seconded. The motion passed unanimously. **Action: Brad Compton will transfer all remaining 22nd Pronghorn Workshop funds to Steve Barton, WAFWA treasurer, to establish a WAFWA sponsored Pronghorn Workshop account.**

STATE STATUS REPORT DATABASE

Bruce Ackerman reported on the progress made updating the state/province status reports. Several states had not provided information including Montana, Nebraska, New Mexico, and Oklahoma. Bruce encouraged those states to provide information as soon as possible. Bruce stated he was working to develop a database that houses all historical state status information, and the database would be available prior to the next Pronghorn Workshop. **Action: Bruce Ackerman will produce a database incorporating all historical state and provincial status information prior to the next workshop.**

OTHER ITEMS

The group discussed responsibility for coordinating the biennial awards, including the Berrendo and Special Recognition awards. It was decided the host agency would be responsible for coordinating awards. Host agencies will be responsible for coordinating the forming of award committees, soliciting nominations, arranging for production of awards, and presenting the awards. **Action: this decision was not based on a vote. This issue should be brought up at the 23rd Pronghorn Workshop business meeting for formal consideration and incorporation into the bylaws.**

The business meeting adjourned at 1:45 PM.

Awards

Awards Presented at the 22md Biennial Pronghorn Workshop, Idaho Falls, Idaho

2006 Berrendo Award

The Berrendo Award is the most significant award offered through the Pronghorn Workshop, an event sanctioned by the Western Association of Fish and Wildlife Agencies. One award is given per workshop, to an individual or group of collaborators who made great contributions to the management or research of pronghorn. Two Berrendo Awards have previously been given out. In 2002, the first Berrendo Award was presented to Jim Yoakum, whereas the 2nd Berrendo Award in 2004 was given to Bart O'Gara. Today, we will honor the 3rd recipient of this prestigious award. The 2006 Berrendo Award recipient is Tom Pojar, from the state of Colorado.

As one of his nominators noted, Tom's career contributions to pronghorn are long overdue for peer recognition. For exceptional and long-term contributions to scientific management and research on pronghorn ecology, Tom is most deserving of recognition by his peers. For more than 25 years, Tom has conducted investigations into population dynamics, herd surveys, and other aspects of pronghorn ecology. A large portion of Tom's long career with Colorado Division of Wildlife was devoted to understanding pronghorn biology. Key to his research, Tom strived to apply his findings to management.

Throughout Tom's career, he has been an active participant in the Biennial Pronghorn Workshops. Ever since 1980, Tom has attended and been involved in every workshop. He chaired the 1990 Workshop in Colorado, at the headwaters of the Colorado River. He has authored more than 20 scientific publications on pronghorn, of which 10 have been printed in the various proceedings of the workshops he attended. Tom has contributed substantially in revising 3 updates of the "pronghorn management guides".

Tom has recently retired from Colorado Division of Wildlife, but he has continued to be actively involved in wildlife issues in Colorado, including pronghorn issues. As one nominator stated, he personifies the old adage, "once a pronghorn biologist, always a pronghorn biologist". The 22nd Pronghorn Workshop proudly recognizes and grants for a life-time career of excellent service to pronghorn and the wildlife profession, the 2006 Berrendo Award to Tom Pojar.

2006 Special Recognition Awards

Up to 4 Special Recognition Awards can be presented at a Pronghorn Workshop, an event sanctioned by the Western Association of Fish and Wildlife Agencies. The first awards, 4 of them, were presented to deserving recipients at the 2002 Pronghorn Workshop in Nebraska. In 2004, in North Dakota, 4 more awards were given to worthy recipients. Today, we will present 3 more Special Recognition Awards. The Special Recognition Award recognizes those who have made significant contributions that aid in the management of pronghorn. The key word is management.

This award is a certificate honoring the accomplishments of an individual or group that made an important contribution towards management of pronghorn, either as a single event or as the accumulation of long-term contributions.

Rick Danvir, Staff Wildlife Biologist/Manager, Deseret Land and Livestock Ranch, Woodruff, Utah

As the nominator stated, we often hear the adage "Good rangeland management is good wildlife management". Here we have a case history for pronghorn. The Deseret Ranch is a large ranch in northeastern Utah and adjacent Wyoming. What management strategies were conducted to take a pioneering herd of wild pronghorn of <100 animals to >700 in 2 decades, and who was the driving force in ensuring that the management strategies actually worked. Two major strategies were undertaken, first, maintain and enhance diversity of plant species and communities of grasses, forbs, and shrubs in healthy condition; secondly, effectively control wild and domestic ungulate numbers within the carrying capacity of the rangeland. As manager of the Deseret Ranch, Rick has ensured that the ranch is accomplishing these major goals. Rick's leadership is responsible for the management of the habitat and the wildlife using that habitat, in coordination with many other resource uses. Under Rick's stewardship of more than 25 years, the coordinated management program has resulted in an effective multiple use program that benefits pronghorn and other wildlife. This is on the ground management that is working and deserves recognition from the 22nd Pronghorn Workshop. We thank Rick for being such a strong manager and believing in multiple use management.

Award Recipients from Pronghorn Workshops

Berrendo Award

2002: Dr. Jim Yoakum, Western Wildlife, retired Bureau of Land Management

2004: Dr. Bart O'Gara, Professor Emeritus, Retired Unit Leader, Montana Cooperative Fish and Wildlife Research Unit, University of Montana (Deceased)

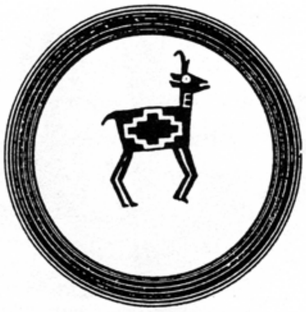
2006: Tom Pojar, retired, Colorado Division of Wildlife

Special Recognition Awards

2002: Karl Menzel, Nebraska; Jorge Cancino, Baja California Sur, Mexico; Bill Rudd, Wyoming; Richard Ockenfels, Arizona

2004: Rich Guenzel, Wyoming; Alice Koch, California; John Hervert, Arizona; Arizona Antelope Foundation

2006: Rick Danvir, Utah; Dr. Fred Lindzey, Wyoming; Dr. Rick Miller, Arizona



Summary of Pronghorn Workshops Held to Date

Meeting Dates and Locations	Number Attending	Chairman	Host Agency
April 14-16, 1965 Santa Fe, NM	18	W. Huey	New Mexico Department of Fish and Game
February 16-17, 1966 Denver, CO	32	G.D. Bear	Colorado Game, Fish and Parks Department
February 5-6, 1968 Casper, WY	97	J.L. Newman	Wyoming Game and Fish Commission
January 27-28, 1970 Scottsbluff, NE	85	K.I. Menzel	Nebraska Game and Parks Commission
June 19-22, 1972 Billings, MT	85	H.O. Compton	Montana Fish and Game Department
February 19-21, 1974 Salt Lake City, UT	52	D.M. Beale	Utah Division of Wildlife Resources
February 24-26, 1976 Twin Falls, ID	68	R. Autenrieth	Idaho Department of Fish and Game
May 2-4, 1978 Jasper, Alberta	84	M.W. Barrett	Alberta Fish and Wildlife Division
April 8-10, 1980 Rio Rico, AZ	64	J.S. Phelps	Arizona Game and Fish Department
April 5-7, 1982 Dickinson, ND	69	J.V. McKenzie	North Dakota Game and Fish Department
April 10-12, 1984 Corpus Christi, TX	45	C.K. Winkler	Texas Parks and Wildlife Department
March 11-13, 1986 Reno, NV	43	M. Hess	Nevada Department of Fish and Wildlife
May 31-June 2, 1988 Hart Mt., OR	43	D. Eastman	Oregon Department of Fish and Wildlife
May 22-24, 1990 Silver Creek, CO	45	T.M. Pojar	Colorado Division of Wildlife
June 8-11, 1992 Rock Springs, WY	91	P. Riddle	Wyoming Game and Fish Commission
April 18-21, 1994 Emporia, KS	49	K. Sexson	Kansas Department of Wildlife and Parks
June 5-7, 1996 Lake Tahoe, CA	75	L. Colton	California Department of Fish and Game
March 23-27, 1998 Prescott, AZ	92	R.A. Ockenfels	Arizona Game and Fish Department
March 14-17, 2000 La Paz, Baja California Sur, Mexico	42	J. Cancino	Centro de Investigaciones Biologicas del Noroeste - Direccion General de Vida Silvestre
March 17-20, 2002 Kearney, NE	85	J.S. Abegglen	Nebraska Game and Parks Commission, U.S. Forest Service, Nebraska National Forest
May 2-4, 2004 Bismarck, ND	76	Bill Jensen, Bruce Stillings	North Dakota Game and Fish Department, U.S. Forest Service, Bureau of Land Management
May 16-19, 2006 Idaho Falls, ID		Brad Compton, Dale Toweill	Idaho Department of Fish and Game

The Logo

EDSON FICHTER

1910 - 1994

Passion and dedication were the hallmarks of Edson Fichter. His passion and love for wildlife and wild places are displayed in lasting memory through his art and writings. Few others in the wildlife profession contributed so much to our understanding and appreciation of wildlife and wild lands.

Edson Fichter's wildlife career spanned over forty years. He was truly one of the founding biologists of wildlife conservation. Most of his career was spent in Idaho.

As a professor of wildlife at Idaho State University, as a wildlife researcher, an artist and a writer he became regarded as a renowned authority on the pronghorn antelope and the sagebrush/grassland ecosystem on which it depended. Pronghorn behavior, population ecology and habitat relationships were among his most noted contributions to our understanding of the pronghorn.

Edson loved to share his knowledge by mentoring and coaching many aspiring biologists. Today, many of his students are among the top in the wildlife management profession.

Edson Fichter was an avid fan of the pronghorn and made significant contributions to the North American Pronghorn Foundation, including a substantial collection of pronghorn artwork. Through his art and writings he has left a legacy of appreciation for the independence of free-ranging pronghorn herds and associated wildlife on sagebrush prairie habitats of western North America.

Courtesy North American Pronghorn Foundation

2006 Workshop Attendees

First Name	Last Name	Affiliation	City	State
Bruce	Ackerman	Idaho Dept of Fish and Game	Boise	ID
Eric	Anderson	Idaho Dept of Fish and Game	Idaho Falls	ID
Anis	Aoude	Utah Division of Wildlife Resources	Hyrum	UT
Al	Arsenault	Saskatchewan Environment	Saskatoon	SK
John	Augsburger	Bureau of Land Management	Boise	ID
Kerey	Barnowe-Meyer	University of Idaho	Moscow	ID
Peggy	Bartels	Bureau of Land Management	Burley	ID
Tom	Becker	Utah Division of Wildlife Resources	Tooele	UT
Jon	Beckmann	Wildlife Conservation Society	Boseman	MT
Chuck	Berdan	Bureau of Land Management	Belle 4che	SD
Kim	Berger	Wildlife Conservation Society	Victor	ID
Joel	Berger	Wildlife Conservation Society	Victor	ID
Regan	Berkley	Idaho Dept of Fish and Game	Jerome	ID
Marcus	Blood	W Civ 75 CEG/CEVR	Hill AFB	UT
Roger	Bredehoft	WY Game & Fish Dept	Laramie	WY
Toby	Boudreau	Idaho Dept of Fish and Game	Pocatello	ID
Clay	Brewer	Texas Parks & Wildlife Dept	Fort Davis	TX
Kim	Brinkley	Los Angeles Zoo	Glendale	CA
Adam	Bronson	Utah Division of Wildlife Resources	Panguitch	UT
David	Brown	Arizona State University	Phoenix	AZ
John	Byers	University of Idaho	Moscow	ID
Jorge	Cancino Hernandez	Centro de Investigatciones Biologicas del Noro Est	La Paz	Baja CS
Michael	Catanach	New Mexico Dept of Game & Fish	Raton	NM
Simon	Chapelle	Lotek Wireless Inc	Newmarket	ON
W. Jack	Clark	Clark & Associates	Centennial	CO
Corey	Class	Idaho Dept of Fish and Game	Pocatello	ID
Michael	Coffeen	USFWS	Phoenix	AZ
Tom	Collom	Oregon Dept of Fish and Wildlife	Salem	OR
Brad	Compton	Idaho Fish & Game	Boise	ID
Todd	Cornia	Desert Land & Livestock Ranch	Woodruff	UT
Rick	Danvir	Desert Land & Livestock	Woodruff	UT
Tom	Donham	Nevada Department of Wildlife	Tonopah	NV
Mike	Dunbar	USDA National Wildlife Res Ctr	Ft Collins	CO
Steve	Elam	Idaho Dept of Fish and Game	Jerome	ID
Dorothy	Fecske	ND Game & Fish Department	Riverdale	ND
Sue	Fairbanks	DNR Iowa State University	Ames	IA
Jeff	Faught	ND Game & Fish Department	Bismarck	ND
Mike	Fisher	USFWS SE Idaho Refuge Complex	Chubbuck	ID
Scott	Gamo	Idaho Dept of Fish and Game	Idaho Falls	ID
E Oz	Garton	University of Idaho	Moscow	ID
Shannon	Gavin	University of Calgary	Calgary	Alberta
Ken	Gray	Nevada Department of Wildlife	Elko	NV

Mike	Grue	Alberta Conservation Association	Lethbridge	Alberta
Rich	Guenzel	Wyoming Game and Fish Dept	Laramie	WY
Jerry	Gulke	ND Game & Fish Department	Bismarck	ND
Vincent	Gwyer	Bureau of Land Management	Salmon	ID
Dan	Halstead	ND Game and Fish Department	Riverdale	ND
Nate	Harling	ND Game and Fish Dept	Dickinson	ND
Louis	Harveson	Sul Ross University	Alpine	TX
Jim	Heffelfinger	AZ Game and Fish Dept	Tucson	AZ
Curtis	Hendricks	Idaho Dept of Fish and Game	Salmon	ID
Robb	Hitchcock	N AM Pronghorn Foundation	Casper	WY
Jill	Holderman	Bureau of Land Management	Boise	ID
Brad	Holliday	Nebraska Game & Parks Commission	Gering	NE
Doug	Howie	ND Game & Fish Department	Bismarck	ND
Mark	Hurley	Idaho Dept of Fish and Game	Salmon	ID
Chris	Jacques	South Dakota State University	Brookings	SD
Jonathan	Jenks	South Dakota State University	Brookings	SD
Bill	Jensen	North Dakota Game & Fish Dept	Bismarck	ND
Kelvin	Johnson	Montana Fish & Wildlife & Parks	Glasgow	MT
Michael	Johnson	ND Game & Fish Department	Bismarck	ND
Roger	Johnson	ND Game & Fish Department	Devils Lake	ND
Paul	Jones	Alberta Conservation Association	Lethbridge	Alberta
Thomas	Keegan	Idaho Dept of Fish and Game	Salmon	IS
Robert	Klaver	USGS/EROS	Sioux Falls	SD
Rod	Klus	Oregon Dept of Fish and Wildlife	Salem	OR
Jerry	Kobriger	ND Game & Fish Department	Dickinson	ND
Alice	Koch	California Dept of Fish & Game	Templeton	CA
Chris	Kochanny	Advanced Telemetry Systems	Isanti	MN
Jesse	Kolar	ND Game & Fish Department	Dickinson	ND
Randy	Kreil	ND Game & Fish Department	Bismarck	ND
Andy	Lindbloom	SD Game, Fish & Parks	Ft Pierre	SD
Fred	Lindzey	Professor Emeritus, University of Wyoming	Laramie	WY
Joe	Lowe	Bureau of Land Management	Idaho Falls	ID
Duane	Lucia	Texas Parks & Wildlife Dept	Lubbock	TX
Kent	Luttschwager	ND Game & Fish Department	Williston	ND
Cindy	Zachmeier	NRCS	Dickinson	ND
Steve	Madsen	Bureau of Land Management	Salt Lake City	UT
Jim	Maskey	University of North Dakota	Grand Forks	ND
Brandon	Mason	ND Game & Fish Department	Bismarck	ND
Phil	Mastrangelo	USDA Wildlife Services	Bismarck	ND
Pat	Mathis	New Mexico Dept of Game & Fish	Las Cruces	NM
Craig	McLaughlin	Utah Division of Wildlife Resources	Salt Lake City	UT
Cal	McCluskey	Bureau of Land Management	Boise	ID
Daryl	Meints	Idaho Dept of Fish and Game	Idaho Falls	ID
Bill	Miller	Arizona State University	Mesa	AZ
Carl	Mitchell	U.S. Fish & Wildlife Service	Wayan	ID
Kim	Morton	Alberta SRD-Fish & Wildlife	Lethbridge	Alberta

Hollie	Myasaki	Idaho Dept of Fish and Game	Nampa	ID
Justin	Naderman	Idaho Dept of Fish and Game	Idaho Falls	ID
Richard	Nelson	Nebraska Game & Parks Commission	North Platte	NE
Richard	Ockenfels	Arizona Game & Fish Dept	Phoenix	AZ
Michael	Oehler	National Park Service	Medora	ND
John	O'Neil	Idaho Dept of Fish and Game	Idaho Falls	ID
Greg	Painter	Idaho Dept of Fish and Game	Salmon	ID
Ray	Parsons	ND Game and Fish Department	Bismarck	ND
Ed	Partee	Nevada Department of Wildlife	Winnemuca	NV
George	Pauley	Idaho Dept of Fish and Game	Kamiah	ID
John	Paulson	USDA Wildlife Services	Bismarck	ND
Matt	Peek	Kansas Wildlife and Parks	Emporia	KS
Tom	Pojar	Colorado Division of Wildlife	Kremmling	CO
Jake	Powell	Idaho Dept of Fish and Game	Nampa	ID
Ryan	Powers	USDA Wildlife Services	Bismarck	ND
Jon	Rachael	Idaho Dept of Fish and Game	Nampa	ID
Bruce	Renhowe	ND Game and Fish Department	Bismarck	ND
Natalie	Rodrigues	AVM Instrument Co	Colfax	CA
Bill	Rudd	Wyoming Game & Fish	Green River	WY
Ben	Rutten	Nebraska Game & Parks Commission	Bassett	NE
Glen	Sargeant	USGS	Jamestown	ND
Tom	Segerstrom	Jackson Hole Land Trust	Jackson	WY
Gary	Schlichtemeier	Nebraska Game & Parks Commission	Alliance	NE
Tobin	Seagel	University of Calgary	Calgary	Alberta
Daly	Sheldon	University of Wyoming	Laramie	WY
Jeff	Short	Idaho Dept of Fish and Game	Idaho Falls	ID
Larry	Sickerson	Montana Dept of Transportation	Helena	MT
Aaron	Sides	Sul Ross University	Alpine	TX
Jason	Smith	University of North Dakota	Grand Forks	ND
Randy	Smith	Idaho Dept of Fish and Game	Jerome	ID
Tim	Smyser	University of Idaho	Moscow	ID
Patricia	Stastny	University of NE - Omaha	Omaha	NE
Jim	Stephenson	Yakama Nation	Toppenish	WA
Bruce	Stillings	North Dakota Game & Fish Dept	Dickinson	ND
Mike	Suitor	University of Calgary	Calgary	Alberta
Dan	Svingen	U.S. Forest Service	Bismarck	ND
Chad	Taylor	Nebraska Game & Parks Commission	Cambridge	NE
Terry	Thomas	Idaho Dept of Fish and Game	Idaho Falls	ID
Terry	Tolbert	Bureau of Land Management	Escalante	UT
Dale	Toweill	Idaho Dept of Fish and Game	Boise	ID
Bruce	Trindle	Nebraska Game & Parks Commission	Norfolk	NE
Brian	Wakeling	Arizona Game & Fish Dept	Phoenix	AZ
Dana	Warnecke	Arizona Game and Fish	Mesa	AZ
Craig	White	Idaho Dept of Fish and Game	Nampa	ID
Sheri	Whitfield	Bureau of Land Management	Idaho Falls	ID
Don	Whittaker	Oregon Dept of Fish and Wildlife	Salem	OR
Jeb	Williams	ND Game & Fish Department	Bismarck	ND

Ryan	Wilson	University of Arizona	Tucson	AZ
Brian	Wolfer	Oregon Dept of Fish and Wildlife	Salem	OR
Tim	Woolley	WY Game & Fish Dept	Savery	WY
Leigh	Work	Wildlife Conservation Society	Verdi	ID
John	Wrede	SD Dept of Game Fish & Parks	Rapid City	SD
Jim	Yoakum	Western Wildlife Consultants	Verdi	NV
Tim	Zachmeier	Bureau of Land Management	Dickinson	ND
Pete	Zager	Idaho Dept of Fish and Game	Lewiston	ID