2004

Proceedings of the 21st Biennial
PRONGHORN WORKSHOP
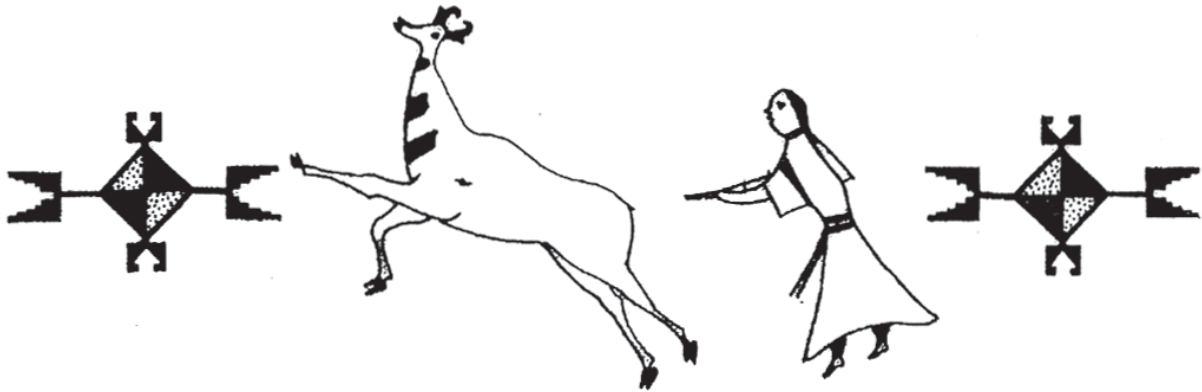### Bismarck, ND

US Forest Service
Bureau of Land Management
North Dakota Game and Fish Department

History of Logo

The drawing shown above (used for the logo) is from the dress of Pretty White Cow. The dress was made in the 1880s or early 1890s.

Pretty White Cow, a Hunkpapa Sioux, was the wife of Spotted Horn Bull; both were present at the battle of the Little Big Horn. Spotted Horn Bull was Sitting Bull's brother. Alone among Sioux Indian women of her time, she was allowed to speak in the Council meetings of Sitting Bull's band.

She was also the only Sioux woman of her time to use realistic, rather than geometric, decorative designs *(R. C. Hollow and H.T. Hoover. 1984. The Last Years of Sitting Bull)*.

This drawing shows a Sioux Woman hunting pronghorn with a rifle.

At the time of the 1885 Census, Pretty White Cow was 45 years of age.

We thank the Historical Society of North Dakota for providing information regarding this drawing.

Proceedings of the

21st Biennial Pronghorn Workshop

2004

May 1 – May 4, 2004

Bismarck, North Dakota

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Financial Contributors

North Dakota Game & Fish Dept.	North American Pronghorn Foundation
U.S. Forest Service	Central Mts. & Plains Section of
Bureau of Land Management	The Wildlife Society
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Arizona Pronghorn Foundation	Telonics, Inc.
	Advanced Telemetry Systems

Special Thanks

Clare Renner (NDGF)
Connie Schiff (NDGF)
Janel Kolar (NDGF)
Carla Turbiville (BLM)

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Dedication
Dr. Bartholomew W. O'Gara
1923-2003

Bartholomew W. O'Gara was born on a farm in Laurel, Nebraska on March 21, 1923. Joining the U.S. Navy I 1941, he served in World War II, the Korean War, and with a variety of shore stations around the world for 20 years.

After his military service, Bart went back to school, receiving a bachelor's degree from Montana State University and a Ph.D. from the University of Montana. His doctoral dissertation was on the reproductive physiology of pronghorn. Bart's publications included all aspects of big game biology and management, particularly predation.

Bart O'Gara was a charter member of the Pronghorn Workshop and attended every biennial meeting for the past 40 years. On May 21, 2003 Dr. Bartholomew W. O'Gara died of a brain aneurysm. The 21st Annual Pronghorn Workshop is dedicated to the life and work of Dr. Bart O'Gara. His knowledge, guidance and quick smile will be missed.
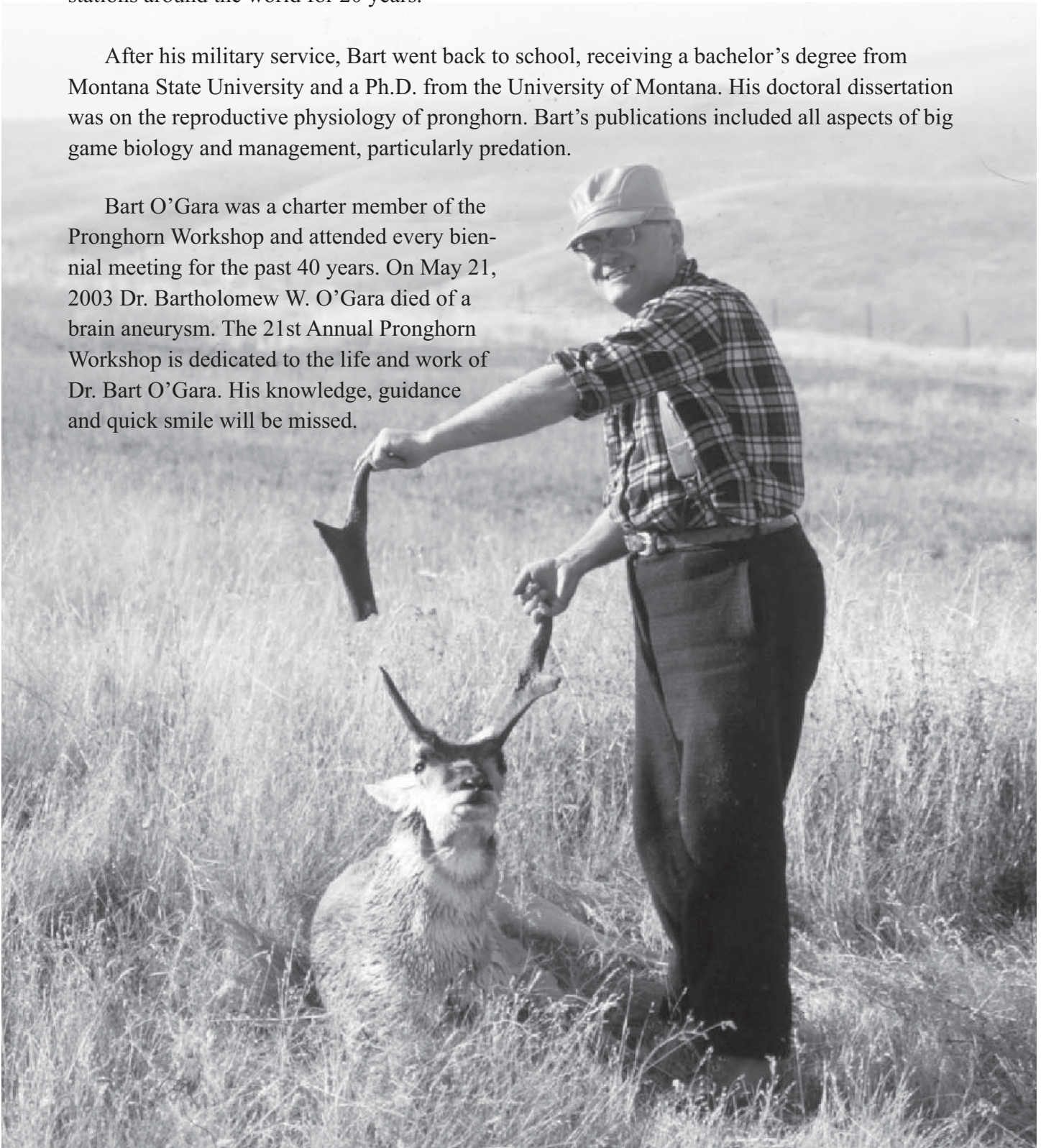
Summary of Pronghorn Workshops Held to Date

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. Autenreith	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

Section I.

Workshop Agenda

21ST BIENNIAL PRONGHORN WORKSHOP
MAY 1 – MAY 4, 2004
BISMARCK, NORTH DAKOTA

Saturday, May 1, 5:00-6:00 PM

5:00 PM – 6:00 PM   Early Registration – Front Lobby

Sunday, May 2, 9:00 AM – 4:00 PM

9:00 a.m. – 4:00 p.m.   Bus tour of Lewis and Clark Interpretive Center, Fort Mandan and Knife River Indian Village.

5:00 p.m.   Registration

7:00 p.m. – 9:00 p.m.   Social – Cash bar and snacks – Picasso/DaVinci Rooms (Sponsored by: Central Mountains and Plains Section of The Wildlife Society and the North Dakota Chapter of The Wildlife Society.)

Monday, May 3, 8:00 AM – 4:15 p.m.

7:30 a.m.   Registration – Rembrandt Room
Continental Breakfast (Sponsored By: Advanced Telemetry Systems, Inc.)

8:30 a.m.   Welcoming & Moderator – Dean Hildebrand, Director, North Dakota Game and Fish Department

8:45 a.m.   **The Role of State Agencies in Pronghorn Management** – *Randy Kreil,* North Dakota Game and Fish Department, Bismarck, ND

9:05 a.m.   **The Role of the National Grasslands in the Northern Great Plains** – *Dan Svingen,* United States Forest Service, Bismarck ND

9:25 a.m.   **An Approach to Regional Habitat Connectivity and Linkage Analysis with Emphasis on Pronghorn and Other Grassland Species: The Prairie Grasslands Analysis Project** – *Cal McCluskey,* Senior Wildlife Specialist, Bureau of Land Management, Boise, ID. Co-authors *Bruce Durtsche,* Wildlife Biologist; *Christopher Benson*, and *Matt Tomaszewski*, BLM National Science and Technology Center, Denver, CO.

9:45 a.m.   Announcements, *Bill Jensen,* North Dakota Game and Fish Department, Bismarck, ND.

9:50 a.m.

National American Pronghorn Foundation Update – *Robb Hitchcock*, North American Pronghorn Foundation.

9:55 a.m.

Arizona Antelope Foundation Update – *David Brown,* Arizona Antelope Foundation

10:00 a.m. – 10:30 a.m.

BREAK (Sponsored by: Advanced Telemetry Systems, Inc.)

10:30 a.m.

State Status Reports – *Bruce Stillings,* Big Game Biologist, ND Game and Fish Department, Dickinson ND.

11:00 a.m.

Mapping Continental Range Distribution of Pronghorn Using GIS Technology – *William F. Jensen,* and *Brian M. Hosek,* ND Game and Fish Department; *William J. Rudd,* Wyoming Game and Fish Department.

11:25 a.m.

Genetic Consequences of Reintroductions: An Example from Pronghorn Antelope in Oregon – *Catherine L. Stephen,* Department of Forestry and Natural Resources, Purdue University; *Donald G. Whittaker,* Oregon Department of Fish and Wildlife; *Don Gillis,* Umatilla Army Chemical Depot; *Lindsey L. Cox,* Department of Forestry and Natural Resource, Purdue University; and *Olin E. Rhodes, Jr.,* Department of Forestry and Natural Resources, Purdue University.

11:55 a.m. – 1:30 p.m.

LUNCH AND BUSINESS MEETING – Picasso/DaVinci Room (see attached agenda)

1:40 p.m.

Wild Ungulates as a Factor Affecting Pronghorn Productivity and Population Levels on Anderson Mesa – *David E. Brown,* Arizona Antelope Foundation; *William Fagan,* Department of Biology, University of Maryland; *Julia Louie,* Department of Biology, University of Maryland; *Henry Provencio,* U.S. Forest Service, Coconino National Forest.

2:05 p.m.

Selection for Early Horn Growth in Pronghorn Males—*Carl D. Mitchell,* U.S. Fish and Wildlife Service; *Christian R. Maher*, Department of Biological Sciences, University of Southern Maine.

2:30 p.m. – 3:00 p.m.

BREAK (Sponsored by: North American Pronghorn Foundation)

3:00 p.m.

Importance of Vegetation Structure and Forage Ability in Habitat Selection by Female Pronghorn and Fawns During the Fawn Hiding Period – *Patricia L. Stastny,* and *W. Sue Fairbanks,* University of Nebraska, Omaha.

3:25 p.m.   **Selection of Wintering Areas During Different Environmental Conditions on the Basis of Shrub Density and Shrub Height** – *Patricia L. Stastny, Joerg Henkel,* and *W. Sue Fairbanks,* University of Nebraska, Omaha.

3:50 p.m.   **The Use of Translocations in Wildlife Management** – *Brian F. Wakeling*, Arizona Game and Fish Department.

Tuesday, May 4, 2004 – 6:00 a.m. – 9:00 p.m.

6:00 a.m.   **Birding Tour** – *Dan Svingen* (Contact Dan at the meeting)

7:30 a.m.   **Continental Breakfast** – Rembrandt Room (Sponsored by: Telonics, Inc.)

8:30 a.m.   **Pronghorn and Predators: A Review** – *Jim D. Yoakum,* Western Wildlife.

8:55 a.m.   **The Peninsular Pronghorn Recovery Plan: 20 Years** – *Jorge Cancino,* Centro de Investigaciones Biologicas del Noroeste; *Ramon Castellanos,* Reserve de la Bioserfa El Vizcaino; *Jeff Holland,* Los Angeles Zoo; *Felipe Ramirez,* and *Victor Sanchez,* Reserve de la Bioserfa El Vizcaino.

9:20 a.m.   **Using GPS-Equipped Telemetry Collars to Assess Pronghorn Movements and Habitat Use in Northern Arizona and Northern Mexico** – *Richard A. Ockerfels, James C. deVos, Jr., Chuck R. Anderson,* and *Sue R. Boe,* Research Branch, Arizona Game and Fish Department.

9:45 a.m. – 10:20 a.m.   **BREAK** (Sponsored by: Telonics, Inc.)

10:20 a.m.   **Pronghorn Recruitment Study: Status Report** – *Scott C. Sprague, Kirby D. Bristow, Tim Rogers, Shelli A. Dubay, Stan C. Cunningham,* and *Richard A. Ockerfels,* Arizona Game and Fish Department.

10:45 a.m.   **Survival of Adult and Neonatal-Aged Pronghorn in Western South Dakota** – *Christopher N. Jacques, Jaret D. Sievers, Jonathan A. Jenks,* Department of Wildlife and Fisheries Sciences, South Dakota State University.

11:05 a.m.   **LUNCH** (on your own)

1:10 p.m.   **Road Effects on Pronghorn Antelope (***Antilocapra americana***) Habitat Use and Behavior in Southern Alberta, Canada** – *Shannin D. Gavin,* Department of Biological Services, University of Calgary, Calgary, Alberta.

1:35 p.m.   **Movement and Dispersion of Pronghorn in Southwestern Wyoming** – *Daly Sheldon,* and *Fred Lindzey,* Zoology and Physiology Department, University of Wyoming.

2:00 p.m.   **Pronghorn and Fences: A Review and New Management Strategies** – *Jim D. Yoakum,* Western Wildlife.

2:25 p.m. – 2:45 p.m.   **BREAK** (Sponsored by: Arizona Antelope Foundation.)

2:45 p.m. – 4:00 p.m.   **General Discussion** – *William J. Rudd,* Wyoming Game and Fish Department and *Fred Lindzey,* Zoology and Physiology Department, University of Wyoming.
– Pronghorn crossing structures.

4:00 p.m. – 4:30 p.m.   **Closing Remarks** – *Jim D. Yoakum*

6:00 p.m.   **Social** – Picasso/DaVinci Rooms
6:30 p.m.   **Banquet** – Picasso/DaVinci Rooms

21ST BIENNIAL PRONGHORN WORKSHOP
BUSINESS MEETING AGENDA

May 3, 2004 11:55 a.m. – 1:30 p.m.

- Website/CD for Proceedings *(Richard Ockenfels)*
- Management Guidelines *(David Brown)*
- Awards *(Richard Ockenfels)*
- Hall of Fame *(Richard Ockenfels)*
- Pronghorn Book *(Jim Yoakum)*
- Special edition of Wildlife Society Bulletin Regarding Pronghorn *(William Rudd or Richard Ockenfels)*
- Next Meeting Location *(William Jensen)*
- What to do with surplus funds from the workshop *(William Jensen)*
- Other Items

Section II.

Status Report

PRONGHORN PROVINCE AND STATE STATUS REPORT

BRUCE A. STILLINGS, Big Game Biologist, North Dakota Game and Fish Department, 225 30th Avenue SW, Dickinson, ND 58601-7227, USA

Abstract: A standardized questionnaire was sent to 16 western states in the United States, 2 Canadian provinces, and Mexico to collect 2003 pronghorn population, survey, and hunt information. We received responses from all western U.S. states, two Canadian provinces, and one from Mexico. Wyoming remains the core of the global pronghorn population with an estimate of 440,000 animals. All states/provinces except Baja California Sur in Mexico have a pronghorn rifle season. Total harvest decreased substantially in 2003 versus 1993. Wildlife/Landowner conflicts are mitigated through depredation payments, transferable licenses, and/or hunter access programs.

INTRODUCTION

A standardized questionnaire was sent to all states and provinces in the United States, Canada, and Mexico known to have free-ranging pronghorn to collect 2003 pronghorn population, survey, and hunt information. Questionnaires were completed by all states in the USA and Canadian provinces, but only Baja California Sur in Mexico.

POPULATION ESTIMATES AND SURVEY METHODOLOGY

Population estimates ranged from 68 in Baja California Sur, Mexico, to 440,000 in Wyoming. All states/provinces conduct aerial surveys to sample population sizes in at least part of their range, while sex/age data are collected using aerial and/or from the ground. The most common survey method was line transects. Pre-season buck-to-doe ratios ranged from a low of 15 bucks per 100 does in Nebraska to a high of 80 bucks per 100 does in Colorado. Pre-season fawn-to-doe ratios ranged from a low of 8 fawns per 100 does in Arizona to a high of 96 fawns per 100 does in South Dakota.

State/Prov.	Population Estimate	Percent Observed	Estimate Method	Survey Type				Survey Method		Time of Year	
				Helicopter	Ground	Fixed-Wing	Land-owner	Aerial	Ground	Aerial	Ground
AB	16,437	16		X				Line Transect		Post-Fawn	
AZ	8,000-10,000	50-70	Model Pop II.			X		Line Transect		Post-Fawn	
CA	5,000	>80	Count			X		Targeted Search & Count		Winter	
CO	58,410	Unknown	Computer Simulation	X		X		Strip Transect, Line Transect, Haphazard/Random Search & Count		Fall, Pre-Fawn	
ID	13,000	Unknown	Count	X	X	X		Line Transect, Targeted, Quadrant Sampling	Targeted Concentration	Pre-Fawn, Post-Fawn	Post-Fawn
KS	2,000	55	Count			X		Line Transect		Post-Fawn, Winter	
MT	N/A	Unknown	Count			X		Strip Transect		Post-Fawn	
ND	9,966	Unknown	Count			X		Strip Transect		Post-Fawn	
NE	6,000-7,000	9	Count		X	X	X	Strip Transect	Trend Routes, Targeted Concentration	Post-Fawn, Winter	Post-Fawn
NM	N/A	Various	Count			X		Strip Transect		Pre-Fawn	
NV	18,000	51	Pop II	X	X			Targeted Search, Haphazard/Random Search	Targeted Concentration	Post-Fawn, Winter	Post-Fawn
OK	1,500	60%	Count		X	X		Strip Transect	Targeted Concentration	Winter	Winter
OR	~25,000	Unknown	Count	X	X	X		Targeted Search & Count, Haphazard/Random Search & Count	Trend Routes, Targeted Concentration Areas	Post-Fawn, Winter	Post-Fawn, Winter
SK	21,600		Program Distance			X		Line Transect		Pre-Fawn	
SD	40,770	33	Count	X	X	X		Line Transect	Targeted Concentration	Pre-Fawn	Post-Fawn
TX	10,305	100	Count		X	X		Strip Transect	Targeted Concentration	Post-Fawn	Post-Fawn
UT	12,000	70	Count		X	X		Strip Transect, Targeted Search & Count	Targeted Concentration	Pre-Fawn	Post-Fawn
WY	439,977	Unknown	Pop II/Dist		X	X		Line Transect		Pre-Fawn	Post-Fawn
MEX	68	60	Count		X	X		Strip Transect, Haphazard/Random Search & Count	Trend Routes	Winter	Fall, Pre-Fawn, Post-Fawn

POPULATION STATUS

Total Population Estimate, 2003

16,437   21,600

9,966

25,000   13,000   439,977

40,770

6,000-7,000

18,000   12,000   58,410

2,000

5,000

1,500

8,000-10,000

68

10,305*
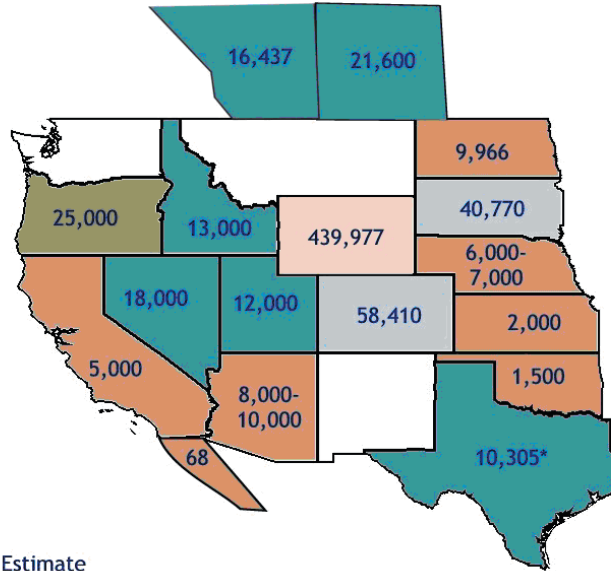
*2002 Estimate

Pre-Season Buck-to-Doe Ratio, 2003

48   52

36 (25-46)

41

46

20-50   21-71

15-30

40-45   35   19-80

32

35

44

Pre-Season Fawn-to-Doe Ratio, 2003

63   60

67 (60-71)

39(13-75)[01]   30-80   27-95

96

18-71

32-34   30   15-63

70

8

42
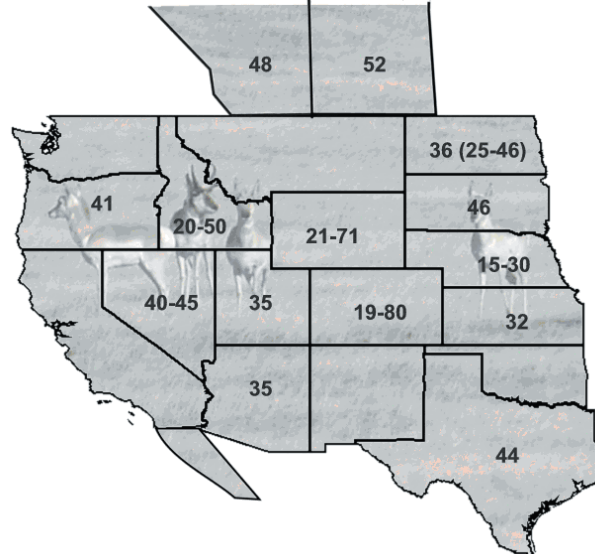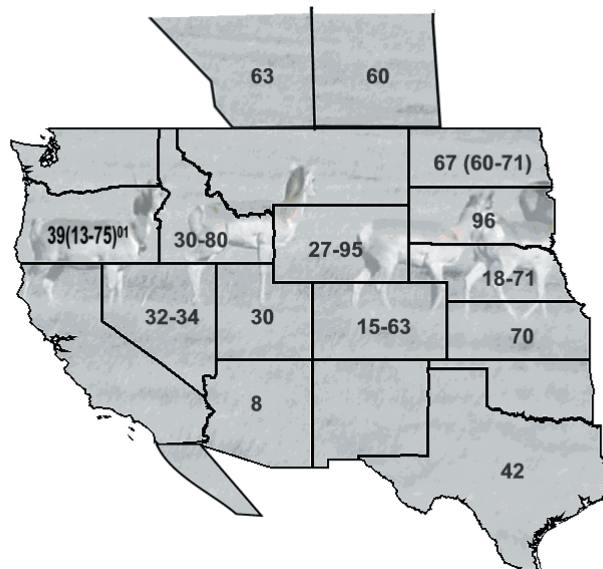
SEASON STRUCTURE

Hunt season structure varied by jurisdiction. Many muzzleloader seasons occurred in conjunction with rifle or archery seasons and/or had their own season following the rifle hunt. Most archery seasons opened prior to firearm season.

State/ Prov.	Rifle Dates	Days	Muzzleloader Dates	Days	Archery Dates	Days	Special Status Report Type	Dates	Days
AB	9/29 – 10/29	15			9/3 – 9/27	22			
AZ	3rd or 4th wk. Sept.	6	3rd or 4th wk. Sept.	4-6	Late Aug./ early Sept.	14	Juniors	3rd or 4th wk. Sept.	6
CA	Aug. & Sept.	9	w/rifle season		August	9	Junior	August	9
							Fund-raising (2 auction tags)	Aug – Sept	51
CO	9/25 – 10/1 or 10/2 - 10/8	7	10/21 – 10/29	9	8/15 – 9/20	37	Youth (fees decreased)	Same	Same
ID	9/25 – 10/24	30	9/25 – 10/24	30	8/15 – 9/15	32	Short Range Weap.	9/25 – 10/24	30
							Youth	9/25 – 10/24	30
KS	10/3 – 10/6	4	9/29 – 10/6	8	9/20 – 9/28	9			
MT	10/13-11/10	29			9/7-10/12	36			
ND	10/3 – 10/19	16 ½			8/29 – 10/12	51 ½			
NE	Oct. 1-16	16	9/20 – 10/5	16	8/20-11/14, 11/24-12/31	109			
NM	8/24 – 10/6 (weekends)	7	8/17-20, 9/14-15 (2 periods)	6	8/24-28 8/10-14	10	Mobility Impaired	8/3-5	3
							Youth	9/28-29	2
NV	8/23 – 9/1	10			8/2 – 8/17	16	Heritage Tag auction	7/15 – 12/31	139
OK	9/26-29 Buck 12/12-15 Doe	4/4							
OR	Mid August	9	Early Sept.	9	Var. Aug. & Sept.	9-11	Youth	Mid-late Aug.	9
							Special Auction	8/1 – 9/30	61
							Special Raffle	8/1 – 9/30	61
SK	10/20 – 10/25	6	9/29 – 10/18	18	9/1 – 10/18	48			
SD	10/4 – 10/12	9			8/16 – 10/31	69			
TX	10/4 – 10/12	9							
UT	9/13 – 9/23	11			8/16 – 9/12	28	Conservation Permits	9/1 – 11/15	76
							Coop. Wildlife Mgmt. Units	9/1 – 11/15	76
							Depredation	As needed	
WY	9/1 – 12/15	10-92	8/20 – 9/30	20-42	8/15 – 9/30	46	One shot hunt		
							Gov/Com. Licenses	Variable	Variable

HARVEST SUMMARY

The tables below summarize harvest data from western states, Alberta, and Saskatchewan. The percent of the population harvested varied from 2% in Saskatchewan to 14% in North Dakota. Bucks comprised the majority of the harvest, ranging from 57 to100%. Does/fawns were not harvested in Arizona, Saskatchewan, and Texas. Where does and fawns were harvested, the percent of total harvest ranged from 3 to 50%.

The number of rifle hunters and harvest generally decreased in 2003 versus 1993. Rifle hunter success remains very high, averaging 77%. Only 9 states had a muzzleloader season, with hunter success ranging from 43 to 86%. The number of archers and harvest has remained relatively stable among states/provinces reporting data for 1993 and 2003. The biggest change in archery hunters occurred in Idaho (96% increase in resident hunters) and New Mexico (60% decrease in total archers).

Total Harvest, 1993 versus 2003
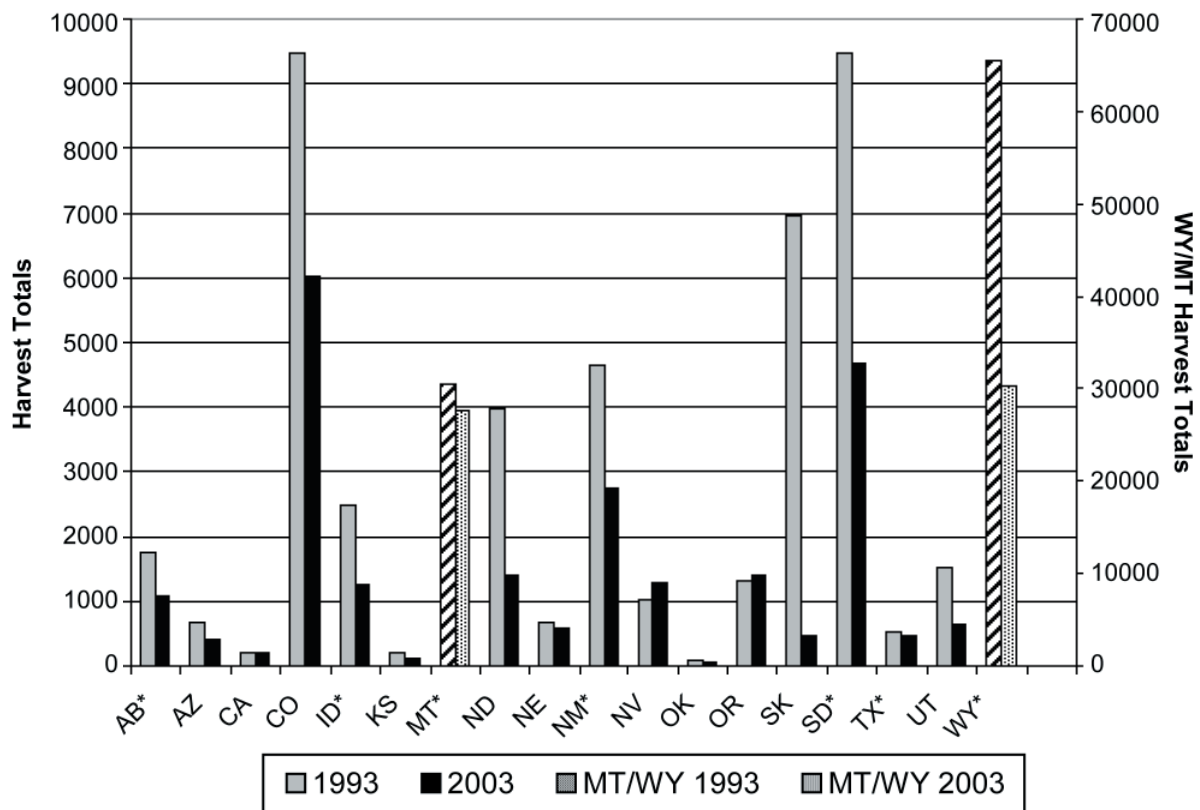
*1993 & 2002 Data

Total Harvest, 2003

State/ Prov.	Population Estimate	Total Harvest	% of Pop Harvested	No. Bucks Harvested	% Bucks Harvest	No. Does/ Fawns Harvested	% Does/ Fawns Harvest
AB[1]	16,437	1090	7	764	70	326	30
AZ	8,000-10,000	415	5	415	100	–	–
CA	5,000	191	4	187	98	4	2
CO	58,410	6021	10	3431	57	2590	43
ID[1]	13,000	1256	10	994	80	262	20
KS	2,000	108	5	88	82	20	18
MT	N/A	27,720	N/A	16,817	61	10,903	39
ND	9,966	1412	14	1155	82	257	18
NE	6,000-7,000	572	9	561	99	11	1
NM	N/A	2744	N/A	2698	98	46	2
NV	18,000	1275	8	1206	95	69	5
OK	1,500	61	4	54	89	7	11
OR	~25,000	1392	6	1200	86	192	14
SK	21,600	456	2	456	100	–	–
SD	40,770	4664	12	2918	63	1746	37
TX	10,305	469	5	469	100	–	–
UT	12,000	644	6	384	60	260	40
WY	439,977	30260	7	21611	71	8649	29

[1]2002 Data

Rifle Harvest

State/ Prov.	Bucks Harvested		Does/Fawns Harvested		# Resident Hunters		#Non-Resident Hunters		Resident Days		Non-Resident Days		% Success	
	1993	2003	1993	2003	1993	2003	1993	2003	1993	2003	1993	2003	1993	2003
AB	984	704[1]	712	326[1]	2334	1279[1]	44	44[1]	3643	2578[1]	--	--	72.7	80.5[1]
AZ	484	303	0	0	632	342	13	30	1466	778	30	68	76	84
CA	189	187	0	0	236	232	--	--	--	--	372	313	81	81
CO	4916	3121	4134	2548	10663	7836	240	176	16527	13948	372	313	83	71
ID	1175	747[1]	1198	216[1]	3650	1334[1]	35	35[1]	11100	3736[1]	200	125[1]	65	68[1]
KS	155	66	31	14	210	104	--	--	263	145	--	--	89	77
MT	15,212	16,586[1]	15,228	10,769[1]	35,279	27,246[1]	11,572	3,483[1]	97,369	77,015[1]	39,206	11,964[1]	73	73[1]
ND	2505	982	1457	202	4536	1462	0	0	9283	3210	--	--	85	81
NE	456	430	121	0	710	771	0	0	--	--	--	--	81	56
NM	4147[2]	2391[1]		46[1]	4638[3]	2692[1,3]			--	4065[1,3]	--	--	89	91[1]
NV	954	1114	47	69	1305	1420	72	76	--	3360	--	156	73	79
OK	72	54[1]	9	7[1]	88	100	--	--	N/A	N/A	--	--	92	61[1]
OR	1235	1104	33	183	1763	1684	--	--	5183	4903	--	--	72	76
SK	2866	336	3719	--	10905	369	--	--	23994	598	--	--	60	83
SD	5019	2720[1]	4348	1724[1]	8987	4495[1]	519	318[1]	16176	8181[1]	955	610[1]	68	68[1]
TX	523	469[1]	0	0	602	580[1]	--	--	5418	5220[1]	--	--	87	81
UT	541	352	914	260	511	320	57	40	1073	544	120	68	95[6],79[7]	98[6],88[7]
WY	33069[4]	20783[1]	32370[4]	8318[1]	21165[4]	14946[1]	28024[4]	16943[1]	58334[4]	51086[1]	86379[4]	51004[1,4]	133[4,5]	91.3[1,4]

[1]2002 Data

[2]Combined Does & Bucks

[3]Combined Resident & Non-Resident Data

[4]Includes all license types

[5]Because of the way the old report lumped kills per hunter, this reflects the fact that hunters killed more than 1 pronghorn in a given year. New information breaks out by license type and gives a more accurate estimate of hunter success.

[6]Buck Hunter Success

[7] Doe Hunter Success

Muzzleloader Season

State/ Prov.	Bucks Harvested		Does/Fawns Harvested		# Resident Hunters		#Non- Resident Hunters		Resident Days		Non- Resident Days		% Success	
	1993	2003	1993	2003	1993	2003	1993	2003	1993	2003	1993	2003	1993	2003
AB	–	–	–	–	–	–	–	–	–	–	–	–	–	–
AZ	80	55	0	0	151	78	2	9	480	215	6	25	53	66
CA	–	–	–	–	–	–	–	–	–	–	–	–	–	–
CO	–	49	–	12	–	142[3]				435[3]			–	43
ID	18	52[1]	5	10[1]	50	139[1]	3	4[1]	220	632[1]	9	12[1]	37	44[1]
KS	–	11	–	4	–	27	–	–	–	74	–	–	–	56
MT	–	–	–	–	–	–	–	–	–	–	–	–	–	–
ND	–	–	–	–	–	–	–	–	–	–	–	–	–	–
NE	0	96	0	0	0	162	0	0					0	59
NM	184[2]	113[1]		0[1]	376[3]	186[1, 3]			–	423[1, 3]			49	61[1]
NV	–	–	–	–	–	–	–	–	–	–	–	–	–	–
OK	–	–	–	–	–	–	–	–	–	–	–	–	–	–
OR	6	41	1	2	30	151			141	847			23	28
SK	200	112	56	0	563	130	0	0	1341	271	0	0[1]	46	86
SD	–	–	–	–	–	–	–	–	–	–	–	–	–	–
TX	–	–	–	–	–	–	–	–	–	–	–	–	–	–
UT	–	–	–	–	–	–	–	–	–	–	–	–	–	–
WY		236[1]		94[1]		169[1]		192[1]						

[1] 2002 Data

[2] Combined Does & Bucks

[3] Combined Resident & Non-Resident Data

Archery Season

Archery Season

State/ Prov.	Bucks Harvested		Does/Fawns Harvested		# Resident Hunters		#Non-Resident Hunters		Resident Days		Non-Resident Days		% Success	
	1993	2003	1993	2003	1993	2003	1993	2003	1993	2003	1993	2003	1993	2003
AB	60	60[1]	2	0[1]	172	147[1]	22	22[1]	595	619[1]	–	–	36	41[1]
AZ	111	57	0	0	662	416	4	17	3371	2457	20	100	18	14
CA	6	4	0	0	23	18	0	0					26	22
CO	346	261	66	30	1330	1093	345	283	5719	5957	1484	1548	29	21
ID	60	195[1]	20	36[1]	540	1059[1]	15	15[1]	2950	5368[1]	50	63[1]	15	31[1]
KS	21	11	3	2	110	108	–	–	440	300	–	–	21	12
MT	N/A	231[1]	N/A	134[1]	N/A	1177[1]	N/A	343[1]	N/A	6019[1]	N/A	1682[1]	N/A	34[1]
ND	–	173	–	55	–	987	–	88	–	5141[3]	–		–	21[3]
NE	78[2]	35		11	492	368[3]							16	13
NM	325[3]	194[1]		0[1]	1429[3]	565[1,3]			NA[3]	1689[1,3]			23	34[1]
NV	27	92	0	0	187	337	14	13	NA	1658	N/A	50	13	26
OK	–	–	–	–	–	–	–	–	–	–	–	–	–	–
OR	31	55	1	7	375	363			1853	1404			9	17
SK	71	8	41	0	454	47	0	0	1666	273	0	0	25	17
SD	87	198[1]	13	22[1]	611	701[1]	114	199[1]	3018	3687[1]	358	951[1]	13.8	25[1]
TX	–	–	–	–	–	–	–	–	–	–	–	–	–	–
UT	61	32	0	0	91	61	10	2	391	366	23	12	60	50
WY		592[1]		237[1]		426[1]		483[1]						

[1] 2002 Data

[2] Combined Does & Bucks

[3] Combined Resident & Non-Resident Data

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.

State/Province	No. NR Rifle Hunters	NR % of Rifle Hunters	No. NR Muzzleloader Hunters	NR % of Muzzleloader Hunters	No. NR Archery Hunters	NR % of Archery Hunters
AB	44[1]	2[1]	–	No season	22[1]	13[1]
AZ	30	8	9	10	17	4
CA	–	0	–	No season	0	0
CO	176	2		0	283	21
ID	35[1]	3[1]	4[1]	3[1]	15[1]	1[1]
KS	–	No season	–	No season	–	No season
MT	3483[1]	11	–	No season	–	No season
ND	0	No season	–	No season	88	8
NE	0	0	0	0		Unknown
NM		22		22		22
NV	76	5	–	No season	13	4
OK	–	0	–	No season	–	No season
OR	–	3		3		3
SK	–	No season	0	No season	0	No season
SD	318[1]	7[1]	–	No season	199[1]	22[1]
TX	–	Unknown	–	No season	–	No season
UT	40	11	–	No season	2	3
WY	16943[1]	53[1]	192[1]	53[1]	483[1]	53[1]

[1]2002

WILDLIFE/LANDOWNER PARTNERSHIPS

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

State/ Prov.	Program Description	Funding	Results
AB	AFSC (Alberta Agriculture Food and Rural Dev.) Wildlife Damage Compensation on Stacked Hay Program	Alberta Gov't. funded	Not readily avail.
	Alberta Sustainable Resource Development – Ungulate Damage Prevention Program – $80,000	$80,000	Variable
AZ	Livestock/Wildlife Issues	$90,000-$100,000 Annually	Reduce livestock/wildlife conflicts
CA	Private Lands Wildlife Habitat Enhancement and Management Area Program	Landowners issued licenses (10 in 2003) that can be sold	Increased landowner tolerance of wildlife
	Game damage	Hunter license fees	Compensates land-owners for damage by pronghorn to growing crops in some situations
	Habitat Partnership Program	5% of pronghorn license revenue on a unit by unit basis	Reduces conflicts between landowners and wildlife
CO	Ranching for Wildlife	N/A	Gives landowners with large contiguous blocks of land the opportunity to enter into coop. agreements with CDOW to manage pronghorn on their lands and possibly generate revenue from use of private lands by hunters
	Depredation compensation	Surcharge on tags	Intent is to sustain higher wildlife populations
	Landowner appreciation program	None	Separate controlled hunts for qualifying landowners
ID	Access Yes!	Donations, lottery for super tags	Private Lands Access Program
NM	"Landower Sign-Up System"	Fees on landowner licenses	Provides for some public access on private land.
NV	Landowner Compensation Tag Program	Landowner issued 1 license for every 50 pronghorn on their private land that can be sold	Increased landowner tolerance of wildlife
MT	Block Management Program	N/A	Hunter access to private land
ND	Private Land Open to Sportsmen (PLOTS)		Landowner compensated for habitat conservation in return for hunter access to private land
OR	Landowners are guaranteed doe tags based on acreage owned.		

State/ Prov.	Program Description	Funding	Results
	Walk-In area program	$5.00 surcharge on all big game license fees	Program generally works well but the areas are hunted very hard and sometimes create uneven harvest distribution. Landowners tend to tolerate more hunters in exchange for less wildlife!
SD	Depredation Food Plot Program	$5.00 surcharge on all big game license fees	Usually done in conjunction with the WIA program and does secure additional private land access for hunting and improves landowner tolerance to some degree.
	Cooperative Wildlife Management Units and Landowner permits	Permits to landowners that can be sold	Reduces conflicts between landowners and wildlife
UT	Depredation payments	Direct payments to landowner for forage consumed comes from license dollars	
	Landowner Coupons	Landowners reimbursed for damage on private land	Reduces conflicts between landowners and wildlife
WY	Depredation payments		

HABITAT ENHANCEMENT PROGRAMS

State/ Province	Habitat Enhancement Program
AB	None
AZ	Juniper removal, forage enhancement
CA	None
CO	Conversion of abandoned center pivot as fields to native vegetation
ID	None
KS	None specific
MT	Conservation easements and long-term leases of priority sagebrush/grassland habitat. Rest rotation grazing systems are employed on most conservation easements.
ND	None
NE	None
NV	Water developments, forage enhancement, fence modifications
OK	None
OR	None
SK	None
SD	None
TX	Technical assistance to private landowners, range improvement (grazing plans, prescribed fires, re-seeding)
UT	Water developments, range enhancement
WY	None specific to pronghorn
MX	None

CURRENT RESEARCH PROJECTS

State/Province	Project
AB	GPS collar telemetry, habitat selection, population dynamics & movements
AZ	Movements, nutrition, disease, habitat-use, factors influencing population declines
CA	Habitat condition in Carrizo Plain
CO	Population dynamics and behavior of a pronghorn herd that naturally immigrated to previously unoccupied habitat
ID	Landscape evaluation, population monitoring
KS	None
MT	None
ND	Home range, habitat-use & preference, survival and cause specific mortality rates of adult does and bucks
NE	None
NM	None
NV	None
OK	None
OR	Genetics
SK	None
SD	Population monitoring techniques
TX	Pronghorn movements in relation to fences and traditional netwire fencing; Habitat –utilization and suitability and movement models
UT	None
WY	GPS collar pronghorn movement study; Effects of gas development; Adult pronghorn mortality study
MX	Population viability assessment

Section III.

Abstracts and Papers

MAPPING CONTINENTAL RANGE DISTRIBUTION OF PRONGHORN USING GEOGRAPHIC INFORMATION SYSTEMS TECHNOLOGY

WILLIAM F. JENSEN, North Dakota Game and Fish Department, 100 North Bismarck Expressway, Bismarck, ND 58501, USA (bjensen@state.nd.us)

BRIAN M. HOSEK, North Dakota Game and Fish Department, 100 North Bismarck Expressway, Bismarck, ND 58501, USA (bhosek@state.nd.us)

WILLIAM J. RUDD, Wyoming Game and Fish Department, 315 Astle Street, Green River, WY 82935, USA (bill.rudd@wgf.state.wy.us)

Abstract: Traditionally range distribution maps for most mammalian species have consisted of little more than a shaded polygon. Geographic Information Systems (GIS) technology offers a wide range of opportunities for displaying information about a species over a landscape scale. We have summarized pronghorn distribution data from three distinct data sets: (1) Late Quaternary archeological data (FAUNMAP Working Group database), (2) E.W. Nelson's "Status of the pronghorn antelope, 1922-1924" (1925), and (3) current range distributions and relative densities of pronghorn for the year 2000. A summary of these data suggest that prehistoric pronghorn distributions mimic current range distributions with some temporary easterly expansions during the late Holocene, pronghorn distributions in the 1920s were primarily limited to the dry steppe and semi-desert habitat types, and current range distributions and densities reiterate the importance of key habitat types. Use of GIS mapping techniques could assist in evaluating genetic variations between populations, help us understand habitat use and environmental constraints, and focus attention on management issues such as habitat fragmentation due to fences and roads. This technique may offer a simple and cost-effective approach to monitoring the status of pronghorn populations. Recommendations include a re-sampling of relative pronghorn distributions at regular intervals, using GIS technology, as a means to monitor generalized trends for pronghorn across the range of the species.

Key words: *Antilocapra americana,* pronghorn, continental range distribution, GIS technology, late Quaternary, archaeology, Canada, Mexico, United States of America.

One initial step in developing a management or research plan on any free ranging animal is the review of range maps; both for selection process of study areas and to evaluate the importance of the area to the species in general. Traditionally range distribution maps for most mammalian species have consisted of little more than a shaded polygon.   As species management

questions reach landscape levels, the scale and detail of range maps used to evaluate these issues necessitate more detailed information. Geographic Information Systems (GIS) technology offers a wide range of opportunities for displaying information about a species over a landscape scale. Additionally, GIS mapping techniques not only allows the production of "pretty maps"; it more importantly permits the display and analysis of data that previously could not be achieved without Herculean efforts. The development of GIS mapping layers for several species of big game (e.g., elk, mule deer, white-tailed deer) is currently underway; however, the GIS mapping of pronghorn *(Antilocapra americana)* range distributions has lagged behind. The intent of this project is to start the process of developing important GIS map layers, on a continental scale, for pronghorn.

The data we present was collected from a wide variety of state and federal agencies, and there are disparities in methodology, types of data, and quality of the information available. Rather than focusing on the data presented in a specific political jurisdiction or a specific management unit, we believe the primary value of this process was to collect the available information on the management unit boundaries so the information pertaining to pronghorn in these areas can be updated and improved over time.

Our initial efforts focused on available data from three specific periods in time: (1) pronghorn faunal remains found in archaeological sites dating from the late Quaternary era (FAUNMAP Working Group 1994; McCabe et al. 2004), (2) E.W. Nelson's report "Status of the pronghorned antelope, 1922-1924" (Nelson 1925), and (3) current range distributions and relative densities of pronghorn for the year 2000.

METHODS

Late Quaternary Archaeological Locations: Information on archaeological sites containing pronghorn remains was gleaned from FAUNMAP, a database documenting late Quaternary distributions of mammal species in the United States (FAUNMAP Working Group 1994). Data provided by FAUNMAP Working Group (1994) includes the archeological site name, geologic age of the site within the Quaternary period (i.e., late Wisconsin, Glacial, full Glacial, late Glacial, early Holocene, Middle Holocene, late Holocene), location (state, county, map quadrangle, latitude and longitude), and precision within the 7.5 minute series Quadrangle (exact, Quadrangle approximate, Quadrangle Precise, Quadrangle in center of county). Most locations given were Quadrangle approximates and Quadrangle precise; therefore locations provided are usually within 3.25 minutes of the actual archaeological site. In addition, the approximate locations of 23 sites in Canada and 36 sites in Mexico were added to the database from information provided in McCabe et al. (2004). The sites derived from McCabe et al (2004), and the metadata provided, lack much of the information provided in the FAUNMAP Working Group (1994) data set. Once mapped, the quadratic kernel function (ArcGIS version 9.0) allowed us to evaluate the relative density of archaeological sites containing pronghorn remains over time and space. Caution needs to be stressed when attempting to interpret the clustering and dispersion of these sites.

E. W. Nelson's Pronghorn Range Distribution (1922-24): In 1925 the U.S. Biological Survey, Department of Agriculture, published the first major survey on the continental distribution and inventory of pronghorn. Nelson (1925) contacted government trappers, provincial and state

wildlife agencies, and local experts for information on the location and numbers of pronghorn in each of the states and provinces of Canada, Mexico, and the United States. Maps provided in these reports range from the identification of very discrete populations of pronghorn in some states and provinces to the more generalized locations in other states and Mexico. In order to develop a more standardize format, Nelson's pronghorn census data was assigned on county-by-county basis for the United States, and more generalized boundaries in Canada and Mexico.

The size and shapes of political boundaries vary widely from state-to-state and country-to-country. In response Nelson's 1925 data was converted to 1:100,000 scale Quadrangles (1/2 by 1 degree in size). From these 100K quadrangles we produced maps displaying the relative pronghorn densities using the quadratic kernel function (ArcGIS version 9.0). Distribution of cluster densities was then compared to other mapping layers in order to look for repeated patterns (e.g., high density of archaeological sites vs. relative density of pronghorn in 1920s, relative density of pronghorn in 1920s vs. relative density of pronghorn in 2000).

Range Distributions and Relative Densities of Pronghorn in 2000: Wildlife professionals in each state and province (Table 1) known to have free ranging populations of pronghorn were contacted to obtain population estimates, by management unit, for the year 2000. It should be noted that size and scale of management units, as well as methods for determining population estimates (e.g., various survey methods, statistical software packages, and license sales), varied by jurisdiction. Where unavailable, management unit boundaries were digitized for Canada and the United States. Areas containing remnant populations of pronghorn in the Republic of Mexico were digitized, based on limited available information, to the best of our abilities. Year 2000 population density estimates for each management unit were than calculated and added to the metadata. Metadata also included source of information, unit name or identification number, and size of unit (i.e., square miles). Some states provided established data files with additional information. A continental GIS layer was compiled with year 2000 population estimates by management unit.

Table 1. A Summary of Information Sources and Data Type Used for 2000 GIS Map of Continental Pronghorn Range Distribution and Densities.

State or Province/ Country	Information Source	Comments
Alberta, Canada	Dale Eslinger (403-528-5205) Alberta Dept. of Environmental Protection	2000 Population Survey
Arizona, USA	Matt Alderson (602-789-3610) Arizona Game and Fish Dept.	2000 survey data. Assumed 50% observation rate. Doubled observed numbers.
California, USA	Richard Shinn & Bob Stafford (530-233-3581) California Dept. of Fish and Game	2000 Population Survey
Colorado, USA	John Ellenberger (970-255-6182) Colorado Div. of Wildlife	2000 Population Survey

Table 1. (continued).

State or Province/ Country	Information Source	Comments
Idaho, USA	Bart Butterfield (208-287-2722) Idaho Fish and Game Dept.	2000 Population Survey
Kansas, USA	Matt Peek (620-342-0658) Kansas Dept. of Wildlife and Parks	2000 Population Survey
Montana, USA	Gary Hammond (406-444-2612) Montana Fish, Wildlife and Parks	2000 pronghorn permit numbers multiplied by three to provide estimate
Nebraska, USA	Bruce Trindle (402-370-3374) Nebraska Game and Parks Commission	2000 Population Survey
Nevada, USA	Mike Cox (775-688-1556) Nevada Div. of Wildlife	2000 Population Survey
New Mexico, USA	Leland Pierce (505-476-8094) New Mexico Dept. of Game and Fish	2000 Pronghorn Management units classified as having high, medium and low densities. Based upon regional densities assigned densities of 1.0, 0.5, and 0.1 animals per sq. mile, respectively
North Dakota, USA	Bill Jensen (701-328-6637) North Dakota Game and Fish Dept.	2000 Population Survey
Oklahoma, USA	Danny Watson (806-339-5175) Oklahoma Dept. of Wildlife Conservation	2000 Population Survey
Oregon, USA	Don Whittaker (503-947-6325) Oregon Dept. of Fish and Wildlife	2000 Population Survey
Republic of Mexico	Rogelio Carrera, Graduate Student, Texas Tech. Univ. (52-612-123-8483) Jorge Cancino, Centro de Investigaciones Biologicas del Noroestes, Baja California Sur Internet Websites	Population estimates based upon several sources. Densities very low. Total population estimated to be about 1000 animals in 2000.
Saskatchewan, Canada	Al Arsenault (306-933-5797) Saskatchewan Environment	2000 Population Survey
South Dakota, USA	John Wrede (605-394-2391) South Dakota Dept. of Game, Fish and Parks	2000 Population Survey
Texas, USA	Clay Brewer (432-426-3770) Texas Parks and Wildlife Dept.	2000 Population Survey
Utah, USA	Tom Becker (801-491-5678) Utah Div. of Wildlife Res.	2000 Population Survey
Wyoming, USA	Tim Woolley (307-383-6082) Wyoming Game and Fish Dept.	2000 Population Survey

RESULTS

Late Quaternary Archaeological Locations: Archaeological sites containing pronghorn remains totaled 271 locations (FAUNMAP Working Group 1994; McCabe et al. 2004). It should be noted that one physical location may contain more than one archaeological site due to repeated

use of the same area over time. For this report, archaeological sites were lumped into four geological ages of the late Quaternary period: (1) late Wisconsin (10,000 to 40,000 ybp; N= 14) and Glacial (10,000 to 20,000 ybp; N= 2 sites) (Figure 1), (2) full Glacial (15,000 to 20,000 ybp; N= 1 site) and late Glacial (10,000 to 15,000 ybp; N=13 sites) (Figure 2), (3) early Holocene (8,000 to 10,000 ybp; N=13 sites) and middle Holocene (4,000 to 8,000 ybp; N= 32 sites) (Figure 3), and (4) late Holocene (500 to 4,000 ybp; N= 182 sites) (Figure 4). All prehistoric archaeological sites containing pronghorn remains are presented in Figure 5. Pronghorn remains found in historic sites (500 ybp to present) were not included in this data set. Of the 271 archaeological sites containing pronghorn 30 were within the state of Wyoming. Additionally, a number of archaeological sites dating from the late Holocene extend outside the historic distributions of this species and into the states of Arkansas, Iowa, Missouri, Oklahoma, Nebraska, and Washington.

E. W. Nelson's Pronghorn Range Distribution (1922-24): Nelson's (1925) map is displayed in Figure 6. When converted to 100k quadrangles (Figure 7), and processed using to quadratic kernel function (ArcGIS version 9.0)(Figure 8), four attributes of the 1922-24 pronghorn densities and distributions stand out; (1) the importance of dry steppe and semi-desert provinces of Bailey's Ecoregions (Bailey 1980), (2) the influences of natural barriers such as major rivers and mountains, (3) the location of small isolated remnant and/or vulnerable pronghorn populations (e.g., Mexico, southern California, south Texas, and Saskatchewan), and (4) the location of important and relatively high density pronghorn range in Wyoming and northwestern Nevada-southeastern Oregon-northeastern California.

Range Distributions and Relative Densities of Pronghorn in 2000: The 2000 pronghorn distribution and relative density map reiterates several of the points mentioned above for Nelson's (1925) map (Figures 9 and 10). These include: (1) the importance of dry steppe and semi-desert provinces of Bailey's Ecoregions, (2) the influences of natural barriers such and major rivers and mountains, (3) the location of small isolated remnant and/or vulnerable pronghorn populations (e.g., California, Mexico, Texas, and Saskatchewan), and (4) the location and relative important of high density pronghorn range in Wyoming and northwestern Nevada-southeastern Oregon-northeastern California. One notable observation is that while current pronghorn distributions and numbers have rebounded from the lows reported in Nelson's (1925) map for much of the continent, the southern distribution of pronghorn has apparently continued to decline. This is particularly true for the Republic of Mexico, southern California, and southeastern Texas (i.e., Brooks, Hidalgo, Jim Hogg, and Webb counties).

Fig. 1. Location of archaeological sites, dating from the Late Wisconsin and Glacial ages of the Pleistocene (10,000 to 40,000 ybp; N= 16), containing pronghorn faunal remains (FAUNMAP Working Group. 1994; McCabe et al. 2004).

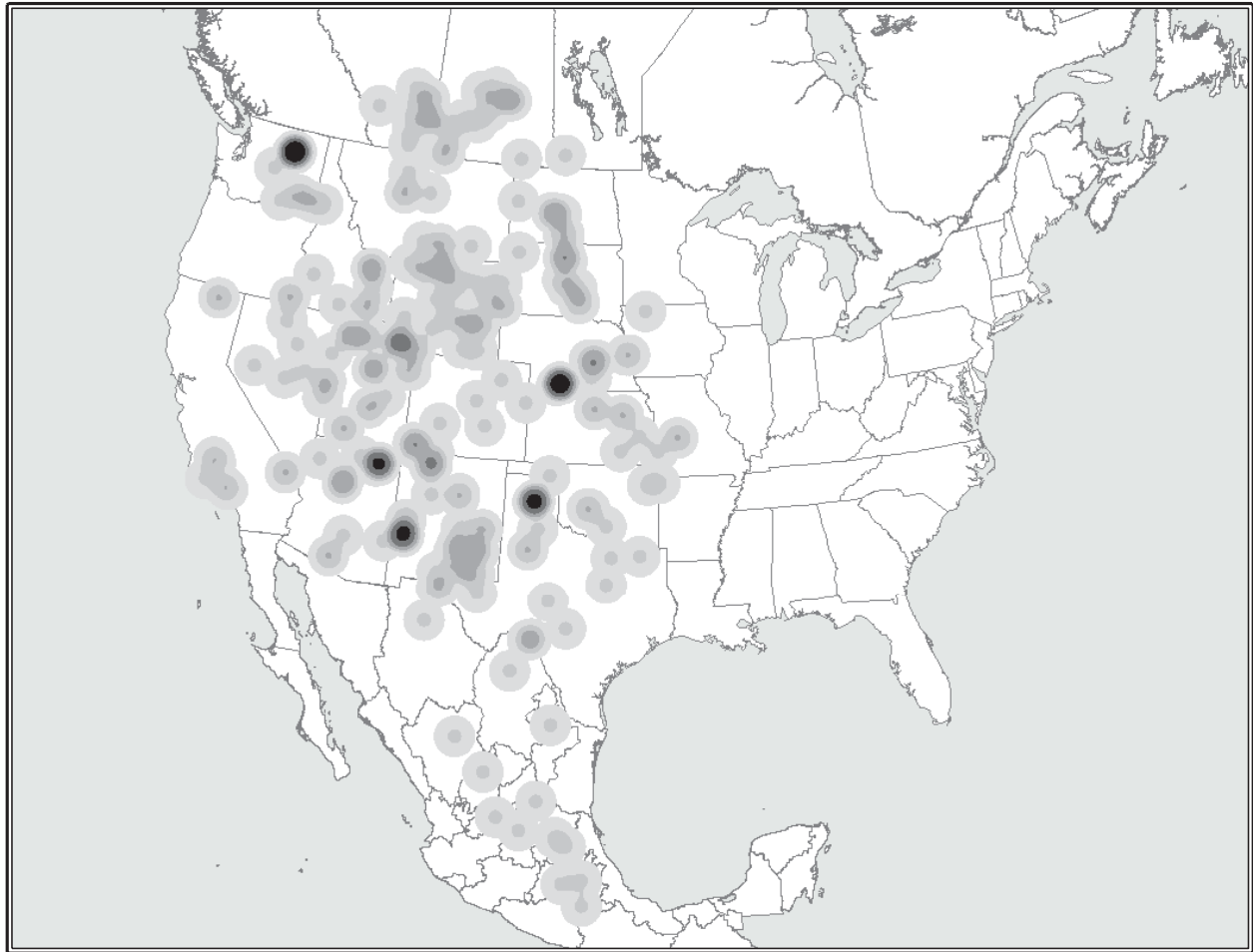**Fig. 2.** Location of archaeological sites, dating from the Full Glacial and Late Glacial ages of the Pleistocene (10,000 to 20,000 ybp; N= 14), containing pronghorn faunal remains (FAUNMAP Working Group. 1994; McCabe et al. 2004).

Fig. 3. Location of archaeological sites, dating from the Early Holocene and Middle Holocene ages (4,000 to 10,000 ybp; N= 45), containing pronghorn faunal remains (FAUNMAP Working Group. 1994; McCabe et al. 2004).

Fig. 4. Location of archaeological sites, dating from the Late Holocene age (500 to 4,000 ybp; N= 182), containing pronghorn faunal remains (FAUNMAP Working Group. 1994; McCabe et al. 2004).

Fig. 5. Location of all archaeological sites, dating from the Pleistocene and Holocene ages (500 to 40,000 ybp; N= 271), containing pronghorn faunal remains (FAUNMAP Working Group. 1994; McCabe et al. 2004). Quadratic kernel function method used to evaluate the distribution and clustering of these sites within a 100 km search radius.
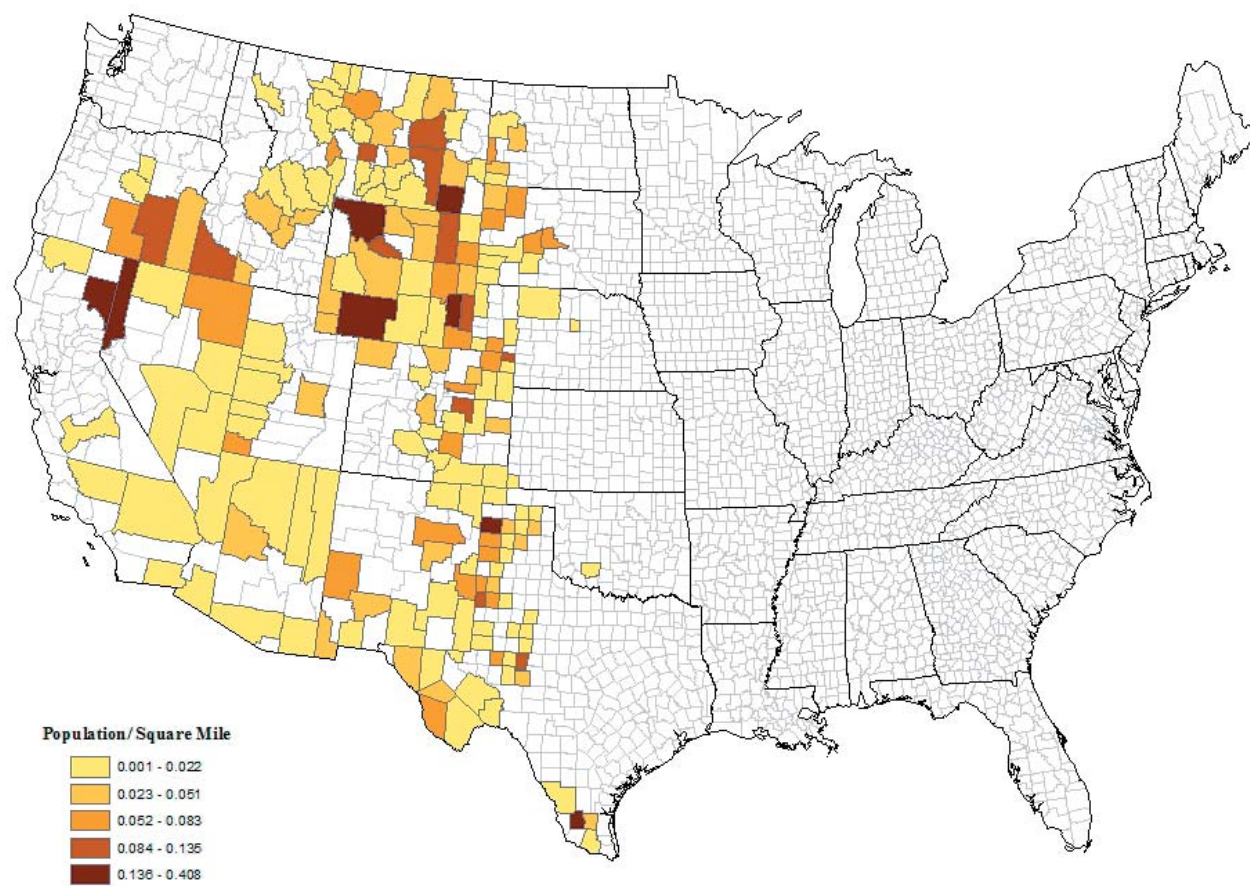
Fig. 6. Relative density of pronghorn populations across the continent in 1922-24, by counties in the United States based upon information provided in Nelson (1925).
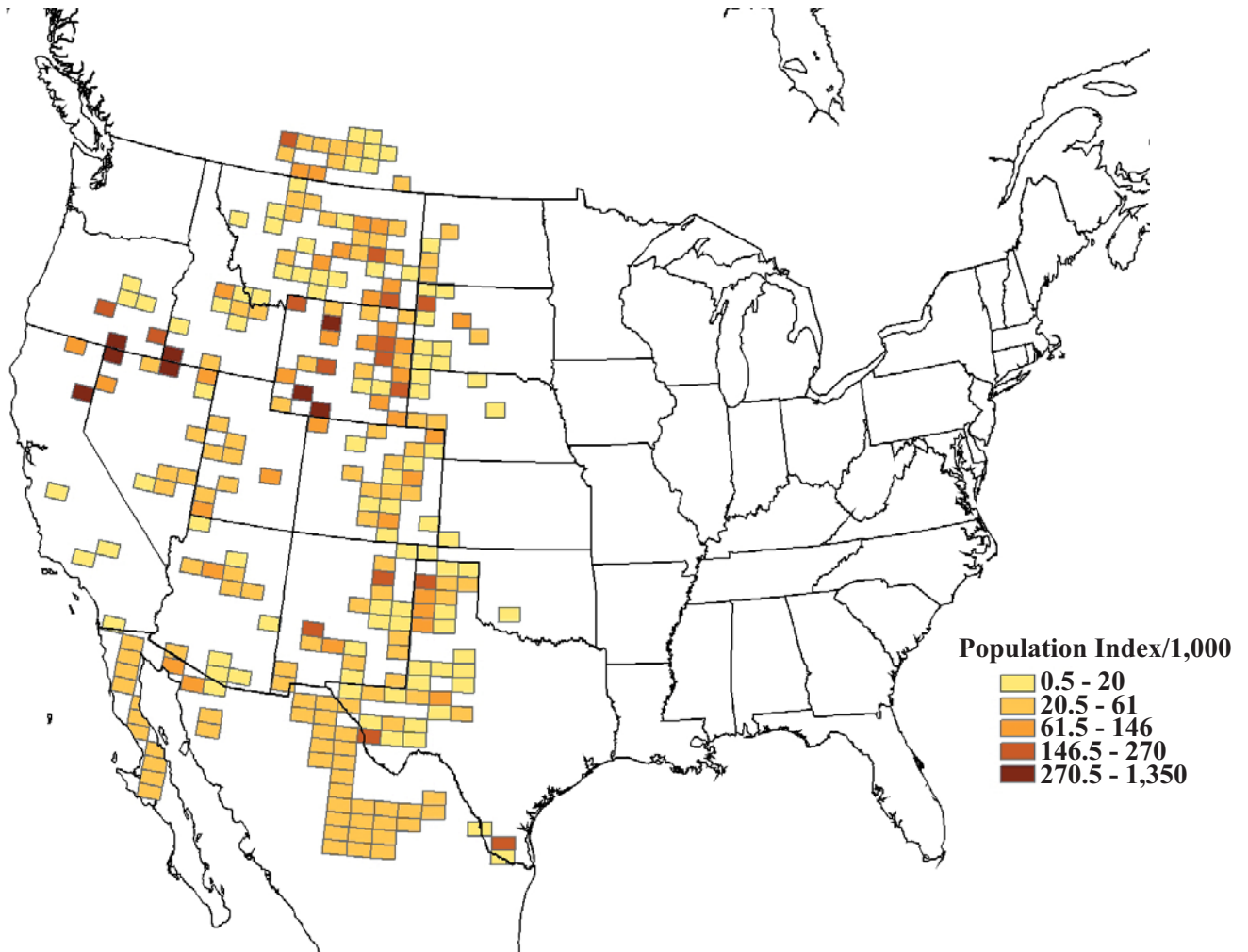
Fig. 7. Relative density of pronghorn populations across the continent in 1922-24, based upon information provided in Nelson (1925). Data presented in Figure 6 and more generalized polygons in Canada and Mexico was converted, via GIS programming, to 100K quadrangles (1/2 by 1 degree in size).
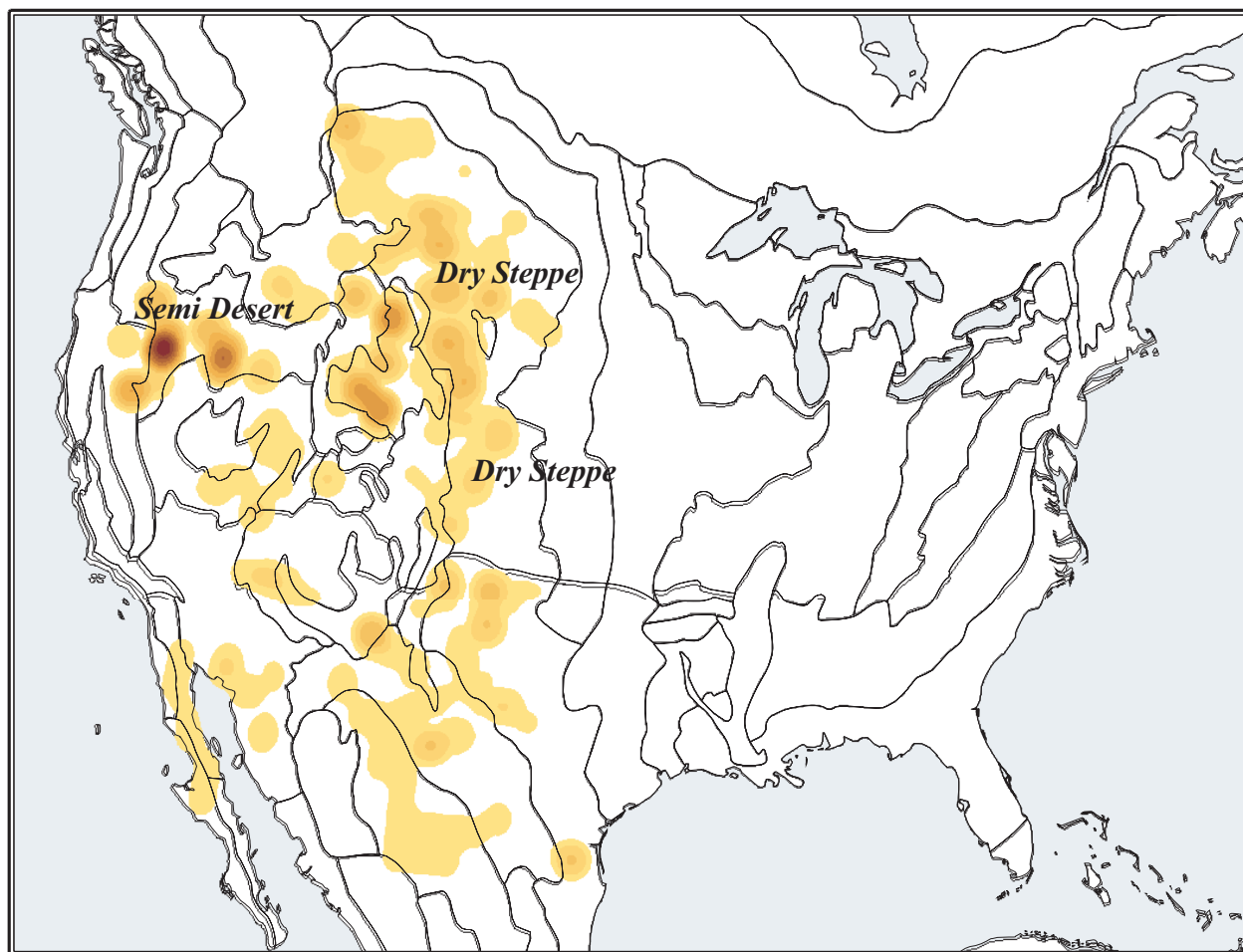
Fig. 8. Relative density of pronghorn populations across the continent in 1922-24, based upon information provided in Nelson (1925). Data presented in Figure 7 converted, via GIS programming, to quadratic kernel function analysis (point matrix at 1/2 degree intervals). Polygons denote boundaries of Bailey's Ecoregions; with densest clustering within the eastern dry steppe, and the western semi-desert provinces.
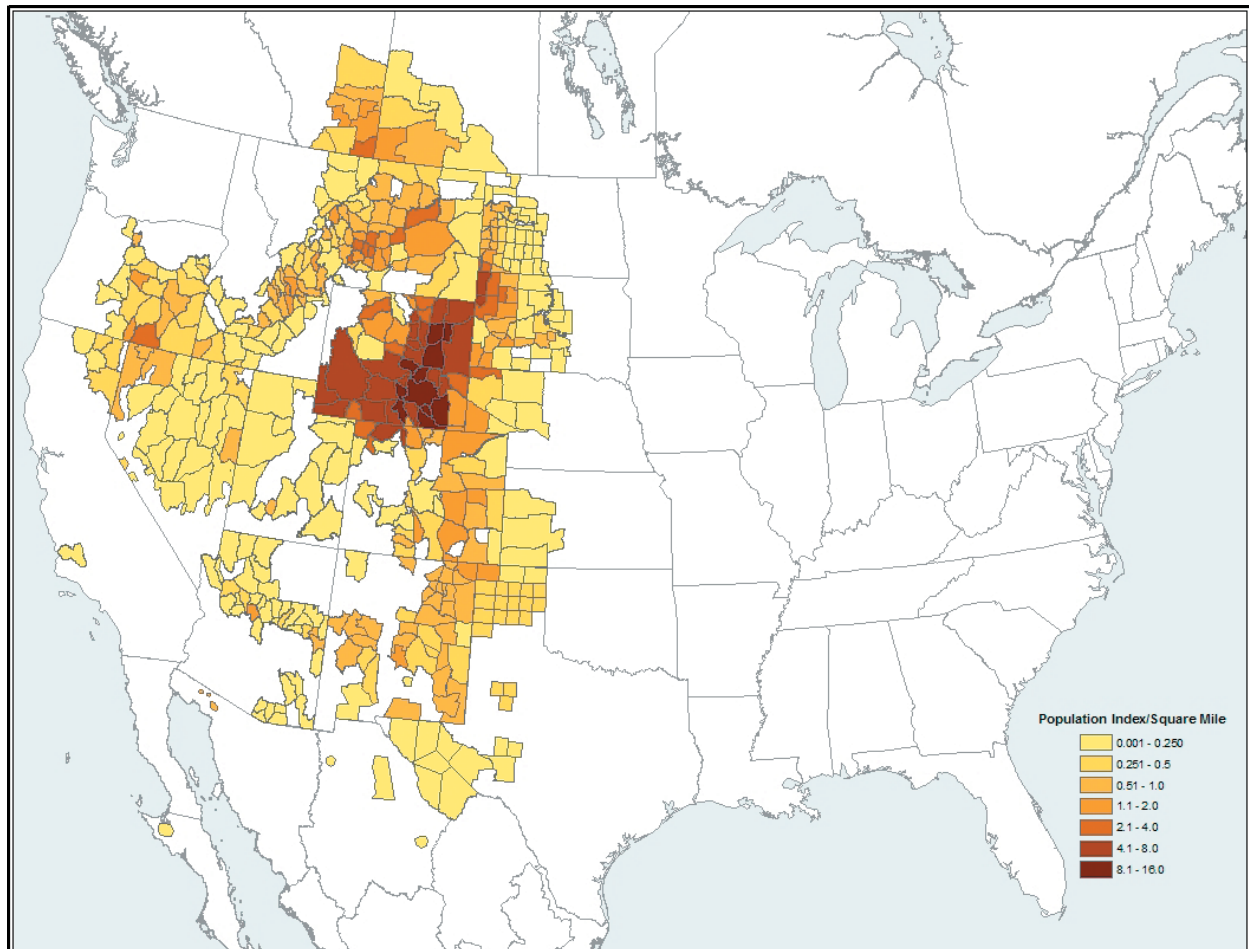
Fig. 9. Relative density of pronghorn populations across the continent for year 2000, based upon information provided by contributors in listed in Table 1. Pronghorn management units in Canada and the United States were used for polygon boundaries. More generalized polygons were used for boundaries in Mexico.
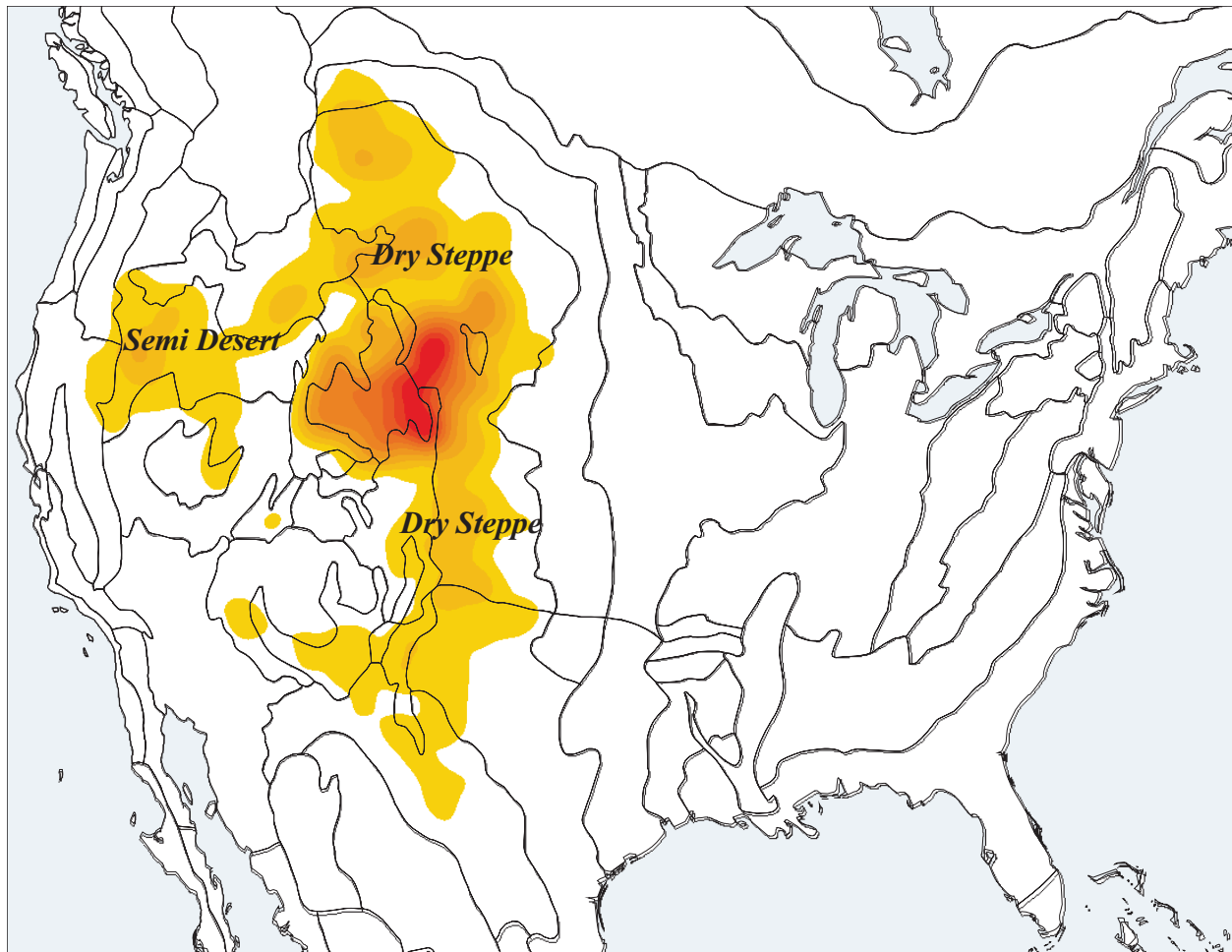
Fig. 10. Relative density of pronghorn populations across the continent for year 2000, based upon information provided by contributors in listed in Table 1. Data presented in Figure 9 was converted, via GIS programming, to quadratic kernel function analysis (point matrix at 1/2 degree intervals). Polygons denote boundaries of Bailey's Ecoregions; again with densest clustering within the eastern dry steppe, and the western semi-desert provinces.

DISCUSSION

Late Quaternary Archaeological Locations: Based upon information recorded for 2,919 archaeological sites evaluated by the FAUNMAP Working Group (1994), a total of 234 Pre-Columbian archaeological sites containing pronghorn bones were identified and mapped within the contiguous 48 United States(>500 ybp). McCabe et al. (2004) identifies 23, 36, and 234 archaeological sites containing pronghorn remains in Canada, Mexico, and the United States of America, respectively. Our data set contains 271 sites. Walker (2000) reported 357 archaeological sites of all ages containing pronghorn bones were identified and map within the contiguous 48 United States; with 49 being Post-Columbian in age (<450 ybp). Lack of information on archaeological sites from Canada and the Republic of Mexico, as well as the discrepancy of 74 sites identified by Walker (2000) in the United States, are weaknesses of this data set.

Although GIS technology allows for the evaluation of the relative density of archaeological sites across the landscape, caution is warranted when interpreting our results. Presence of pronghorn remains usually just consists of one or two individuals. Closely concentrated sites often denote long-term occupation of a site (i.e., caves) or Plains Farmer and other village sites along river systems. Additionally, it is not beyond the realm of possibility that these early hunters may have saved and moved the jaws or skulls of an animal unique to their experience.

Archaeological sites containing pronghorn remains that are located outside the current range distribution are primarily found along the eastern edge of the Great Plains and central Mexico. The loss of pronghorn from much of the Mexican range is most likely due to excessive human exploitation (O'Gara and McCabe 2004). However, loss of pronghorn from their eastern Pre-Columbian range may be due to temporary changes in climate. During the middle and late Holocene (8,500 to 500 ybp) the Great Plains experienced a prolonged period of drought conditions, accompanied by associated vegetative changes (Wendland et al.1987). These climate and vegetation changes during the late Holocene led to the temporary eastern expansion of pronghorn range as far east as Arkansas and Missouri (Walker 2000).

There are 12 archaeological sites containing pronghorn bonebeds (i.e., five or more individual pronghorn represented); of which six are located in the Great Basin region of southwestern Wyoming (Lubinski 1999). It is interesting to note that evidence of communal hunting was apparently increasing about 700 ybp (Lubinski 2000), and that several of these sites are located along seasonal pronghorn migration routes that would have provided the Indian inhabitants of the area some level of predictability for organizing and timing a hunt (Miller and Sanders 2000; Sanders 2000). At other sites (e.g., pits and enclosures) early hunters took advantage of natural barriers provided by the landscape features such as the convergence of drainage systems (Sundstrom 2000). Additionally, the relative abundance of other big game species also played a role in the amount of effort put into hunting pronghorn (McCabe et al. 2004). We also need to remember that the presence and type of faunal remains found in archaeological sites are also dependent upon the relative distribution and activities of pre-Columbian American Indians, and where archaeologists have looked.

Captain William Clark noted in his journal (August 29, 1806) "with regard to game in general, we observe that the greatest quantities of wild animals are found in the country lying between two nations at war" (Martin and Szuter 2002). Martin and Szuter (2002) "view humans as a crucial variable influencing the range of terrestrial megafauna at any time, past or present". However, these views of late prehistoric and early historic game sources and sinks are not universally accepted (Lyman and Wolverton 2002). Additionally, that portion of eastern Montana that is referred to as a war zone for neighboring hostile tribes, supported high pronghorn densities in both Nelson's (1925) map and the our 2000 map. It is interesting to note that in the eastern half of Montana, a region where both Nelson's 1925 and our current 2000 mapping effort suggest relatively high pronghorn densities, there have been few archaeological sites excavated, with only four sites containing pronghorn remains (FAUNMAP Working Group 1994). This region was reported by Lewis and Clark to support high populations of Bison (Bison bison), elk (Cervus elaphus), deer (Odocoileus spp.), as well as pronghorn (Martin and Szuter 2002; McCabe et al. 2004).

In contrast, pre-Columbian Indians on the Plateau region of eastern Washington based their economy on fish, gathering wild plants, and limited big game hunting. Prior to European settlement, bison and bighorn sheep (Ovis canadensis) were not found in this region, and mule deer numbers were limited (McCabe et al. 2004). Pronghorn numbers in Washington were relatively low in post-Columbian times, yet 17 archaeological sites in Washington contained pronghorn remains (11 at Chief Joseph Dam, along the Columbia River) (FAUNMAP Working Group 1994). On their trip west, Lewis and Clark reported (October 11, 1805) that local Indian tribes hunted pronghorn on both sides of the Snake River near the confluence with the Clearwater River (McCabe et al. 2004). During their return trip (April 27, 1806), Clark stated that the Walla Walla Indians reported plenty of pronghorn in the area (McCabe et al. 2004), perhaps in the war zone south of the Columbia River (Martin and Szuter 2002). It is, however, plausible that a hunter-gather society in eastern Washington, based heavily on a fishing economy and coupled with the aid of horses and trade rifles, could extirpate a marginal pronghorn population in what is now the state of Washington. The barrier of Columbia and Snake Rivers would greatly limit re-colonization of the area by southern herds. Therefore, the prehistoric and modern pronghorn distribution maps appear to provide evidence for both sides of this debate.

E. W. Nelson's Pronghorn Range Distribution (1922-24): Despite its limitations, Nelson's map provides a unique snapshot in time regarding continental pronghorn distributions. The loss of pronghorn in southern Texas, and the dramatic decline in pronghorn range in southern California point out the vulnerability of this species to extirpation despite conservation efforts. It is not surprising that the pronghorn populations in the Republic of Mexico, with limited resources available to devote to wildlife conservation and enforcement, have suffered continual population declines since the 1920s. The southern declines may reflect larger trends for pronghorn inhabiting the most southern extent of their range. Nelson's (1925) map also reinforces the importance of dry steppe and semi-desert habitat types, and the influences of natural barriers such and major rivers and mountains on pronghorn densities and distributions.

Range Distributions and Relative Densities of Pronghorn in 2000: The 2000 map reiterates points and concerns raised by Nelson's (1925) map (i.e., the importance of specific habitat types, and natural barriers). An obvious weakness of the data set is the lack of information in a number of states about pronghorn numbers within Indian Reservations and military installations. The map does provide another snapshot in time, and the basis for making broad generalizations about "potential" pronghorn numbers within areas not surveyed. For example, based upon densities in surrounding management units in Arizona and Utah, the 32,000 square mile Hopi and Navajo reservations in northeastern Arizona, northwestern New Mexico, and southeastern Utah (no current information available) may on average hold the potential of supporting about 0.1 pronghorn per square mile or roughly 3,200 pronghorn. This crude estimate equates to about 30% of Arizona estimated pronghorn population.

This range-wide approach may be useful for long term tracking of pronghorn populations. It could be used for the identification of habitat loss or shifts in habitat quality. In addition, it may help identify segments of the populations that have either become fragmented or are in danger of becoming so. This GIS approach may also useful for the identifications of environmental factors or impacts that are affecting pronghorn on a range-wide basis such as drought, habitat fragmentation, or even energy development. GIS technology provides for a range of scales of analyses as well as the ability to incorporate new layers of information.

Future Uses of the Database: As previously mentioned, a variety of methods, survey techniques, and software packages were used to derive the reported pronghorn population estimates. We need to keep in mind that each estimate has its own inherent variability, strengths and weaknesses. However, the information presented is the best currently available regarding the unit-by-unit continental density and distribution of pronghorn. We believe the real value of GIS mapping pronghorn range will not come from what we have done, but from the refinements and development of the database by others. The Western States and Provinces Mule Deer Mapping Project (CD made available March 2005, Utah State University RS/GIS Laboratory) can serve as the basis for what this database can become.

Landscape scale management questions could be addressed efficiently and accurately using this approach. Future use and refinement of this data could be used to answer questions such as: (1) where are the information gaps about pronghorn across their range distribution, (2) where transplants may or may not be warranted (e.g., southern Texas and Washington), (3) where were there potential genetic bottlenecks for pronghorn populations, (4) where are states dealing with similar habitat and biological issues influencing pronghorn populations, (5) how human-caused activities, such as coal-bed methane development, subdivisions, and fence barriers are affecting regional pronghorn distributions, and (6) what areas support high and low fawn recruitment rates? By probing for patterns, on a landscape scale, future research may be able to better focus on what factors may be influencing demographic characteristics of these populations. We recommend that the IAFWA update this database on a regular basis (<10 year intervals), and that a permanent website be found to maintain this database. The Biennial Pronghorn Workshop might be a logical group to assist with this recommendation.

The North Dakota Game and Fish Department has agreed to store and provide access for to this data for researchers and managers on a temporary basis. We hope this database will find wider use and applications to improve research and management of pronghorn across the continent.

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GENETIC CONSEQUENCES OF REINTRODUCTIONS: AN EXAMPLE FROM PRONGHORN ANTELOPE IN OREGON

CATHERINE L. STEPHEN, Department of Forestry and Natural Resources, Purdue University, West Lafayette, IN 47907, USA.

DONALD G. WHITTAKER, Oregon Department of Fish and Wildlife, 3406 Cherry Avenue NE, Salem, OR 97303, USA.

DON GILLIS, Umatilla Army Chemical Depot, Hermiston, OR 97838

LINDSEY L. COX, Department of Forestry and Natural Resources, Purdue University, West Lafayette, IN 47907, USA.

OLIN E. RHODES, JR., Department of Forestry and Natural Resources, Purdue University, West Lafayette, IN 47907, USA.

Abstract: Seventeen pronghorn were reintroduced onto Umatilla Army Base in Oregon 41 years ago with no subsequent translocations or immigration into this fully enclosed area. We explored the genetic signature this event left on the population using a combination of microsatellite genotypes and mtDNA sequencing data. We compared the present day Umatilla herd to its source population and a southeastern Oregon population we felt was distinct. We found the reintroduced population had sharply lower genetic diversity compared to its source. Additionally, there was significant haplotypic and genotypic differentiation between the reintroduced population and its source (GST = 0.063, FST = 0.079) that was approximately 3.5 times that found between the source and the southeastern population (GST = 0.018, FST = 0.021). The Umatilla population increased rapidly after its initial founding event providing an opportunity to retain much of its original genetic diversity. Thus, it is likely the observed loss of diversity was primarily a function of the low number of founders and stochastic losses of diversity in subsequent generations rather than a prolonged bottleneck. The founding effect, stochastic shifts in allele frequencies each generation, restricted gene flow, and variance in the segregation of alleles related to a polygamous mating system have contributed to the significant differentiation observed between the Umatilla herd and its source.

ELK AS A FACTOR AFFECTING PRONGHORN PRODUCTIVITY AND POPULATION LEVELS ON ANDERSON MESA, ARIZONA

DAVID E. BROWN, Department of Life Sciences, Arizona State University, PO Box 874501, Tempe, AZ 85287, USA, E-Mail Address: debrown@imap3.asu.edu

WILLIAM FAGAN, Department of Biology, University of Maryland, College Park, MD 20742, USA

JULIA LOUIE, Department of Biology, University of Maryland, College Park, MD 20742, USA

HENRY PROVENCIO, U. S. Forest Service, Coconino National Forest, Mormon Lake Ranger District, Flagstaff, AZ. 86001, USA

Abstract: Pronghorn (*Antilocapra americana*) rarely if ever remove sufficient forage to affect cattle, and ever since Bűechner (1950) reported "overgrazing by cattle appears to have little effect upon the pronghorn," wildlife managers have stressed the compatibility of the 2 species. Although pasturing of domestic sheep has been shown to sometimes be detrimental to pronghorn (Yoakum et al.1995), effects of expanding populations of large, wild ungulates on pronghorn remain relatively uninvestigated. We addressed this knowledge gap, by examining possible effects of a rapidly expanding elk (*Cervus elaphus*) population on a declining pronghorn population on Anderson Mesa, Arizona. We found a strong negative (r^2=0.41, $p<0.001$) correlation between estimated elk biomass and pronghorn productivity independent of rainfall and other variables. This correlation, together with data from other semiarid, grassland areas, could suggest that expanding populations of large, wild ungulates may result in a reduction in pronghorn population levels, and that the decline in pronghorn productivity on Anderson Mesa may have been due to an insufficient quantity of quality vegetation, particularly during late winter and early spring.

No area in Arizona is associated with pronghorn antelope as much as Game Management Unit 5, which includes Anderson Mesa. Three of the top 5 pronghorn trophies in the 11th edition of the Boone and Crockett Club's "Records of North American Big Game" (Beyers and Bettas 1999) are from Coconino County which contains Anderson Mesa. More than 25% of all pronghorn in the "Millennium" edition of the Arizona Wildlife Federation's trophy book (Lewis 2000) either came from Anderson Mesa, or from areas restocked with animals from Anderson Mesa. Anderson Mesa was the site of the state's first legal pronghorn hunt in 1941, and has been a focal point for pronghorn research since the 1950s (e.g., Arrington and Edwards 1951, Neff and Woolsey 1980, Gay 1984, Neff et al. 1985).

Anderson Mesa and surrounding habitats have been heavily grazed by cattle and sheep since the early 1880s. Nelson (1925) estimated <100 pronghorn as occupying Anderson Mesa in 1923, due primarily to unregulated hunting. At the same time, local newspapers such as the Flagstaff *Champion* were reporting a near cessation of large scale range fires. Then, concurrent with legal protection, reduced livestock grazing, predator control, and high fur prices, pronghorn numbers rebounded until the population was estimated at between 4,000 and 5,000 animals (U.S.Forest Service annual reports; Appendix 1). As the population recovered, legal hunting was resumed on this portion of the Coconino National Forest with annual harvests ranging from >500 animals during good years to none during hunt closures (Appendix1).

Pronghorn productivity and population trends on Anderson Mesa have fluctuated since 1950. But despite juniper (*Juniperus* spp.) control projects, intermittent coyote *(Canis latrans)* control, and cessation of sheep grazing, pronghorn numbers have generally decreased since 1960 due to poor fawn survival (Neff and Woolsey 1979, 1980). After some initial success at increasing fawn survival by aerial gunning coyotes prior to the fawning season (Neff et al. 1985), pronghorn productivity declined severely after 1985, prompting demands for reduced livestock numbers, more intense predator control, and increased juniper clearing. Yoakum (2003), however, determined that the most pressing concerns regarding the ability to sustain historic populations of pronghorn on Anderson Mesa were unhealthy vegetation conditions, and the inadequacy of existing vegetation relative to pronghorn requirements for nutritious forage and fawn concealment. He considered these deficiencies to be the result of various ecological factors including insufficient precipitation, wildfire suppression, encroachment by woody plants, changes in forage composition, and especially, intense competition for nutritious forage with wild and domestic ungulates.

Although both cattle and elk were potential competitors with pronghorn for forage, we were particularly interested in evaluating the possible effects of elk competition due to greatly increased elk numbers after 1980 and a series of mild winters that allowed elk to concentrate on Anderson Mesa during late winter and early spring. We realized that livestock numbers, while less variable during this period, influenced the effects of forage consumption by elk in that any competition measured would be cumulative to the effects of cattle. Hence, we also tested relative correlation of pronghorn productivity with all of the large ungulates present. Should a significant correlation between pronghorn productivity and ungulate numbers exist, we hypothesized that significant increases in ungulate competition might also influence other species such as mule deer *(Odocoileus hemionus),* and that influxes of elk and other large wild ungulates might measurably impact pronghorn populations elsewhere.

STUDY AREA

Nearly all of the 1,950 to 2,200 m. high plateau, commonly referred to as Anderson Mesa, is contained within the boundaries of the Coconino National Forest (Figure 1). This 1,036 km² (400 mi²) study area of volcanic basalt, a rocky substrate commonly referred to as *malpai* or "bad lands, " includes 11 major grazing allotments, in which Forest Service personnel monitor range conditions and regulate livestock numbers. Those areas in Unit 5 below 1950 m are a checkerboard of state and private lands. All of Unit 5 is subjected to livestock grazing, and range conditions, while variable from year to year, and allotment to allotment, have suffered from a notice-
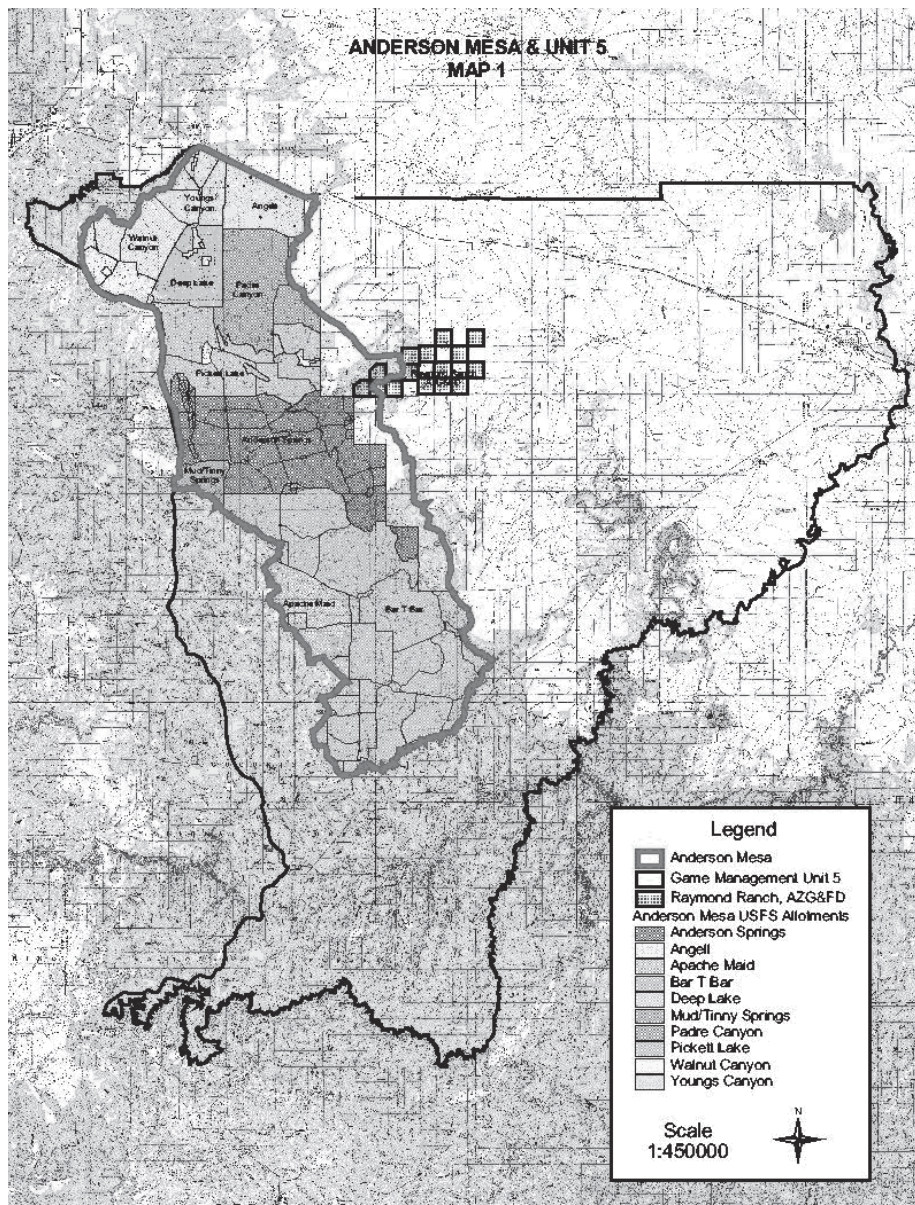
Fig. 1. Anderson Mesa and Game Management Unit 5.

able encroachment of woody species as determined from time-lapse photography and vegetation maps (Richard Miller, Arizona Game and Fish Department, personal communication). There have been no sheep in the unit since 1962.

Named after an early settler, Anderson Mesa receives an annual average precipitation of about 50 cm (19.5 in), and the primary vegetation is intermountain grassland (Brown 1994) interspersed with stands of ponderosa pine (*Pinus ponderosa*) and pinyon (*Pinus edulis*)-juniper woodland. Perennial streams are lacking, and natural water sources are limited to a few springs and numerous intermittent lakes supporting herbaceous vegetation. In addition to pronghorn, Anderson Mesa is an important area for mule deer and wild turkey (*Meleagris gallopavo*), and since 1970, home to 1 of Arizona's premier elk herds.

Mean minimum temperatures at Mormon Lake and Flagstaff are about -1ºC and the mean January minimum is -9ºC. On average only 99, frost-free days occur annually (Koss et al. 1988). A majority of the precipitation comes during the months of October through March, and snow occurs regularly. Winter temperatures can be severe and, at least in some years, most of the pronghorn on Anderson Mesa appear to move east and northward off the Mesa to lower elevations where other pronghorn are present (Richard Ockenfels, Arizona Game and Fish Department, personal communication). Significant winter mortality of pronghorn has nonetheless been recorded on the winter range, the lowest elevations of which barely exceed 1,500 m. (Arrington and Edwards 1951, White 1969). In addition to varying numbers of pronghorn, elk, deer, and cattle being seasonally present on Anderson Mesa, these same species are also found on the "winter range" where bison are year-long residents on the fenced 60 km² Raymond Ranch Wildlife Management Area (Table 1) operated by the Arizona Game and Fish Department (AGFD).

Although not all of the pronghorn in Unit 5 fawn on Anderson Mesa, most of the Mesa's pronghorn are contained within this 4,488 km² (1,733 mi²) unit (Fig. 1). In addition to conducting aerial surveys and collecting harvest data for pronghorn in this area since 1950, the AGFD conducts annual surveys in Unit 5 for elk, mule deer, bison, and turkey. Although survey procedures have varied over time, sufficient samples have usually been available to provide indices to productivity and population trends (Figures 2 and 3).
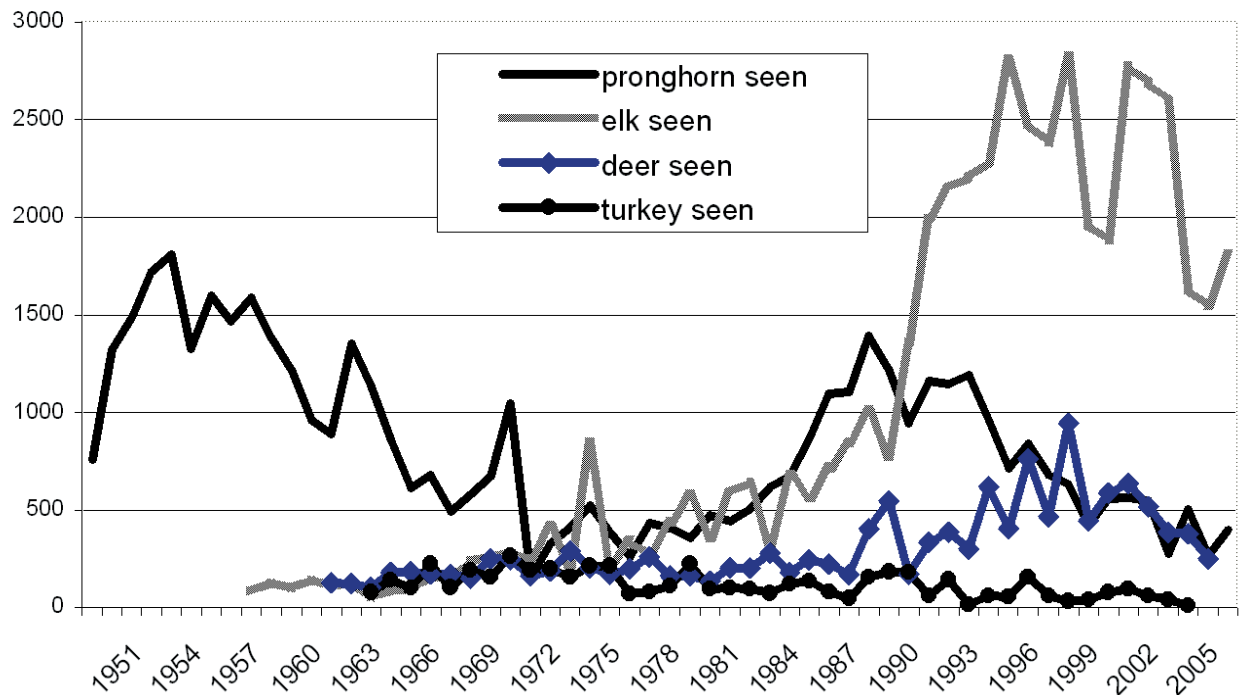

Fig. 2. Pronghorn, elk, mule deer and turkeys seen in Unit 5, Arizona 1950-2003
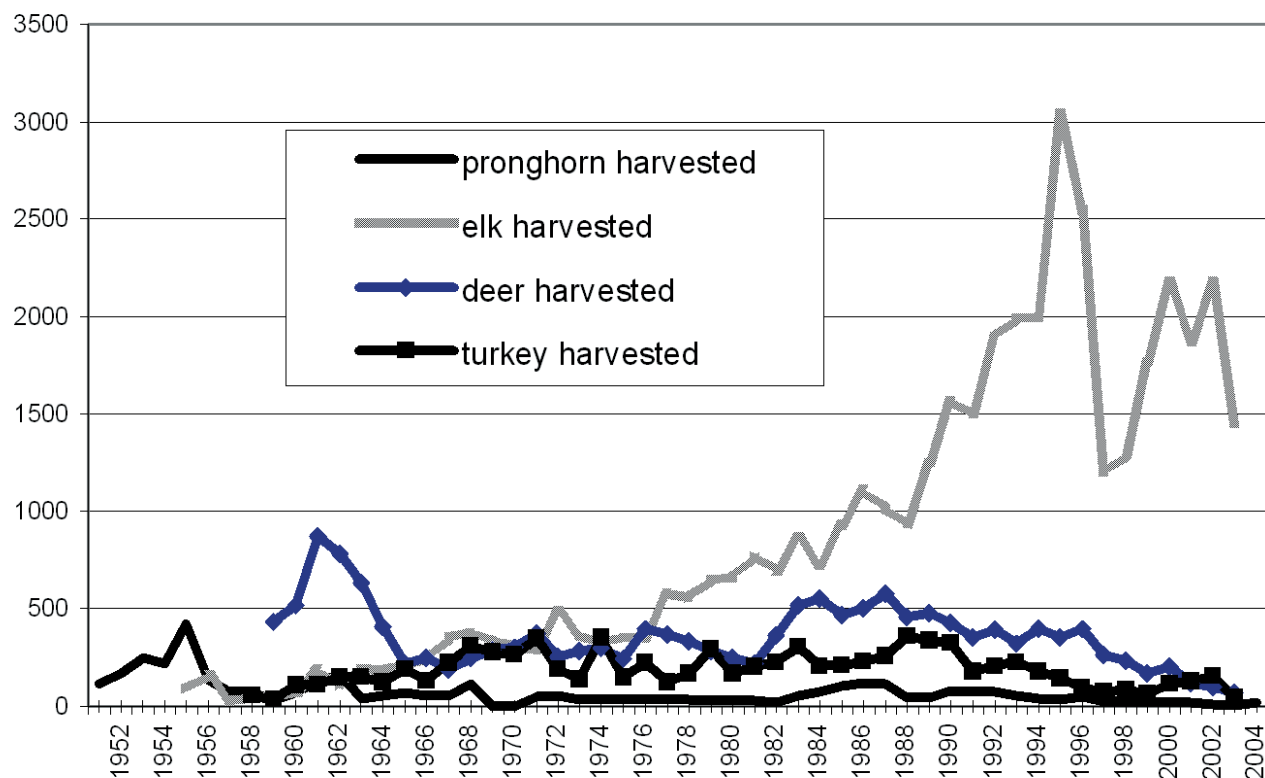
Fig. 3. Pronghorn, elk, mule deer and turkeys harvested in Unit 5, Arizona 1950-2003

METHODS

To identify trends in ungulate numbers we calculated population estimates for all of the ungulates present in unit 5 since 1950 (Table 1). After consultation with Tom Britt (retired Arizona Game and Fish Department Region II Supervisor) we based these estimates on the approximations that:

1. 70% of the pronghorn in Unit 5 are seen on surveys each year,
2. 17% of the elk in Unit 5 are harvested each year, and
3. 50% of the buck mule deer population is harvested each year and the mean buck:doe ratio is 1:6.

Table 1. Estimated pronghorn, elk, mule deer, bison, cattle and sheep populations and biomass for Game Management Unit 5, 1950, 2002.

Year	No. of Prong.	Pronghorn Biomass in 100 Kg	Est. elk per AGFD model	Est. # Elk	Elk Biomass in 100 kg	Est. # Deer	Deer Biomass in 100 kg	Bison	Bison Biomass in 100 kg	Cattle	Cattle Biomass in 100 kg	Sheep	Sheep Biomass in 100 kg	Total Biomass in 100 kg
2002	380	169	8184	7,240	17,231	804	482	88	393	5,289	25,810	0	0	44,085
2001	719	320	9192	10,890	25,918	1,356	814	100	447	7,496	36,580	0	0	64,079
2000	400	178	10828	9,340	22,229	1,440	864	90	402	7,729	37,718	0	0	61,391
1999	780	347	11464	10,905	25,954	2,400	1,440	92	411	7,668	37,420	0	0	65,572
1998	809	360	10970	8,825	21,004	1,968	1,181	103	460	7,608	37,127	0	0	60,132
1997	796	354	10274	6,435	15,315	2,796	1,678	92	411	7,150	34,892	0	0	52,650
1996	601	267	10493	5,975	14,221	3,144	1,886	71	317	7,094	34,619	0	0	51,310
1995	909	405	11685	12,730	30,297	4,752	2,851	85	380	7,428	36,249	0	0	70,182

Table 1. (continued).

Year	No. of Prong.	Pronghorn Biomass in 100 Kg	Est. elk per AGFD model	Est. # Elk	Elk Biomass in 100 kg	Est. # Deer	Deer Biomass in 100 kg	Bison	Bison Biomass in 100 kg	Cattle	Cattle Biomass in 100 kg	Sheep	Sheep Biomass in 100 kg	Total Biomass in 100 kg
1994	973	433	12804	15,215	36,212	4,224	2,534	113	505	7,367	35,951	0	0	75,635
1993	1199	534	12647	9,970	23,729	4,776	2,866	116	519	7,306	35,653	0	0	63,300
1992	1017	453	11696	9,950	23,681	3,852	2,311	119	532	7,247	35,365	0	0	62,342
1991	1377	613	11268	9,480	22,562	4,716	2,830	114	510	7,389	36,058	0	0	62,573
1990	1699	756	10218	7,485	17,814	4,212	2,527	111	496	7,893	38,518	0	0	60,112
1989	1637	728	10141	7,820	18,612	5,136	3,082	113	505	5,995	29,256	0	0	52,182
1988	1659	738	9565	6,235	14,839	5,724	3,434	116	519	6,087	29,705	0	0	49,235
1987	1354	603	5437	4,665	11,103	5,484	3,290	113	505	6,186	30,188	0	0	45,688
1986	1736	773	5938	5,095	12,126	6,912	4,147	109	487	6,291	30,700	0	0	48,233
1985	1986	884	6439	5,525	13,150	6,012	3,607	107	478	6,392	31,193	0	0	49,312
1984	1581	704	5402	4,635	11,031	5,604	3,362	107	478	6,493	31,686	0	0	47,261
1983	1566	697	4213	3,615	8,604	6,636	3,982	93	416	6,595	32,184	0	0	45,881
1982	1233	549	5029	4,315	10,270	6,228	3,737	89	398	6,697	32,681	0	0	47,634
1981	963	429	4044	3,470	8,259	4,344	2,606	91	407	6,798	33,174	0	0	44,875
1980	880	392	4499	3,860	9,187	2,604	1,562	103	460	6,900	33,672	0	0	45,273
1979	720	320	3840	3,295	7,842	2,976	1,786	97	434	7,332	35,780	0	0	46,162
1978	634	282	3770	3,235	7,699	3,432	2,059	96	429	6,988	34,101	0	0	44,571
1977	674	300	3246	2,785	6,628	3,984	2,390	120	536	7,379	36,010	0	0	45,865
1976	510	227	3347	2,875	6,843	4,428	2,657	139	621	7,770	37,918	0	0	48,265
1975	583	259	2028	1,740	4,141	4,740	2,844	167	746	9,067	44,247	0	0	52,238
1974	619	275	2069	1,775	4,225	2,868	1,721	208	930	9,000	39,780	0	0	46,931
1973	370	165	1882	1,615	3,844	3,552	2,131	214	957	9,262	40,938	0	0	48,034
1972	556	247	2115	1,815	4,320	3,372	2,023	275	1,229	9,167	40,518	0	0	48,338
1971	743	331	2815	2,415	5,748	3,024	1,814	215	961	8,685	38,388	0	0	47,241
1970	591	263	1678	1,440	3,427	4,452	2,671	239	1,068	8,044	35,554	0	0	42,984
1969	469	209	1789	1,535	3,653	3,624	2,174	227	1,015	9,547	42,198	0	0	49,249
1968	219	97	1952	1,675	3,987	3,456	2,074	215	961	9,262	40,938	0	0	48,057
1967	1494	665	2220	1,905	4,534	2,928	1,757	220	983	9,000	39,780	0	0	47,719
1966	960	427	2045	1,755	4,177	2,268	1,361	223	997	8,312	36,739	0	0	43,701
1965	830	369	1399	1,200	2,856	2,964	1,778	192	858	8,550	37,791	0	0	43,653
1964	701	312	1253	1,075	2,559	2,628	1,577	202	903	7,785	34,410	0	0	39,760
1963	973	433	1061	910	2,166	4,872	2,923	212	948	7,785	34,410	1490	1,430	42,310
1962	876	390	1131	970	2,309	7,596	4,558	253	1,131	8,977	39,678	1600	1,536	49,601
1961	1240	552	612	525	1,250	9,384	5,630	218	974	8,325	36,797	1750	1,680	46,883
1960	1621	721	1078	925	2,202	10,428	6,257	208	930	9,082	40,142	1547	1,485	51,737
1959	1929	858	420	360	857	6,204	3,722	206	921	9,220	40,752	1593	1,529	48,640
1958	1269	565	268	230	547	5,148	3,089	212	948	9,298	41,097	1640	1,574	47,820
1957	1376	612	227	195	464	4,862	2,917	205	916	9,372	41,424	1687	1,620	47,954
1956	1730	770	152	130	309	4,564	2,738	192	858	9,449	41,765	1773	1,702	48,143
1955	1984	883	903	775	1,845	4,270	2,562	172	769	9,525	42,101	2740	2,630	50,789
1954	2269	1,010	501	430	1,023	3,976	2,386	152	679	9,595	42,410	2786	2,675	50,183
1953	2094	932	466	400	952	3,682	2,209	132	590	9,675	42,764	2833	2,720	50,166
1952	2280	1,015	408	350	833	3,388	2,033	112	501	8,546	37,773	3770	3,619	45,774
1951	1897	844	350	300	714	3,094	1,856	92	411	8,761	38,724	2926	2,809	45,358
1950	2589	1,152	291	250	595	2,800	1,680	358	1,600	9,902	43,767	3450	3,312	52,106

Elk population estimates based on AGFD model from 1988 through 2002; estimates <1988 = 17% of annual harvest.

Bison numbers were derived from annual AGFD post-hunt censuses on Raymond Ranch. The Forest Service and Diablo Trust (a ranching coalition) provided estimates of the number of permitted livestock on Anderson Mesa for those years when such data were available. When such numbers were unavailable, we estimated 50% of the cattle permitted on the Coconino National Forest were on Anderson Mesa during the summer months (May through September) and that all or most non-marketed livestock wintered in Unit 5 off the Mesa. These estimates were then submitted to the Diablo Trust for adjustments of livestock numbers based on particular case histories. Because some cattle were undoubtedly present off the Mesa all year, these Unit 5 estimates are thought to be conservative.

To test the hypothesis that ungulate numbers are either negatively or positively correlated with pronghorn recruitment and population trends, we sought to quantify total ungulate foraging values in Unit 5 each year. To do this, we calculated the total biomass for each ungulate species based on mean sex ratios for Unit 5 animals and the following sex-specific biomass estimates for Arizona animals:

- Pronghorn buck= 50 kg; doe=43 kg; mean @ 25 bucks:100 does = 44.5 kg (98 lbs).
- Elk bull = 317.5 kg; cow = 227 kg; mean @ 20 bulls:100 cows = 238 kg (525 lbs).
- Mule deer buck = 70 kg; doe = 57 kg; mean @ 17 bucks:100 does = 59 kg (130 lbs).
- Bison bull = 612 kg; cow = 430 kg; mean @10 bulls:100 cows = 447 kg (985 lbs).
- Cattle bull (1950-74) = 560 kg; cow/calf = 430 kg; mean @10 bulls:100 cows = 442 kg (974 lbs).
- Cattle bull (>1975) = 612 kg; cow/calf = 476 kg; mean @10 bulls:100 cows = 488 kg (1076 lbs).
- Domestic ewe sheep = 59 kg + 37 kg lamb = 96 kg (212 lbs).

Productivity estimates for pronghorn and mule deer (given as ratios of fawns per 100 does) were obtained from pre-hunt surveys. In contrast, estimates of biomass for pronghorn, elk, and other ungulate species were obtained from fall hunting season statistics. Consequently, our analyses of the effects of ungulate biomass on pronghorn and deer productivity and biomass must reflect the differential timing of productivity and biomass components. We therefore opted to structure all productivity analyses using a 1-calendar-year lag. That is, we explored the dependence of pronghorn and mule deer productivity in year t + 1 on ungulate biomass the previous fall (~6-12 months earlier). In contrast, we always explored the dependence of pronghorn and mule deer biomass in the fall of year t on ungulate biomass estimates from the same fall. Our trend analyses were robust to these assumptions: if we analyzed same-year productivity-biomass relationships (i.e., with a 0-yr lag) instead of those with a 1-yr lag, none of the results changed qualitatively.

We performed separate regressions of time series of pronghorn productivity (i.e., fawns per 100 does) and pronghorn biomass against time series of elk biomass, livestock biomass, and "Total Ungulate Biomass (TUB)." Total biomass for each ungulate species in a given year was the product of this per capita and the estimated population size that year. "TUB" represents the sum of the total ungulate biomass across all ungulate species, excluding the focal species. For example, in an analysis of ungulate impacts on pronghorn productivity, TUB sums the biomass of each ungulate species except pronghorn. In this way, TUB is a gauge of total potential interspecific competition. Other analyses compared effects of intraspecific competition.

After comparing elk biomass trends, livestock biomass trends, and TUB trends with lagged (1 year) pronghorn productivity and pronghorn biomass, these same variables were then tested against mule deer productivity and biomass trends.

Logistic regressions were used to characterize dependence of pronghorn and mule deer productivity on ungulate biomass. In contrast, linear regressions were used to explore correlations of pronghorn and mule deer biomass on biomass of other ungulate species.

Because studies in other areas have shown a significant relationship between winter precipitation amounts and pronghorn productivity (Brown et al. 2002), we conducted several analyses in which seasonal or annual precipitation were assessed as predictors of pronghorn productivity in Unit 5. Analyses involving rainfall the previous summer, over winter (October through Mach) rainfall, and rainfall during the spring growing season were conducted separately.

RESULTS

The Unit 5 database clearly indicates a negative correlation of pronghorn recruitment with total ungulate biomass (excluding pronghorn) the previous fall ($r^2 = 0.29$, $P < 0.001$). The majority of this negative relationship is attributable to a 90-fold decrease in pronghorn recruitment concurrent with a 117-fold increase in elk biomass (Fig. 4; $r^2 = 0.48$, $P < 0.001$). In contrast, no strong relationship between pronghorn biomass and TUB (excluding pronghorn) the previous fall was evident ($r^2 = 0.004$, $P = 0.67$). Likewise, no strong relationship between pronghorn biomass and elk biomass alone was evident ($r^2 = 0.049$, $P = 0.11$).
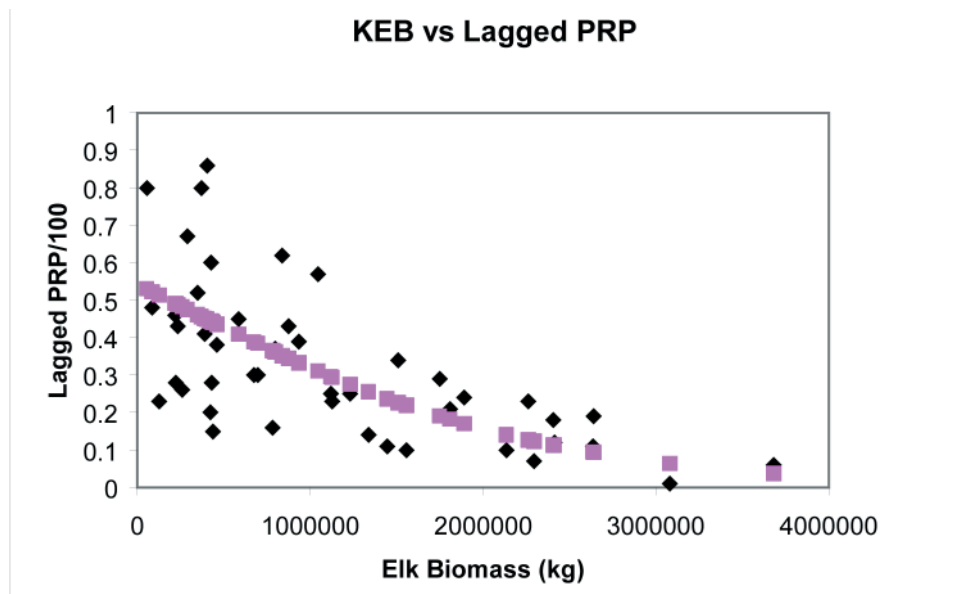

Fig. 4. Elk biomass (KEB) vs. pronghorn recruitment (PRP) lagged 1 year. Unit 5, Arizona, 1950-2003.

To a lesser extent, the same negative relationship holds for the correlation between mule deer recruitment and biomass with total ungulate biomass ($r^2 = 0.15$, p < 0.02). The majority of this multi-species correlation, however, appears due to the relationship between deer recruitment and elk biomass. Deer recruitment declined 4.4-fold across the same 117-fold range of elk biomass (Fig. 5; $r^2 = 0.23$, P< 0.001). Nonetheless, a strong relationship between mule deer biomass and total ungulate biomass the previous fall (excluding mule deer) is evident ($r^2 = 0.052$, $P = 0.099$), even though a relationship between mule deer biomass and elk biomass alone is absent ($r^2 = 0.042$, $P = 0.14$).
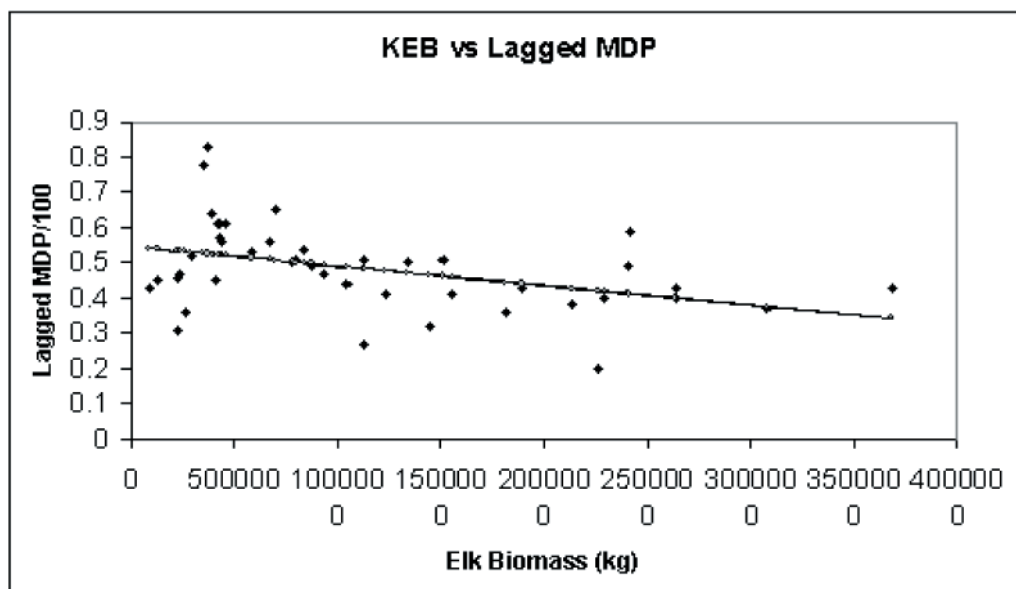
Fig. 5. Elk biomass (KEB) vs mule deer recruitment (MDP) lagged 1 year, Unit 5, Arizona, 1950-2003.

Over the 53 years of the database, elk, mule deer, and pronghorn exhibited different responses to such changes in environmental conditions such as drought and grazing intensity. In a given year, eliminating any effect due to inter-year variations in precipitation, elk recruitment almost always exceeded pronghorn recruitment. This was almost exclusively so during the last few decades (Fig. 6). The only years in which pronghorn recruitment greatly exceeded elk recruitment were 1950-56, 1959, 1969, and 1970. Recruitment ratios for elk and pronghorn are uncorrelated ($r = 0.09$, N.S.). In contrast, recruitment ratios for mule deer and elk exhibited far less variation from each other within years (Fig. 6) and are significantly correlated ($r = 0.64$, P< 0.001). In 1969, 1970, and again in 2001, mule deer recruitment greatly exceeded elk productivity. Given the similarities between elk and mule deer recruitment rates, it is not surprising that mule deer recruitment exceeded pronghorn recruitment nearly every year (Fig. 6), with 1959 providing the only serious departure from this pattern. Even though there was little correlation between elk and pronghorn recruitment rates, the recruitment rates mule deer and pronghorn were correlated ($r = 0.40$, $P = 0.002$).
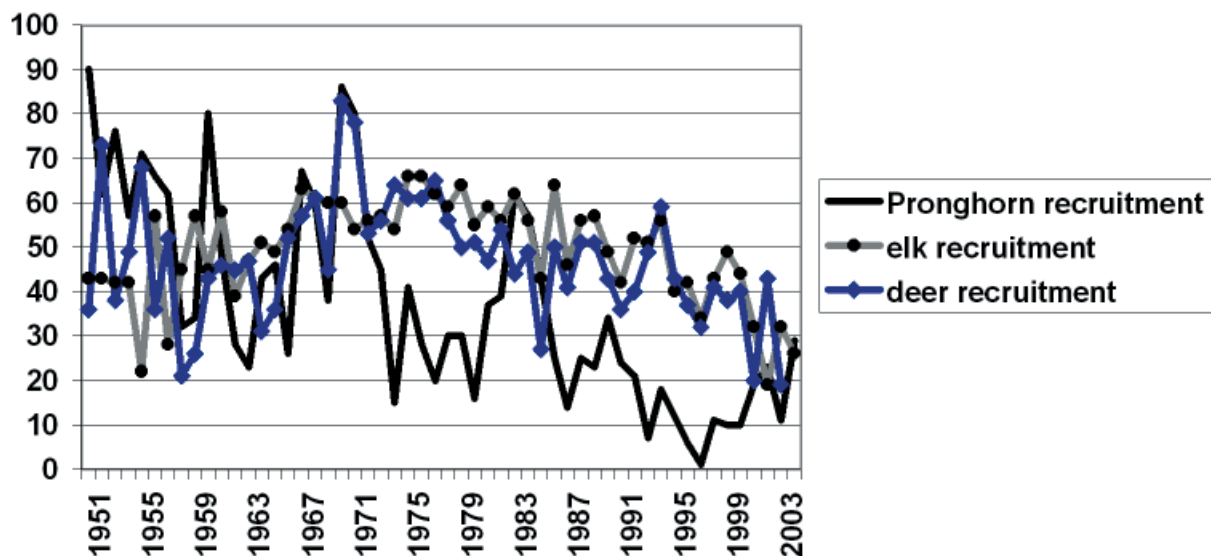
Fig. 6. Pronghorn, elk, and mule deer productivity in Unit 5, Arizona, 1950-2003.

Pronghorn biomass was significantly related to pronghorn recruitment ($r^2 = 0.21$; $P < 0.01$). This relationship would indicate that fawn survival importantly contributed to population numbers and trends as postulated by Neff and Woolsey (1979). The lack of a negative relationship between these 2 variables would also indicate that pronghorn recruitment was not density dependant on an intraspecific basis.

Although aerial gunning of coyotes appeared to result in improved pronghorn recruitment in 1982 and 1983, little improvement was noted after treatments in 1988 and 2002, and results in 2003 are unclear. Comparison between areas treated for coyotes and similar-sized control areas on Anderson Mesa in 2002 and 2003 showed no significant (P>0.05) differences in 2002 and both positive and negative differences in 2003 so that the relationship between these 2 variables remains ambiguous (Richard Miller, Arizona Game and Fish Department, personal communication).

No relationship was noted between pronghorn recruitment and/or population trend with any of the seasonal precipitation combinations tested. Seasonal drought is nonetheless a factor in that winter rainfall amounts < 2 in were always followed by poor recruitment (Table 1, Brown et al. 2002). These data support the hypothesis that competition for nutritious forage, especially during late winter and early spring months, may be a factor limiting pronghorn recruitment and population size in Unit 5 (Yoakum 2003). Pronghorn productivity in Unit 5 is significantly reduced when elk biomass is high (Fig. 4). Although livestock and bison constitute the largest collective biomass (Fig. 7), and consume the largest amount of forage, increased competition with elk was the primary measurable cause of the decline in pronghorn recruitment. This low recruitment, coupled with the impacts of drought, appears responsible for the decline of the Anderson Mesa pronghorn population during the 1990s. Further evidence of this phenomenon was the heavy use of browse plants by elk prior to pronghorn arriving on Anderson Mesa in spring (Fig. 8). Physiological and spatial advantages of elk over mule deer on winter and intermediate ranges have been well summarized by Keegan and Wakeling (2003) and Wisdom et al. (2004). Presumably, these same traits would also afford elk substantial advantages over the diminutive pronghorn.
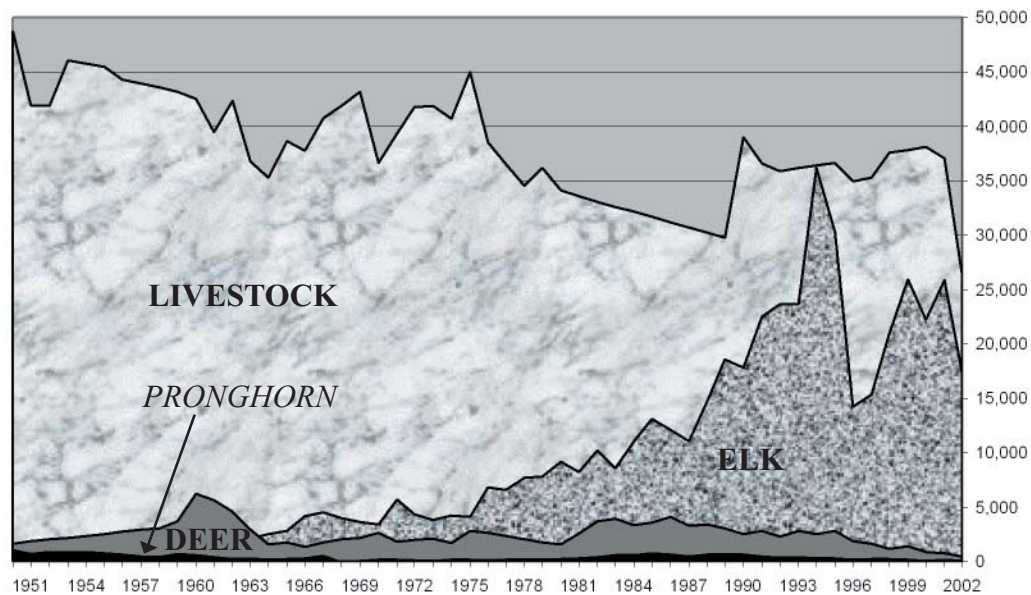
Fig. 7. Collective biomass of pronghorn, elk, deer, bison, and livestock biomass in Unit 5, Arizona, 1950-2002.

Fig. 8. All-thorn *(Lycium pallidum)* shrubs recently damaged by elk. Photo taken during early spring of 2001. Numerous elk pellets were found amongst the shrubbery and many of these plants were dead by the summer of 2003.

DISCUSSION

The Anderson Mesa Pronghorn Management Plan adopted by the AGFD and CNF (2004) in conjunction with permittees, conservation groups, and other stakeholders, recognizes the apparent effect of elk competition and the need to improve quantity and quality of forage. This adaptive management plan, which is revised each year, calls for mechanical removal of junipers from thousands of acres of former grassland, reseeding these areas with native grasses and forbs, resting or deferring key pastures from livestock grazing, and reducing elk populations in Unit 5. Moreover, an elk population reduction hunt schedule, established during the 2001 hunt season, may be bearing fruit in that there was a significant improvement in pronghorn recruitment in 2003 (Appendix 1). These efforts, coupled with 2 large natural fires in 2003, and reduction of bison numbers on Raymond Ranch, should allow pronghorn productivity on Anderson Mesa to again reach historic levels. Nonetheless, given the inherent inter-annual variability of pronghorn recruitment, a sustained, multi-year effort will be necessary for this assortment of management activities to translate into a persistent increase in pronghorn population numbers.

Should the hypothesis that pronghorn recruitment on Anderson Mesa has been kept below maintenance levels due to inadequate vegetation quality brought on by increased use of wild and domestic ungulates prove valid, this phenomenon could explain recent pronghorn population declines in such problem areas as Yellowstone National Park (Boccadori and Garrott 2002; elk) and Sheldon National Wildlife Refuge in Nevada (Bennett 2002; feral horses and burros).

ACKNOWLEDGEMENTS

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Appendix 1. Wild ungulate survey and harvest data in Game Management Unit 5 compared to estimated live-stock numbers, 1949-2003 x 1. Precipitation, drought severity index, survey and hunt, and other Unit 5 management information, 1949-2003.

Year	Oct.-Mar. Precip.	July PDSI*	Prong. seen	FF:100 DD	Prong. Taken	Elk seen	Calves: 100 CC	Elk taken	Deer seen	FF:100 DD	Deer taken	Bison	Calves: 100 CC	Est. Cattle	Est. Sheep	Management Notes
2003	8.07	-4.04	397	29	11	1685	26	1492	234	39	57	75	44			Coop. management measures implemented
2002	3.79	-5.76	266	11	5	1545	32	1448	249	19	67	104	63	5289	0	Extreme drought; some aerial gunning
2001	10.69	1.18	503	23	9	1635	19	2178	377	43	100	100	53	7496	0	Public concern over pr management
2000	5.35	-5.41	280	19	16	2603	32	1868	386	20	120	90	51	7,729	0	AWF questions management of A. M.
1999	6.58	1.3	546	10	15	2691	44	2181	518	40	200	92	59	7668	0	1999-2004 are drought years
1998	10.99	2.82	566	10	22	2775	49	1765	637	38	164	103	68	7608	0	Some aerial gunning of coyotes
1997	6.85	0.24	557	11	22	1882	43	1287	589	41	233	92	60	7150	0	
1996	2.76	-5.05	421	1	24	1963	34	1195	443	32	262	71	56	7094	0	Very dry winter
1995	14.64	0.28	636	6	46	2828	42	2546	944	37	396	85	72	7428	0	
1994	12.95	-0.9	681	12	36	2382	40	3043	467	43	352	113	75	7367	0	Prop. 200 bans trapping on public land
1993	32.02	4.22	839	18	40	2481	56	1994	763	59	398	116	79	7306	0	
1992	18.44	4.67	712	7	57	2814	51	1990	404	49	321	119	83	7247	0	
1991	13.1	-0.25	964	21	75	2288	52	1896	622	40	393	114	70	7389	0	
1990	9.24	0.21	1189	24	74	2203	42	1497	302	36	351	111	63	7,893	0	
1989	8.64	-3.52	1146	34	80	2152	49	1564	384	43	428	113	74	5995	0	Aerial gunning of coyotes
1988	13	4.27	1161	23	44	1995	57	1247	335	51	477	116	75	6087	0	Aerial gunning of coyotes
1987	11.87	3.46	948	25	44	1359	56	933	168	51	457	113	84	6186	0	Aerial gunning of coyotes
1986	13.9	1.78	1215	14	116	771	46	1019	546	41	576	109	85	6291	0	
1985	14.42	4.8	1390	25	120	1011	64	1105	403	50	501	107	81	6392	0	
1984	6.18	1.62	1107	43	103	846	43	927	169	27	467	107	74	6493	0	
1983	18.75	4.86	1096	57	73	717	56	723	224	49	553	93	74	6595	0	Aerial gunning of coyotes
1982	17.27	2.06	863	62	53	567	62	863	247	44	519	89	59	6697	0	Aerial gunning of coyotes

Appendix 1. (continued).

Year	Oct.-Mar. Precip.	July PDSI*	Prong. seen	FF:100 DD	Prong. Taken	Elk seen	Calves: 100 CC	Elk taken	Deer seen	FF:100 DD	Deer taken	Bison	Calves: 100 CC	Est. Cattle	Est. Sheep	Management Notes
1981	8.74	0.33	674	39	21	678	56	694	181	54	362	91	59	6798	0	Trapping + aerial gunning of coyotes
1980	22.43	5.01	616	37	28	306	59	772	279	47	217	103	81	6,900	0	Coyotes trapped
1979	21.9	5.53	504	16	33	642	55	659	201	51	248	97	66	7332	0	Coyotes trapped
1978	17.32	2.29	444	30	28	593	64	647	202	50	286	96	60	6988	0	Coyotes trapped
1977	5.24	-2.11	472	30	30	356	59	557	135	56	332	120	80	7379	0	Coyotes trapped; last fire on A.M.(200 ac.)
1976	13.43	1.86	357	20	36	578	62	575	163	65	369	139	61	7770	0	
1975	12.43	1.96	408	28	35	438	66	348	160	61	395	167	42	9067	0	1974--1977 drought years
1974	6.95	-3.09	433	41	38	271	66	355	259	61	239	208	77	9000	0	Elk numbers increasing
1973	28.09	6.14	259	15	33	340	54	323	198	64	296	214	85	9262	0	Building of 345 KV powerline on AM 1080 banned; Grapevine allotment open to grazing
1972	8.97	-3	389	45	32	214	57	363	170	56	281	275	56	9167	0	
1971	5.41	-5.1	520	52	56	847	56	483	207	53	252	215	77	8685	0	severe drought
1970	11.31	-1.9	414	80	49	186	54	288	290	78	371	239	70	8,044	0	
1969	16.5	0.37	328	86	0	419	60	307	187	83	302	227	no data	9547	0	Closed season
1968	12.13	-0.24	153	38	0	245	60	335	162	45	288	215	60	9262	0	Est. 80% loss from Jan. storm/no hunt
1967	11.53	-1.8	1046	60	112	280	61	381	245	61	244	220	71	9000	0	
1966	14.98	-0.51	672	67	56	261	63	351	248	57	189	223	56	8312	0	
1965	12.75	3.17	581	26	50	237	54	240	150	52	247	192	80	8550	0	
1964	7.29	-2.73	491	46	67	148	49	215	169	36	219	115	71	7785	0	Harvest Includes 3 does
1963	6.47	-5.11	681	43	51	158	51	182	173	31	406	212	75	7785	1490	Unit 5 divided into 5A & 5B; dry
1962	14.57	-1.59	613	23	41	90	47	194	183	47	633	253	54	8977	1600	Major p-j control project pleted Harvest includes 60 does; 34 pr translocated
1961	9.39	-2.61	868	28	163	88	39	105	179	45	782	218	68	8325	1750	
1960	9.85	-2.12	1135	48	122	53	58	185	102	46	869	208	59	9,082	1,547	
1959	6.3	-4.23	1350	80	69	129	45	72	120	43	517	206	69	9220	1593	83 pronghorn translocated; dry
1958	15.43	-0.78	888	34	27	110	57	46	129	40	429	212	72	9298	1640	

Year	Oct.-Mar. Precip.	July PDSI*	Prong. seen	FF:100 DD	Prong. Taken	Elk seen	Calves: 100 CC	Elk taken	Deer seen	FF:100 DD	Deer taken	Bison	Calves: 100 CC	Est. Cattle	Est. Sheep	Management Notes
1957	9.33	0.78	963	32	74	143	45	39				205		9372	1687	
1956	5.51	-3.42	1211	62	76	99	28	26				192		9449	1773	drought year
1955	6.22	-1.87	1389	66	131	130	57	155				172		9525	2740	drought year
1954	9.49	-1.64	1588	71	421	85	22	86				152		9595	2786	
1953	5.6	0.85	1466	57	219		42					132		9675	2833	Increased fencing and stock tank building
1952	16.3	3.67	1596	76	248		42					112		8546	3770	Severe winter storm in fall of 1952 Drought: 167 pr + 175 bison removed
1951	4.12	-4.26	1328	62	166		43					92		8761	2926	1950-51
1950	8.86	-1.85	1812	90	114		43					358		9,902	3,450	4000 pr. est. on C.N.F. 166 bison to R.R.
1949	14.55	3	1717	79	243		37					146				Big snowstorm in January
* Palmer Drought Severity Index																

SELECTION FOR EARLY HORN GROWTH IN PRONGHORN (*ANTILOCAPRA AMERICANA)* MALES

CARL D. MITCHELL, U.S. Fish and Wildlife Service, 74 Grays Lake Road, Wayan, ID 83285. carl_mitchell@fws.gov

CHRISTINE R. MAHER, Department of Biological Sciences, University of Southern Maine, 96 Falmouth Street, Portland, ME 04104. cmaher@usm.maine.edu

Abstract: Recently, multiple investigators have documented that male pronghorn (*Antilocapra americana*) can attain large horn size at 2-4 years of age, which is younger than peak horn or antler size achieved by other similar sized ungulates. We believe aspects of pronghorn biology, ecology, behavior and evolution can explain this phenomenon. Early physical maturation (maximum body length and mass, large horn size) of males, combined with flexible breeding strategies, allows individuals with these traits more opportunities to breed. Large horns play a role in pronghorn social interactions but other characters (body size, cheek patches, vigor, and experience) are more important. Therefore, we believe large horn size is part of a suite of characters associated with early maturation, rather than being selected for *per se.* Most ungulates are physiologically capable of reproducing at young ages but are prevented from doing so because of competition with larger, or more experienced males in the population. Early breeding by physically and physiologically mature individuals also may allow populations to recover rapidly from periodic episodes of high mortality characteristic of dynamic grassland ecosystems. Reproduction by younger but mature pronghorn would also favor selection for early adult characteristics.

INTRODUCTION

Life histories reflect tradeoffs in allocating resources toward growth or reproduction, including both current and future reproduction (Stearns 1992). Many factors can influence these allocations, such as resource availability, competition for resources or mates, predation rates, and environmental fluctuations or disturbance (Komers et al. 1997, Lytle 2001, Reznick et al. 2002). Ungulate life histories often involve allocating energy toward growth at younger ages, with reproduction delayed until animals reach maximum body sizes (Geist 1971, Clutton-Brock et al. 1982, Spinage 1986, Stewart et al. 2000, Hudson and Haigh 2002). Male ungulates may reach physiological maturity (i.e. produce viable sperm) at 16-24 months (O'Gara 1978, 1990; Komers et al. 1997, Hudson and Haigh 2002); yet, they do not attain maximum body size and often do not breed successfully until much later ages (Geist 1971, Lott 1979, Clutton-Brock et al. 1982, Spinage 1986, Komers et al. 1997, Hudson and Haigh 2002, Mysterud et al. 2003).

An understanding of life histories bears directly on management and conservation decisions (Caughley 1976, Ferguson and Lariviere 2002). Ungulate populations often are managed implicitly or explicitly to produce adequate numbers of male animals with large horns or antlers to harvest, while maintaining post-harvest male:female ratios adequate to support desired demographic

characteristics (densities, reproduction, recruitment, and population growth). Until recently, with little data for support, wildlife managers assumed that pronghorns needed at least 4-5 years to grow the largest sized horns (Kitchen and O'Gara 1982, O'Gara 1990). Under those guidelines, managers attempting to provide "mature" males for harvest would try to manage for an abundance of males at least 4-5 years old.

We agree that long-lived populations should be managed for a complete age structure of young, medium, and old-aged animals for several reasons. Older males may reduce length of the breeding season (Geist 1971, 1991; Mysterud et al. 2002, Holand et al. 2003), may increase calving synchrony (Mysterud et al. 2002), may sire higher quality neonates (Saether et al. 2003), and may reduce immature breeding behavior and female harassment (Geist 1971, 1991). However, we suggest that an extended age structure is not needed to provide large horn size for trophies in pronghorns.

Pronghorns typically achieve large horn sizes at earlier ages than other ungulates, with the largest horns often found on 2-4 year old males (Wright 1994, Min 1997a, Mitchell and Maher 2001, Brown et al. 2003). These studies documented nonlinear relationships between horn length and age in pronghorns from different populations. They found a generally rapid increase in male horn size until ages 2-4 years, and a leveling off or decline at older ages. Wright (1994) also mentioned that the largest horns in a small sample of Montana pronghorns came from 3-year-old males. Although data are still limited, we believe an examination of pronghorn biology, ecology and behavior explains why pronghorn males may attain large horn size at a relatively early age compared to other ungulates. This model focuses on early maturation and flexible breeding strategies, which allow populations to recover rapidly from periodic episodes of low reproduction or high mortality inherent in dynamic prairie ecosystems.

We define maturity as the entire suite of physiological, morphological and behavioral traits that allow an animal to compete with others of the same sex for breeding opportunities. Physiological characteristics include producing adequate levels of testosterone and other hormones to stimulate appropriate physical and behavioral actions, producing fertile sperm, emitting appropriate scents from skin glands, and accumulating sufficient fat reserves to support rutting activities. Morphological traits refer to having attained sufficient body size and mass, horn size adequately large to use for display and/or to engage in intrasexual fighting, secondary sexual characteristics (i.e. black cheek patches), and an overall "vigorous" condition (Byers et al. 1994). Behavioral traits include being practiced enough to engage in intersexual behavior (herding, chasing, tending, courting and copulation), as well as scent marking, intrasexual displays and/or fighting.

EARLY MATURATION
We believe that large horn size potential (not always realized) at an early age comprises part of a generally rapid maturation process in pronghorns. Pronghorns grow quickly, and fawns are nearly adult sized by 5 months of age (Byers 1997). Male pronghorns mature physiologically and morphologically by 2 years of age. Testis weight in 2-year old males matches or exceeds that of older males (Mitchell 1980, O'Gara 1990), and males produce viable sperm at 1.5 years of age (O'Gara 1978). Furthermore, adult body size and mass of 1.5-2 year old males overlap those of older animals (Mason 1952, Mitchell 1980, Smith and Beale 1980).

In many cervids, and at least some bovids, antler or horn size is positively correlated with body size or mass (Bubenik 1990, Geist 1998), although allometric equations differ phylogenetically and geographically. Thus, if pronghorns attain adult size or mass at relatively young ages, their horn size also should be large at that time. Min (1997a) noted that horn size increased with head size, an index of body size, in male pronghorns.

Pronghorn males also may exhibit adult behavior patterns by their second breeding season. We observed a 1.5 year old male (with horns <15 cm long) tending and herding a female in north-central Montana, although we did not observe copulation (C. D. Mitchell and C. R. Maher, personal observations), and a 1.5 year old male was observed copulating with a female in central California (C. R. Maher, personal observations).

Pronghorns tend to be short-lived, with relatively few males exceeding 9-10 years of age (O'Gara 1990, O'Gara and Yoakum 1992). Rapid physical growth, early sexual maturity, and relatively short life span all suggest selection for physical and behavioral attributes that contribute to successful competition for mates at an early age. Early reproduction is one factor that can increase lifetime reproductive success (Clutton-Brock 1988).

FLEXIBLE BREEDING STRATEGIES

O'Gara (1990) suggested younger male pronghorns seldom had a chance to breed in normal age and sex structured populations exhibiting a resource defense (= territorial) mating strategy. However, pronghorns use a variety of mating systems (Kitchen and O'Gara 1982; O'Gara 1990; Maher 1994, 2000; Byers 1997), and because of differences in forage quantity and quality, skewed sex or age structure, or human disturbance, the classic notion of a few dominant males monopolizing all breeding females does not always exist (Copeland 1980, Kitchen and O'Gara 1982, Deblinger and Alldredge 1989, Byers 1997, Maher 2000). During our studies (Maher 1994, Maher and Mitchell 2000, Mitchell and Maher 2001) pronghorns used a group defense (= harem) mating strategy (Maher 1994, 2000). Defense of a stationary site may involve choosing different strategies from a fixed suite of behaviors (e.g. more male-male display, combat) than defending a mobile group of females (e.g. more chasing).

Flexible breeding strategies in unpredictable environments mean that in some circumstances young male pronghorns could breed. If such environmental conditions are common, then selection should favor attributes that allowed young male pronghorns to capitalize on those opportunities, resulting in animals that matured earlier so they could reproduce sooner. This strategy would require rapid attainment of adult body size and weight, reproductive function, and secondary sexual characteristics (e.g. horn size) that improved competition for resources. Pronghorns exhibit all these characteristics, showing adult characters at age 2-3 years.

STOCHASTIC ENVIRONMENTS AND PERIODIC MASS MORTALITY

Models suggest that when environmental disturbances cause high mortality they have profound effects on life history strategies, and resulting population structures play a larger role in life history evolution (Lytle 2001). We believe habitats inhabited by pronghorn, both historically (i.e.

savannah, Geist and Francis 2001) and recently (i.e. short- and mixed grass prairie, shrub-steppe, and desert, O'Gara 1978, O'Gara and Yoakum 1992), contributed to selection for early maturation. These habitats experience extreme variation in climate (i.e. temperature, precipitation, winds, evaporation), vegetation productivity, and available surface water (Garrison et al. 1977). High mortality during extreme weather conditions is still common across the geographic range of pronghorns (Hoover et al. 1959, Hailey et al. 1966, Martinka 1967, Barrett 1982, Bradybaugh and Howard 1982, Byers and Kitchen 1988, Byers 1997, Geist and Francis 2001). Indeed, these events, which include severe droughts and winter storms, should be expected, given that prairie, steppe, and desert ecosystems typically undergo extreme environmental fluctuations between years (Garrison et al. 1977).

Even if older animals survived disproportionately, once normal reproductive rates resumed, the age structure of those populations would be skewed towards younger animals (Byers and Kitchen 1988). Selection for physical and behavioral attributes that permit breeding at early ages is beneficial for individuals and populations under these conditions. Given that unpredictable environments regularly lead to mass mortality and skewed age structures, we believe pronghorns have evolved to exploit these conditions. Under these circumstances, male pronghorns may have evolved to take advantage of naturally fast growth rates and reached maturity at an early age (2-3 years), allowing them to compete for breeding opportunities.

WHY HORN SIZE MATTERS

Why should pronghorn biologists and managers care about horn growth patterns? Gavin (1991) suggested that understanding why animals behave as they do provides insight into population dynamics. A better understanding of horn structure and growth patterns in modern pronghorn provides better insight into their ecology and behavior.

We believe that horns developed and evolved primarily for intraspecific use (e.g. display, dominance or combat) rather than as weapons against predators. Pronghorns evolved other methods of dealing with predation (Byers 1997), and they can outrun most potential predators (Kitchen and O'Gara 1982, Byers 1997). The structure and orientation of pronghorn horns indicate that they probably developed as weapons for use in intraspecific combat (Geist 1966, Bubenik 1990), and they also function as visual and olfactory sources of information (Bubenik 1990, O'Gara 1990). Furthermore, horns probably are not as energetically costly to grow as antlers are, so growing large horns do not detract from body growth (O'Gara 1971, Brown 1990, O'Gara 1990).

Pronghorn males may evaluate other males' horn size during interactions (O'Gara 1990). Presumably, horn size is important in common male-male interactions such as "lowered head", "broadside display", "walking parallel", or "touching horns" (Kitchen 1974, Kitchen and Bromley 1974). All of these behavior patterns include components where horns are highly visible and where horn size might be accentuated by positioning of the head and ears. Similar displays in elk (Cervus canadensis), moose (Alces alces), and bighorn sheep (Ovis canadensis) apparently involve evaluating size of an opponent's antlers or horns (Geist 1971, 1982, 1998; Bubenik 1987). Pronghorn displays may have similar functions, at least under some circumstances. Researchers generally have assumed that larger horned pronghorn males dominate smaller horned males

(O'Gara 1990), as is often true for other ungulates (Geist 1971, 1982). However, during our studies of a pronghorn population using group defense mating strategies, we observed smaller horned males chasing larger horned males (C.R. Maher and C.D. Mitchell, unpublished data). Selection may favor different horn sizes in different populations displaying higher male:female ratios or using a resource defense mating strategy (e.g. more fighting may mean larger horns are advantageous). Also, different herds may have different horn potential due to genetics or nutrition.

O'Gara (1990) also suggested that horns function in intersexual interactions, such as male displays toward females that accentuated horn size, along with other secondary sexual characteristics. If males with larger horns were more successful breeders, we might expect selection for large horns regardless of age. However, female pronghorns do not select for large horn size in males. They select for "vigorous" males (Byers et al. 1994, Byers 1997) and/or for large cheek patches (Min 1997b). Regardless of selection pressure for early maturation, the role of horn size in pronghorn behavior needs further evaluation.

J. A. Byers (personal communication) has suggested that horn shape (e.g. wide versus narrow) may be more important than length, and that males may not accrue any advantage to having horns larger than average for the population. Certain horn configurations could be disadvantageous when applied against other configurations. For example, narrow horns might fit inside an opponent's wider horns, allowing the wider horned animal to "hook" more effectively. Short, stout horns might provide better mechanical strength and leverage than long, thin horns. Large, hooked prongs distally located might provide better parrying and protection than smaller, rounded prongs located proximally. Body mass and previous experience also should be important factors in fighting (Geist 1971, 1991).

Combat in pronghorns is usually rare, at least in herds using a resource defense mating strategy. Kitchen and Bromley (1974) found only 10 of 1877 (0.005%) observations involved fights. However, fights can be life threatening when they occur. Of 15 fights observed in two studies, 5 (33%) resulted in serious injuries (O'Gara 1990). Byers (1997) also noted the seriousness of fights, with 10 males (12%) fatally injured or killed during 82 fights.

Horn size and shape have some function in pronghorn behavior, but we are uncertain if it is a strong, or necessarily obvious, role. Males with larger horns do not always dominate males with smaller horns. Horns may be important primarily in male-male interactions (O'Gara 1990), although they may also play only a secondary (evaluating opponents) or tertiary (actual fighting) role. Horn size alone does not appear to be a good indicator of female selection (Byers et al. 1994). Additional observations of wild pronghorns, or controlled experiments with captive animals, might shed more light on exactly how, and in what specific situations, horns are used. We hope future researchers will examine horn size and shape, in addition to other physical (e.g. age, condition, body size and mass) and behavioral (e.g. group or resource defense mating strategy) characteristics.

CONCLUSIONS

We propose that large early horn size in pronghorns evolved from a combination of physical, behavioral and environmental factors. Pronghorns are relatively small ungulates with rapid

growth rates, and males often reach adult size and mass at 2 years of age. Many ungulates attain maximum horn or antler size when they reach maximum body size or mass, which happens early in life for pronghorns. Periodic mass mortality due to extreme weather events is common in pronghorn habitats and probably provided additional selection for early maturity. Horn sheaths are less costly to grow than antlers, and pronghorns would not likely suffer losses in body size by growing adult sized horns early in life. Horns serve valuable functions in pronghorn social interactions, but very large horns may not provide significant benefits, although this has not been examined.

RESEARCH NEEDS

We believe the relationship between horn size and age warrants further study in other pronghorn populations, in different environmental conditions, across longer time frames, and especially using random sampling. Such research could provide insights to links between horn size and other body dimensions (e.g. head and limb length, mass). Other factors including annual or cohort variations due to maternal, neonatal and annual spring nutrition, genetics and social structure also may influence horn size.

Specific examples include:
1. Investigate relationships between pronghorn age, body size, mass, and horn size using true random sampling in different areas (G. A. Sargeant, personal communication). Samples need not come from harvested animals but could use live animals captured for other studies. This could also be done using captive animals (see below) if using a population with marked fawns followed through life.
2. Confirm age/size/mass-horn size relationships in other geographic areas under different harvest regimes, using random sampling, check stations or taxidermists. Some index to body size (e.g. head length, body length, limb length, chest girth) should be incorporated to adjust for differences in body size.
3. Conduct research (preferably controlled experiments with captive animals) to determine the relationship of horn growth and size with body size, mass, prenatal and post-partum nutrition, genetics, maternal effects, seasonal population density, social status, condition (fat reserves, parasites), and external environmental factors (weather, forage, minerals).
4. Conduct research, using both captive and wild pronghorns, to experimentally document the role(s) of horns, including size and shape, in male-male interactions and in mate choice, documenting population sex and age ratios, and mating strategies used.

MANAGEMENT IMPLICATIONS

Managers often use horn characteristics to infer nutritional status, genetic attributes, and general fitness and to measure sex and age ratios, which are useful parameters for making harvest and other management decisions (Mitchell and Maher 2001). Thus, wildlife managers and biologists should understand what "normal" horn size means, both at the species and individual population level.

Managers should be concerned with horn size because of hunters' potential selection for particular males, which can have several consequences. Hunters' selection of large horned male pronghorns could result in smaller mean horn size within the larger population (Fichter and Autenrieth 1978, Coltman et al. 2003). Hunters also could eliminate unusual colors and horn

morphologies from herds (O'Gara 1990). Furthermore, over-harvesting animals with attributes can lead to genetic changes in populations (e.g. large horns or antlers; Hartl et al. 1991, Harris et al. 2002).

In our view, managers should aim for an extended normal age structure consisting of young, prime, and senescent individuals in wild ungulate populations. Many ecological relationships among age, reproduction and behavior described in other ungulates have not yet been documented for pronghorns, but we expect many of these same relationships to hold true, at least for some populations. Several researchers have demonstrated that male pronghorns in some populations acquire adult sized horns, and even maximum horn growth, by age 2-4 years (Wright 1994, Min 1997a, Mitchell and Maher 2001, Brown et al. 2003). This phenomenon may necessitate revision of pronghorn harvest goals and objectives in relation to pronghorn population demographics. It also has implications for monitoring and managing the harvest of translocated pronghorn populations, in that new populations might produce large males for harvest more rapidly than managers previously thought possible. Finally, it provides additional information on pronghorn ecology that should be useful to managers monitoring pronghorn harvest and population status through check station or other harvest data.

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    WE DEDICATE this paper to the memory of Dr. Philip Wright, Dr. Bart O'Gara and Dr. Dale Lott, who encouraged us in our investigations and offered their advice and encouragement along the way.

IMPORTANCE OF VEGETATION STRUCTURE AND FORAGE AVAILABILITY IN HABITAT SELECTION BY FEMALE PRONGHORN AND FAWNS DURING THE FAWN HIDING PERIOD

PATRICIA L. STASTNY, University of Nebraska-Omaha, Biology Department, 6001 Dodge Streets, Omaha, NE 68182-0040 pstastny@hotmail.com

W. SUE FAIRBANKS, University of Nebraska-Omaha, Biology Department, 6001 Dodge Streets, Omaha, NE 68182-0040

Abstract: During parturition, female pronghorn must find an area that provides adequate cover for her offspring during the hiding phase of life, as well as adequate forage during the nutritionally demanding time of lactation. Areas with greater vegetative cover would provide adequate hiding for the offspring, but may be limited in the amount of preferred forb species available. Therefore, females could be forced into a trade-off between their own nutritional needs and the protective cover needs of their neonates. We investigated selection of habitat by females, and microhabitat selection by fawns, during the hiding period in a grassland pronghorn population in Nebraska. During the summers of 2001 and 2002, topographical, meteorological, and vegetation characteristics of the surrounding area were measured along 100-m transects centered on fawn bed-sites (early and late bed-sites) and random points. Fawns selected bed-sites with greater surrounding vegetative cover with decreased visibility at the height of a bedded fawn at 25m in 2002. Females selected areas for first bed-sites that had significantly greater biomass of forbs and grasses in 2002. Logistic regression analyses suggest that fawns select bed-sites based on structure preferences whereas females select areas based on forage. Additional analyses will also be discussed.

SELECTION OF WINTERING AREAS DURING DIFFERENT ENVIRONMENTAL CONDITIONS ON THE BASIS OF SHRUB DENSITY AND SHRUB HEIGHT

PATRICIA L. STASTNY, University of Nebraska-Omaha, Biology Department, 6001 Dodge Streets, Omaha, NE 68182-0040. pstastny@hotmail.com

JOERG HENKEL, University of Nebraska-Omaha, Biology Department, 6001 Dodge Streets, Omaha, NE 68182-0040

W. SUE FAIRBANKS, University of Nebraska-Omaha, Biology Department, 6001 Dodge Streets, Omaha, NE 68182-0040

Abstract: During the winter of 2002, radio-collared pronghorn does were located on a regular basis in the area of the Oglala National Grasslands, NE to determine winter ranges used. Early winter conditions were characterized by little to no snow accumulation, but in mid-March, a snowstorm left approximately 36cm of snow accumulation in the study area. This change in snow depth was associated with increased mortality and a dramatic shift in habitat use by pronghorn. We compared shrub density among areas used by pronghorn during severe winter conditions, mild winter conditions, and overall availability within the study area. Maximum heights of shrubs were compared between severe and mild winter conditions. Areas with greater shrub abundance, especially silver sagebrush (*Artemisia cana*), were selected during severe winter conditions. Overall shrub height did not differ significantly between severe and mild wintering areas; however the heights of both silver sagebrush and rabbitbrush (*Chrysothamnus nauseosus*) were significantly taller in severe wintering areas compared to mild wintering areas. The opposite trend was seen for snowberry spp. (*Symphoricarpos spp.*). Visibility differences among these three areas approached significance. Our results show that during times of severe winter conditions, pronghorn select areas with increased shrub density and increased height of selected shrubs. These areas of greater shrub density and shrub height were not selected during the mild winter conditions, possibly due to the decreased visibility in these areas for predators. These results suggest that areas with shrubs, particularly silver sagebrush and rabbitbrush, may be important to ensure pronghorn survival in periods of heavy snow. Most of these areas used by pronghorn during severe winter conditions were located on private lands. Therefore, implementation of management strategies on public lands that would increase availability of this important component of pronghorn winter habitat may decrease mortality during severe winter conditions.

THE USE OF TRANSLOCATIONS IN WILDLIFE MANAGEMENT

BRIAN F. WAKELING, Arizona Game and Fish Department, Game Branch, 2221 West Greenway Road, Phoenix, AZ 85023 USA; bwakeling@azgfd.gov

Abstract: Translocations of free-ranging wildlife have been used in restoration efforts for many wildlife species, although little evaluation has occurred on the success of those efforts. Translocations have been touted as the management tool responsible for the restoration of turkey *(Meleagris gallopavo)* and bighorn sheep *(Ovis canadensis),* and to a lesser extent to pronghorn *(Antilocapra americana)* and elk *(Cervus elaphus).* There are functionally 3 management objectives (rationales) for conducting translocations: (1) to establish a population of wildlife where currently none exists, (2) to reduce the numbers of wildlife within the source habitat for the translocation, or (3) to augment an existing population of wildlife with a translocation. Under management objective 1, a translocation may occur to reestablish a population that has been extirpated, or it may occur to expand the range of a wildlife species beyond its historic range. Under management objective 2, translocations may occur to reduce populations where hunting is not an acceptable management tool, or where wildlife is a nuisance or causing depredation on agricultural products. Under management objective 3, translocations may occur to improve genetic diversity of the population, increase numbers, satisfy vocal customer segments that complain of low abundance, or provide the perception that wildlife management is responsive. Implicit with any management action is the responsibility to monitor that action and ascertain that that action is attaining the desired management objective. Under management objective 1 and 2, monitoring the effect can be relatively simple. Does a population now exist at the end of some definitive time period where it did not prior to the action? Did the reduction in animals result in a reduction in complaints or a reduction in resource impact? For management objective 3, measuring that effect is much more problematic. Accurately measuring population demographic parameters can be expensive and detecting a change in those parameters is difficult because most of our classic population monitoring uses techniques with relatively low statistical power. Rarely do we measure genetic diversity prior to transplants, and even more rarely do we measure it after the translocation to determine if it had the desired effect. Published literature indicates that translocated deer (*Odocoileus* spp.) experience high mortality during the first year following a translocation, usually >50%. Little information is available on the effects to the existing population at the release site as a result of transplanted animals. It is incumbent on management agencies to inform the public that translocations into established populations has not been demonstrated to be largely successful, that increased risk of disease transmission exists, and that management activities aimed at modifying other limiting factors, like carrying capacity, water availability, neonatal nutrition, and overall habitat quality would yield greater results in improving population abundance. Should we attempt translocations of free-ranging wildlife to augment existing populations, it is also incumbent on us to test for changes in genetic diversity, survival of translocated wildlife, and demographics of resident wildlife at the release site as part of a thorough evaluation of supplemental translocations as a management tool.

Resource managers have used translocations to reduce wildlife abundance in source habitats (O'Bryan and McCullough 1985, Cook et al. 1993), augment existing populations believed to be below carrying capacity (DeBloois 1998), and establish populations where animals did not exist (Maehr et al. 1999). Although translocations are not used extensively in the current management of many species, transplants are still a common management tool used for pronghorn to address perceived abundance concerns.

In the published literature, relatively few translocations have completely met the objectives of the translocation. For instance, translocations designed to reduce the density of deer in the source habitat implicitly assume high post-release survival of translocated deer in the release habitat (i.e., deer were translocated in lieu of hunting surplus animals). Establishing self-sustaining populations at unoccupied sites seems relatively successful, but this objective is rarely the rationale for a translocation of cervids since elk were reestablished throughout the West using source stock from Yellowstone in the 1920s. Objectives of supplemental translocations aimed at augmenting an existing population include population growth, increased recruitment, increased survival, or improved genetic diversity. These factors are rarely measured and are plagued with accuracy, bias, and cost issues.

High post-release mortality during the first year seems characteristic of most translocations (Drummond 1995, Wakeling 2003). Causes of high mortality are numerous. Mortalities can occur as a result of capture, transit, post-release capture-related myopathy, unfamiliarity with the habitat, and social interaction.

SOURCE OF MORTALITY

Capture mortality. To translocate wildlife, animals must first be captured. Pronghorn have been captured using immobilizing drugs (Beale and Smith 1967, Copeland et al 1978, O'Gara 1987, Kreeger et al. 1999), corral traps (O'Gara and Yoakum 1992), linear tangle nets, cannon nets (Amstrup et al. 1980), surround nets (Reeves 1982), and net guns (Barrett et al. 1982).

For most wildlife, capture mortality is generally <5%. For instance, 12 of 215 deer died after capture and prior to translocation on Angel Island, California, 5 of which were attributed to pre-existing conditions (poor health) (O'Bryan and McCullough 1985). One of 86 deer died during capture efforts in Utah (DeBloois 1998). For pronghorn, mortality directly tied to capture can be higher than for other species. For instance, pronghorn may die at relatively high rates (30-60%) as a result of injuries from falls when captured in nets fired from helicopters (Arizona Game and Fish Department, unpublished data). Chalmer and Barrett (1977) reported that of 475 pronghorn captured in a drive net, about 29 (6%) died of acute trauma.

Transit injury. Animals may also die or be injured during transit from the capture to the release site. Most studies do not report this loss separately, but these losses are generally pooled

with capture deaths. DeBloois (1998) reported 3 of 86 deer were lost during this phase of a translocation. DeBloois (1998) further indicated ranges of mortality from 0-50% could be expected for the capture-transit phase.

Post-release capture-related myopathy. Strictly speaking, myopathy is a muscle disease expressed as a direct result of stress and does not include injury from transit or handling. This cause may be responsible for the greatest proportion of mortality in translocation efforts, although many post-translocation deaths are not investigated soon enough to definitively attribute cause. Rongstad and McCabe (1984) suggested capture myopathy could be difficult to identify and might exceed a quarter of the animals handled. Chalmer and Barrett (1977) attributed 89 (18.8%) mortalities from 475 pronghorn handled in drive nets to capture myopathy. Mortality during the first 2 months following translocation is commonly high (O'Bryan and McCullough 1985, Drummond 1995, Ishmael et al. 1995).

Habitat unfamiliarity. Deaths following release have been attributed to lack of knowledge of release habitats by the translocated animals. For example, 13 of 17 human-induced deaths following the Angel Island deer translocation were due to collisions with vehicles (O'Bryan and McCullough 1985). Jones and Witham (1990) found similar results in Illinois and attributed vehicular collisions with habitat unfamiliarity. They also suggested losses to hunters (and presumably predators) might be partially attributed to naivete of translocated deer. In another study, as many as 44% of translocated deer left the release area and moved back toward their source home ranges (Nelson 1984). Homing behavior has been blamed for the loss of radio contact with some deer after release (DeBloois 1998).

Social interaction. Translocations may alter normal social interactions both within the translocated herd and among the resident animals in the release habitat. Translocations may disrupt existing territories at the release site by the placement of new individuals in occupied habitats; disrupting territories has been demonstrated to increase mortality in neonatal white-tailed deer fawns (Ozoga et al. 1982). Further, translocated female deer may have reduced reproductive success immediately following translocation (DeBloois 1998). Timing of translocation may be important to minimize negative social interactions.

DISCUSSION

Many factors influence the outcome of a translocation effort. Nelson (1984) observed homing tendencies (i.e., returned to site of capture) in white-tailed (*Odocoileus virginianus*) deer translocated <20 km. Miller and Ballard (1982) observed longer range (>20 km movement) homing in brown bears (*Ursus arctos*) in Alaska. Rocky Mountain bighorn sheep (*Ovis canadensis*), translocated <30 km along the San Francisco River in Arizona, also demonstrated substantial homing when 10 of 11 radiomarked animals returned to their former ranges (Arizona Game and Fish Department, unpublished data). Distance moved may play an important role in site fidelity for translocated animals, as could habitat continuity or suitable contiguous terrain.

Survival of translocated animals often seems reduced for at least the first year when compared with that of resident animals. Caribou (*Rangifer tarandus*) survival was lower in trans-

planted caribou than in self-sustaining populations (Compton et al. 1995). Further, translocated elk have been shown to have lower survival rates than did resident elk in the release habitat (Stussy et al. 1994). Augmenting an existing population may be problematic, because the factors influencing the decline of the existing population may be density dependent, such as forage availability. A review of deer literature by Ballard et al. (2001) identified that predator control efforts were more successful when prey were below carrying capacity. A similar relationship may exist with translocations. When habitat conditions are suitable, even nonreproducing mollusks have been shown to begin reproducing again (Heinricher and Layzer 1999). Habitat quality and suitability influence translocation success.

Nutritional stress has influenced the success of some transplants. O'Bryan and McCullough (1985) tested deer extensively after removal from Angel Island and found declining body condition over time following translocation. Truett et al. (2001) recommended providing a food subsidy for prairie dog (*Cynomys* spp.) translocations to reduce dispersal and elevate survival. Gould's turkeys (*Meleagris gallopavo mexicana*) held in a quarantine facility for 30 days where they were fed a commercial poultry feed ad libitum had limited mortality 60 days post release (2 of 14 died; Arizona Game and Fish Department, unpublished data), whereas free-released Gould's turkeys experienced mortality rates >60% during the first 60 days post-release without the quarantine and supplemental feeding (Wakeling 1998).

Timing and technique of capture also seem to influence post-release survival. Olterman et al. (1994) documented high survival in transplanted moose (*Alces alces*) following capture with a net gun. Stussy et al. (1994) speculated that capture timing might influence survival by moving animals during periods when they are not nutritionally stressed.

RECOMMENDATIONS

Wolf et al. (1996) used a logistic regression approach to identifying characteristics of successful translocations for a variety of species. Those characteristics included releasing animals within the core of their historical range within good-to-excellent habitat. Native game species were often successfully translocated, especially if they were omnivores. The larger number of animals released positively influenced success of the translocation. Wolf et al. (1996) also found that the reproductive potential of the animal, the number and duration of the releases, and the source (wild vs. captive bred) did not influence translocation success. Griffith et al. (1989) had previously concluded that wild captured animals were more likely to establish self-sustaining translocated populations.

Based on this review of the literature, I believe many translocation efforts encountered unexpected difficulties in post-release survival. Further, post-release monitoring is has not identified the impacts of supplemental translocations or resident populations at release sites. Monitoring post-release survival is insufficient to determine translocation success, but population survival rates, changes to resident survival rates, changes to population recruitment, and changes to resident habitat use need to be monitored pre- and post-release to detect the success of the effort. Dovlev et al. (2002) used this approach to determine short-term effects of repeated introductions of Persian fallow deer (*Dama mesopotamica*), but this approach must be used in habitats where resident animals are marked prior to translocations. Similarly, Mock et al. (2001) evalu-

ated the genetic diversity of Gould's turkey populations in Arizona's Huachuca Mountains and concluded that supplemental releases in this area might benefit that population. Conversely, a decision should be made consciously concerning intentional intermixing of genetically distinct populations that may represent separate subspecies (Reat et al 1999, Rhodes. et al 1999). Genetic analyses would be useful before concluding that genetic diversity is a concern with a population (O'Callaghan 1993).

Before augmenting existing populations exhibiting poor recruitment or survival, habitat conditions should be evaluated. Habitat improvements may be less expensive to implement and yield greater returns in the long term than simply translocating more pronghorn into an area. Translocations can yield positive public relations, but should be consistent with management objectives for an area.

Agencies should decide how and when a translocation should be conducted before public pressure forces decisions. If conducted, translocations should occur during periods when nutritional stresses are minimal and use capture techniques that further reduce stress on the animals to the extent possible. Agencies should consider a commitment to post-release monitoring so that management actions provide a learning opportunity that may influence future actions. Agencies also must consider the implications of translocations on the transmission of important diseases like Chronic Wasting Disease (Williams et al. 2002).

ACKNOWLEDGEMENTS

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PRONGHORN NEONATES, PREDATORS AND PREDATOR CONTROL

JAMES D. YOAKUM, Western Wildlife, Post Office Box 369, Verdi, Nevada 89439-0369, USA.

HARLEY G. SHAW, Juniper Institute, Post Office Box 486, Hillsboro, New Mexico 88042, USA.

THOMAS M. POJAR, Wildlife Consultant, Post Office Box 1114, Kremmling, Colorado 80459, USA.

REGINALD H. BARRETT, Department Environmental Science, Policy and Management, 137 Mulford Hall, University of California, Berkeley, California 94720-3114, USA.

Abstract: More than 34 investigations provide data regarding interactions of pronghorn fawns with predators. Twelve were biotelemetry studies revealing predation removed from 5 to 81 percent of pronghorn fawns (mean = 53%) for different years and habitats. Ecological factors contributing to predation included weather, vegetation cover, predator density, available alternate prey, fawn health and others. Although various investigations indicated that effective predator control programs at times increased the fawns to does ratio (ff:100dd), these programs rarely resulted in increased herd size. Predation of neonates did not appear to be the most important limiting factor for most herds. Predation was a common mortality factor for free-roaming pronghorn but influenced herd numbers less on rangelands in healthy vegetative condition. Therefore, managers seeking strategies to increase herd size should advocate enhancement of vegetation for preferred forage and quality fawn concealment cover. Proposals for future predator control programs to increase pronghorn fawn survival should include: (l) an assessment of ecological conditions and control options; (2) a cost/benefit analysis; (3) a comprehensive herd management plan; and (4) coordination with cooperating agencies and interested public. Based on a review of more than 60 years of research reports, 14 conclusions and recommendations for pronghorn-predator management are provided.

INTRODUCTION

Pronghorn (*Antilocapra americana*) and predators have coexisted on rangelands of North America for millions of years (Byers 1997). Both still occupy many of the same habitats today. More than 34 investigations regarding relationships of predators to pronghorn fawns have been produced (Tables l-4). These studies substantiate that predators commonly prey on pronghorn neonates (fawns up to three months of age). However, a nagging management question has been whether chronic predation on neonates is generally an important regulator of pronghorn populations.

In this paper, we propose that predation is a natural mortality factor influenced by density dependency of both prey and predator and ecological carrying capacity. Because predation of neonates is common, it should not be labeled a limiting factor until long-term ecological investigations are completed. Ultimately, the goal of predator control is to increase the pronghorn population, but increased fawn survival alone may not accomplish this goal. This distinction is critical in evaluating benefits of predator control.

We have synthesized research and management data that span more than 60 years regarding the effects of predators and predator control practices on the survival of pronghorn neonates. The subject is complicated by lack of adequate biological information and a history of economic pressures, personal prejudices, hidden agendas, political interferences, and diverse public attitudes. A comprehensive review of pronghorn-predator relations was compiled to 2000 by O'Gara and Shaw (2004), however, it lacked conclusions and recommendations. Our report adds new findings as of 2005 and provides conclusions and recommendations.

In the interest of furthering rational debate about the pronghorn fawn survival issue, the objectives of this review are:

1. To assess literature pertaining to pronghorn-predator relations.
2. To evaluate the effects of predator control practices on summer pronghorn ff:100dd ratios.
3. To assess the influences of predator control on fawn survival and herd size.
4. To recommend pronghorn/predator management strategies to enhance pronghorn populations.

EARLY LITERATURE: 1940 TO 1998

Connolly (1978:394) listed 31 reports for 8 ungulates including 7 for pronghorn. He found that: "Because of conflicting public attitudes over ungulate and predator management objectives, as well as the increasing costs of predator control, careful biological and economic justification is required for the exercise of predator control. In general, predator control is justified in big game management only when it will produce substantial ungulate increases at reasonable cost without undue damage to other environmental values and when the increased production will be used. In some cases, control may produce long-range benefits for the predator itself."

Linnell et al. (1995:218) reviewed 73 radiotelemetry studies of predation on wild ungulate fawns in North America of which 15 (20%) pertained to pronghorn. These authors stated, "The large magnitude of predator-induced neonate mortality demonstrates that predation could act as a strong limiting factor on a population's rate of increase. However, as no studies have provided convincing evidence of density-dependent neonatal predation, its role in regulating populations is unknown."

Eighteen references from 1944 to 1997 provide data on pronghorn mortality studies including predation (Table l). Most did not use radiotelemetry. All were from marginal pronghorn habitats with low herd densities compared to prime habitats with high densities (western Montana,

Wyoming, Colorado, and North and South Dakota). Generally, the studies stated predator control increased summer fawn survival.

Twelve studies for 8 states and 1 province used radiotelemetry (Table 2). Except for Colorado, all studies were conducted on rangelands with chronically low fawn recruitment. Of 760 fawns instrumented, 382 deaths were attributed to predation – 227 coyote, 76 bobcat, 6 cougar, 51 golden eagle and 22 unknown.

Three studies were on the National Bison Range (NBR) in western Montana (Table 3). These data were segregated from Table 2 because McNay (1980) and Byers (1997) suggested that fences aid predation. The National Bison Range's external boundary contains a 2.4 m high woven wire fence. However, free-ranging fawn predation averaged 53 percent, whereas the 3 studies on the National Bison Range averaged 59 percent.

One enclosure study of coyote control resulted in increased pronghorn numbers. The Oregon State Game Commission translocated 17 pronghorn to the Umatilla Ordinance Depot in 1959. The herd failed to increase until 1971 when 135 coyotes were removed (Oregon State Game Commission 1972). With continued coyote control, the herd increased to more than 100 by 1976.

RECENT REPORTS: 1998 TO 2005
Four recent reports have reviewed the effects of predator control on pronghorn fawn survival.

Pronghorn Management Guidelines (Lee Et Al. 1998):
Researchers and managers from Canada, Mexico and the United States have been meeting since 1965 to exchange information regarding the biology and management of pronghorn. Workshop attendees developed Pronghorn Management Guides (Authenrieth 1978), which have been updated twice (O'Gara and Yoakum 1992, Lee et al. 1998). These guides provided the following recommendations regarding predator control for enhancing pronghorn populations.

"In treating a problem situation where pronghorn populations are reduced and predators are prevalent, the following guides should be used:

"Determine the pronghorn herd parameters that are desirable. This may be in terms of total number, rate of recruitment to the herd, age classes, etc. Determine the year-round distribution of pronghorn and the habitat types involved. Consider other population influences including, but not limited to, morality factors.

"If a factor such as predation is determined as a significant inhibitor of a pronghorn herd, the cost of actually controlling predators in the short-term must then be balanced against the long-term return.

"If it is determined that the increase in pronghorn justifies the cost, predator control should be done on those herd units here documentation indicates predator reduction would be beneficial in meeting management objectives."

Arizona Report (Shaw 2000):

   The Arizona Antelope Foundation funded a review of literature and management data dealing with predator control to benefit pronghorn in Arizona. Shaw (2000) reviewed historic and current state-wide predator control practices on pronghorn habitats. He reported that areas with intensive predator control programs during the 1940s and 1950s had higher ff:100dd ratios than areas without control practices. He noted fawn survival 30 to 40 years earlier in areas treated with predicides was often higher than reported in the recent decade with aerial gunning for coyotes. A long-term downward trend in fawn survival, independent of predator control history, suggested that ecological processes in addition to predation were influencing pronghorn numbers. Shaw stated the state's greatest weakness was failure to adequately document the response of coyotes, alternate prey, and other predator populations to control practices. He also concluded that coyote control must be repeated at least every other year to be effective in elevating pronghorn fawn survival.

Pronghorn-predation model (phillips and white 2003):

   This report presents a population model to help resolve a management controversy for the Hart Mountain National Antelope Refuge (HMNAR) in Oregon involving proposed lethal control of coyotes to increase pronghorn fawn survival. The report projected that 2 years of intensive coyote control could help maintain the pronghorn population on the HMNAR at 1,200 but would not likely allow it to increase to 2,100. However, 3 years of control may be effective in keeping the herd above the threshold of 1,200 for about 10 years. Our findings indicate that there have been recent natural and man-caused habitat changes affecting approximately 20 percent of pronghorn habitat on the HMNAR. These changes involved removal of domestic and feral livestock foraging and increased wild-prescribed fires. These recent perturbations have set back plant community succession to stages more favorable to pronghorn. Since these changes, the HMNAR pronghorn population has reached its largest recorded size in 60 years--without the control of predators. This provides strong evidence that pronghorn populations can increase without predator control and that vegetation condition is a more important factor influencing population size.

Pronghorn Predator Chapter (O'gara And Shaw 2004):

   A comprehensive report of interactions between pronghorn and predators was provided by O'Gara and Shaw (2004:337-377). They concluded:

   "Predation generally was thought to be important in regulation of pronghorn numbers, and the role of western rangeland conditions and nutrition seldom were considered. Although coyote and other predators can be important decimating factors under certain circumstances, by the beginning of the 21st century few biologists considered predation a major problem facing pronghorn.

   "In most areas, human activities, such as strip mining, subdivisions, fences, livestock grazing and irrigation projects destroy more pronghorn through habitat destruction and restricted access to critical habitats, than could predators.

   "Predator control can make a difference in pronghorn fawn survival, but not necessarily in the stability of the population.

"Control of predators to benefit big game populations often involves wholesale reduction of predators over a large area; even if desirable, such control seldom is economically feasible.

"For aerial gunning (of coyotes) to be effective, it must be maintained on at least a biennial basis. This is probably true of all other forms of coyote control as well.

"They (studies listed in Table 60) illustrate that (pronghorn) population growth and size in a given area, under most conditions, is related to habitat quality (mostly nutrition)--not summer ff:100dd ratios. This is very important to remember when considering predator control as a management option."

Finally, these authors reported that only one study (Canon 1993) has suggested predator control was effective in increasing the size of an endemic pronghorn herd.

Current Research Programs:

Several predator control projects to increase pronghorn fawn recruitment are in the development state or are ongoing. A coyote control program in Nebraska resulted in increased ff:100dd ratios (Menzel 1992); however, 2 years later he reported that the project failed to increase herd size (Menzel 1994). Nevada began a control program in 2000 but reported in 2002 that it was unsuccessful in increasing herd size (Hack and Menzel 2002). Arizona started a study of coyote abundance and behavior in 2004 (Arizona Antelope Foundation 2004). A research project has been proposed to study the effects of predation on chronically low fawn recruitment on Antelope Island in the Great Salt Lake, Utah (Schmidt 2004). A pronghorn neonate mortality project is in progress on the HMNAR.

The pronghorn literature now consistently recommends that agencies first assess other ecological factors, particularly the health of the habitat, before controlling predators (Udy 1953, Hinman 1959, Beale and Smith 1973, Connolly 1978, Barrett 1982, Pyrah 1987, Yoakum 2002, O'Gara and Shaw 2004). Also repeatedly recommended, are comprehensive herd management plans prior to conducting predator control programs (Connolly 1978, O'Gara and Yoakum 1992, Linnell et al.1995, Lee et al. 1998, Yoakum 2002, O'Gara and Shaw 2004).

SYNTHESIS
Predators During Historic Times:

Yoakum (2002) and O'Gara and Shaw (2004) compiled lists of animals that prey on pronghorn neonates including: coyote (*Canis latrans*), wolf (*Canis lupus*), bobcat (*Lynx rufus*), mountain lion (*Felis concolor*), badger (*Taxidea taxus*), red fox (*Vulpes fulva*), and golden eagle (*Aquilla chrysaetos*). Pronghorn neonates are commonly preyed on by coyotes, bobcats, and golden eagles. Of these, coyotes are the major predator (Tables 2-4). Canon (1993) reported cougars killed 6 of 78 fawns monitored in Texas. The on-going pronghorn study on the HMNAR attributed 3 mortalities of 169 fawns monitored to predation by cougars.

Ecological Factors Contributing to Predation:

Ecological factors contributing to the rate of pronghorn mortality due to predation include: (1) weather patterns, (2) density of pronghorn, (3) quality of forage for pronghorn, (4) fences restricting mobility of pronghorn, (5) density of predators, (6) availability of alternate prey, (7) vegetation height and density, (8) presence of livestock and wild ungulates, (9) incidence of disease, parasites, and other health agents.

Annual weather variation is an important variable impacting survival of pronghorn neonates via predation and other sources of mortality. For example, cold damp weather and blizzards during fawning season can cause indirect fawn mortality by stress or direct mortality from cold and snow (Dan Alanso, HMNAR Refuge Manager: personal communication 1996). Poor fawn survival in Oregon, 1991, was attributed to drought and associated predation (Van Dyke and Willis 1992).

In Idaho, fawns bedded in tall vegetative cover (76-137 cm) suffered higher predation than fawns bedded in lower vegetation (20-25cm) (Bodie 1979). A similar relation was observed in Nevada by McNay (1980).

Available prey species directly impact survival and density of predators. In south central Oregon, sagebrush voles (Lemmicus curtatus) were believed to be the primary winter food for coyotes (Dunbar and Giordano 2000). These authors proposed that fire to reduce shrubs would also reduce the coyote prey base and, therefore, result in indirect coyote control while setting back succession improving vegetation conditions for pronghorn.

Fences (barbed or woven) can impede pronghorn mobility, thereby contributing to greater vulnerability to predation (Byers1997). Coyotes have also been observed chasing fawns against fences and catching them in Nevada (McNay 1980).

Factors other than predation can limit pronghorn populations. Therefore, if some other factor is limiting the population, then no amount of predator control will likely result in increased herd density (Beale and Smith 1973, Connolly 1978, Barrett 1982, O'Gara and Yoakum 2002, O'Gara and Shaw 2004).

Pronghorn Density Dependency and Predation:
Long-term pronghorn trends have been related to density dependency in pronghorn herds in California, Nevada and Oregon (Hess 1986, 1999), Montana (Pyrah 1987), Oregon (Kohlmann et al. 1999), and Utah and Wyoming (Danvir 1999). Thirty years of pronghorn surveys and fawn: doe ratio data were evaluated for Great Basin environments (Hess 1986). Pronghorn production and mortality factors were correlated with long-term herd trends, and Hess (1986:53) concluded: "High rates of fawn predation, starvation, abandonment, and weak fawn syndrome are more likely symptoms of relatively high population densities than causes of low fawn survival rates. Pronghorn populations that are frequently subjected to winter related episodic mortality often have higher summer fawn ratios consistent with density dependency." Twelve years later, Hess (1999) further correlated these biological and environmental relationships and reached the same conclusions. Kohlmann et al. (1999) likewise studied herd population dynamics in Oregon and concluded pronghorn populations appeared regulated by density dependent mechanisms.

A 13-year pronghorn research project in central Montana concluded that fawn survival was highest where herd density was lowest (Pyrah 1987). In northeast Utah and adjoining land in Wyoming, a 19-year study found that the population increased from 90 adults to >850. Although coyotes were abundant, they were negatively correlated with same-year ff:100dd ratios, and fawn

survival was more strongly influenced by pronghorn density and summer precipitation. Pronghorn densities and ff:100dd ratios were limited by winter severity and interspecific competition for summer forage (Danvir 1999).

These long-term population studies plus 3 more case-histories (Anderson Mesa, Arizona; HMNAR, Oregon; Parker Mountain, Utah) provide quantitative data that support the hypothesis that pronghorn herds are generally regulated by density dependent mechanisms tied to carrying capacity set by habitat conditions. These studies stress that ff:100dd ratios are not always the best parameter for projecting future herd size.

It is now understood that a population may exhibit 2 equilibrium points. The concept of a "predator pit" alludes to a situation where, given certain circumstances, predators may limit a prey population to a point below food-based carrying capacity (Bergerud et al. 1983, Messier 1994). Criteria needed for a predator pit include: (1) presence of alternate prey, (2) a healthy prey population, (3) high rate of mortality by predation, and (4) historic evidence of a significantly larger prey population. It has been suggested that the pronghorn situation at the HMNAR may be an example of a predator pit (Dunbar et al. 1999, Cougar Management Guidelines Working Group 2005). However, we found (Table 4, Figure 3) that the HMNAR case meets criteria (1) and (2), but not (3) or (4). The predation rate at HMNAR (49%, Table 4) is typical for the species (53%, Table 2). There are no historic data to suggest that pronghorn numbers were ever substantially higher at HMNAR. Therefore, we disagree that the HMNAR case is an example of a predator pit. The National Bison Range pronghorn population may meet the criteria for a predator pit (Table 3). However, this herd was translocated to a fenced area that encloses prey but not predators (O'Gara and Malcolm 1988). Therefore it is not a fully natural situation.

Questionnaires To Management Agencies:

Questionnaires have been used to gather knowledge and experiences of various agencies managing pronghorn (Table 5). During the 1950s, management agencies in California, Nevada and Oregon were reporting years of alleged chronic low fawn survival. The question was – do other agencies experience similar low fawn recruitment? A questionnaire was sent to state wildlife agencies with pronghorn in the United States (Foree 1959). Fifteen questions addressed forage conditions, predation, population size and trend, mortality factors, and other management issues. Survey results listed quality of habitat (vegetation, water, and fences) as the most important factor affecting pronghorn numbers. Predation and disease were not mentioned as being significant factors. Generally, agencies attribute population declines to droughts, winter kills and malnutrition.

The Wildlife Management Institute (Washington, D.C.) surveyed provincial and state wildlife agencies in 2000. The survey included questions on predation to identify which agencies financed predator control. Sixteen western U.S. states responded: 10 contributed funds (Table 5), 6 did not (Wildlife Management Institute 2000). Results of a similar questionnaire are reported by Hack and Menzel (2002).

Public Attitude Surveys:

A nation-wide survey of United States public attitudes towards coyote control was conducted in 1976 (Arthur 1981). The public disapproved of killing predators for population control, indiscriminate shooting or trapping of coyotes, and overwhelmingly disapproved of poisoning. Given a choice of control methods, most respondents preferred nonlethal methods; the most acceptable lethal control technique was aerial gunning. This is also the most economic of the currently legal alternatives (Gum et al. 1978).

Two decades later, more nation-wide public surveys were conducted. Each concluded that wildlife managers needed to consider current information on public attitudes concerning predators and predator control practices. One survey was a random sample of United States households regarding attitudes towards control practices for coyotes, bobcats, raptors and other medium-sized predators (Messmer et al. 1999). Strong support was expressed for predators' rights to exist. The public supported predator control more readily if it was used "surgically" rather than applied broadly. Most respondents believed predators should be protected and even reintroduced to areas where they were extirpated. The public supported the position that maintaining predator populations is more important than earning a living from the land. Most respondents agreed that predator control may be necessary at times, but they believed there usually were better options than lethal practices for solving predation problems.

A survey by Reiter et al. (1999) reported that the public strongly supported public education and research about non-lethal control practices. They were less supportive of lethal control methods. Lethal practices were generally considered more inhumane than non-lethal methods. Predator control practices used on western rangelands included trapping, snares, poisons, and aerial gunning – all lethal methods rated as less humane and therefore generally opposed.

Long-term Case Histories:

Long-term (15 years or longer) investigations can be a more effective assessment of management programs than short-term (1-3 year) studies. Long-term studies account for the influence of a broad range of ecological factors. Four examples of long-term pronghorn-predator relationship studies in different biomes are summarized below.

Yellowstone National Park: Yellowstone National Park (YNP) is one of the largest remaining semi-natural ecosystems in pronghorn country with native predators. An historical account and status report of the YNP pronghorn population was provided by Scott (1986). Herds were thrifty during the 1950s and 1960s; reductions were accomplished by trapping and translocations. Populations rebounded following reductions demonstrating a density dependent response despite a variety of natural predators including coyotes, bobcats, bears (Ursus horribilis), cougars and golden eagles. However, little published information is available relative to the specific effects of predators on pronghorn within YNP.

Herds declined precipitously during the 1990s from 600 to 200 (Clark 2001, Borcadori 2002). Reasons for the decline are open to speculation. Scott (1986) suggested interactions with

vegetative conditions were responsible for fluctuating herd size. In 1968 YNP implemented a policy allowing wildlife populations to exist without human interference to the maximum extent possible (Clark 2001). Clark (2001) described a pilot mortality study indicating that coyote predation of neonates may be causing low pronghorn recruitment rates. Alternatively, Boccadori (2002) suggested poor nutrition from low production of herbaceous forage due to forage competition with bison (Bison bison) and elk (Cervus elaphus) on pronghorn winter range could be the problem.

Reintroduction of wolves to YNP in 1995 has likely affected predation on pronghorn. During the first 5 years following wolf translocations, 1,200 wolf kills of wild ungulates were reported (S. Murphy, personal communication: 2000). Seven of these were pronghorn – one adult buck and 6 fawns. A change in predator relations with pronghorn may be in progress. Coyotes have been the primary predator of pronghorn neonates, but with a roughly 50 percent decrease in coyote numbers since wolf reintroduction, the effects of coyote predation on pronghorn may diminish.

Anderson Mesa, Arizona: Population data and information on predators on Anderson Mesa in east central Arizona span >45 years (Figure 2). A herd size of 3,000 or more was reported during the 1930s--possibly the largest contiguous herd in the state. However, numbers declined to 250 to 400 during the 1990s. Ff:100dd ratios also declined from an average of 70:100 to less than 40:100. This decline precipitated a 5-year research project in the 1970s. Results indicated fawn production was healthy, diseases and parasites were few, and coyote predation was largely responsible for declining herds (Neff and Woolsey 1979).

Anderson Mesa has been subject to predator control programs since the 1940s (Arrington and Edwards 1951). Trapping and poison baits were extensively used during early years. A presidential mandate in 1972 banned the use of the poison, compound 1080, for controlling predators. State wildlife agency surveys disclosed a continued downward trend and poor recruitment; predation of fawns was implicated as the primary reason (Yoakum 2002).

Arizona's authorized gunning statute was used in a follow-up study to determine the effects of coyote removal by aerial gunning (Neff et al. 1985). Coyote control prior to fawning was credited with bringing about a ff:100dd increase from 43 in 1980 to 67 in 1983. This conclusion was based on the fact that no other pronghorn herd in the same general area received intensive aerial gunning, and no other pronghorn herd experienced a comparable gain in fawn survival.

The Anderson Mesa pronghorn population was monitored for 3 decades, and predation was repeatedly implicated as the limiting factor. Periodic coyote aerial gunning was initiated in 1981 (Figure 2); the population still plummeted and ff:100dd ratios remained chronically low. Killing coyotes apparently did not result in a larger pronghorn population. Malnutrition rather than predation may have been the limiting agent (Yoakum 2002). A pronghorn food habits study in 2003-04 for the Mesa and nearby Garland Prairie supports this hypothesis (Miller and Drake 2004). "The Garland Prairie diets had a significantly higher proportion of forbs and lower quantities of grasses than the Anderson Mesa herd...The Garland Prairie herds had significantly higher DAPA

levels across all biological periods, indicating higher rumen microbial activity most likely related to a higher diet quality. This higher nutritional condition during critical periods of reproduction could account for the higher fawn recruitment on Garland Prairie (Miller and Drake 2004:21)."

Hart Mountain National Antelope Refuge, Oregon: Pronghorn population and ecological data are available from the HMNAR for >50 years. Herd size has fluctuated from lows of <350 in the 1950s to highs of >2,400 in the 2000s (Figure 3). 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. During the late 1960's, a resource management plan that prescribed livestock foraging as a management tool to enhance vegetation for wildlife was initiated (U.S. Fish and Wildlife Service 1970).

An environmental impact statement (EIS) from the early 1990s reported that >90 percent of shrublands were in late successional stages, and riparian sites and meadows were deteriorated; these conditions were not considered quality habitat for pronghorn (U.S. Fish and Wildlife Service 1994). Because of the EIS, permitted livestock foraging was terminated and new fire management strategies were incorporated into the updated management plan. The fire management program is now intended to simulate natural disturbances to increase early- and mid-succession vegetation stages that are more favorable for pronghorn. These management practices appear to have contributed to the HMNAR pronghorn herd increasing to all time highs.

Predator control was conducted annually during the 1940s to 1967. Trapping was used extensively along with various other control techniques including den hunting, poisoning, and ground and aerial shooting. For this period of more than 20 years, the pronghorn population was the lowest in the Refuge's history (Figure 3). The intensive predator control program was terminated in 1967. From 1968 to 2004, pronghorn increased to >2,400.

The EIS that resulted in management changes also provided an analysis of the 1940 to 1967 predator control program in relation to pronghorn herd performance. It concluded: "Apparently fawns that survived because of predator control died of other causes between late summer and spring." (U.S. Fish and Wildlife Service 1994:2 Appendix J-35).

When biological events are not recognized or remembered, mistakes can be repeated. This almost occurred on the HMNAR. In 1995, the pronghorn ff:100dd ratio in late July was 1:100; this was the lowest record for the Refuge. Coyote observations by refuge personnel were frequent and management concluded pronghorn survival was at risk. An Environmental Analysis Report prescribed limited aerial gunning (10 to 15%) of coyotes prior to fawning seasons for 3 consecutive years (U.S. Fish and Wildlife Service 1995). The proposal was met with an outcry of public alarm and the filing of a court injunction. The U.S. Fish and Wildlife Service canceled the proposed operation.

In 1996, the HMNAR manager initiated a pronghorn neonate mortality study using radiotelemetry (Gregg et al. 2001). The research is now the longest radiotelemetry study of pronghorn

fawn mortality to date. Of 347 fawns instrumented, known mid-summer mortality credited to predators has averaged 49 percent (Table 4). Although high neonatal losses to predation were common, the herd size nearly doubled over the 10-year study (Figure 3). In 1997, the U.S. Fish and Wildlife Service began drafting a comprehensive management plan for pronghorn with guides for predator control based on recent data (Dunbar 1999).

Our findings indicate management on the HMNAR from 1995 to 2005 has contributed to the following: (1) Lethal predator control programs have not been authorized. (2) Domestic live-stock have been excluded since 1991. (3) Feral horses have been removed since the mid-1990s. (4) Wildfires and prescribed burns have altered >20 percent of shrub dominated rangeland to mixtures of grasses, forbs and shrubs. (5) Precipitation has been average. (6) Forb diversity and abundance have increased >200 percent; thus, critical nutritional forage for neonate survival has increased. (7) Number of pronghorn observed during summer surveys in 2003 and 2004 were respectively 2,444 and 2,474 (The 2004 summer survey resulted in the highest number of prong-horn counted on the Refuge since establishment 68 years ago). Evidently the influence of chang-ing ecological factors during the last decade on the refuge has changed vegetation conditions. Apparently, increasing the carrying capacity has resulted in higher ff:100dd ratios and herd size without lethal predator control.

Parker Mountain, Utah: An unpublished case of increased pronghorn herd size with low intensity predator control was reviewed in November 2004 (Yoakum 2004). Parker Mountain, in central Utah, is administered by the U.S. Forest Service, the U.S. Bureau of Land Management, state school lands and private ranchers (U.S. Bureau of Land Management 1978). Vegetation is largely a buffalo grass *(Buchloe dactyloides)* community rated in fair to poor ecological condition due to decades of intensive foraging by cattle and domestic sheep. Vegetation composition was estimated to be 20 percent grasses, 20 percent forbs and 60 percent shrubs, with height averaging 38cm – ideal conditions meeting pronghorn habitat requirements (Yoakum 2004).

Many reservoirs were developed for livestock that were also used by wildlife. Limited pred-ator control programs have existed for years to accommodate domestic sheep producers. Preda-tors included coyotes, bobcats, cougars, and golden eagles. Elk, mule deer and pronghorn are native, but pronghorn were extirpated during pioneering times. Forty years ago the area received a translocation of some 50 pronghorn, and now the herd is >3,000. More than 10,000 pronghorn have been removed via sport hunting and translocation over the 4 decades. The herd has averaged 80ff:100dd for 4 decades--one of the highest ratios recorded for Great Basin habitats. The area is a "pronghorn factory" that could be used as a model for multiple use management of wildlife and livestock in similar Great Basin environments.

ASSESSMENT
Pronghorn Production and Recruitment:
Pronghorn produce an average of 190 fetuses per 100 does at birth, and females continue to produce at this rate throughout life – even in old age (O'Gara 1968). Actual recruitment of yearlings, however, is lower due to fawn mortality from all sources. The 50-year data set from the HMNAR indicates that a summer ff:100dd ratio of 15 to 20 can sustain a population given the

normal mortality factors for this particular site. Similarly, summer recruitment of 15-20 ff:100dd was found to maintain the pronghorn herd on the National Bison Range (O'Gara and Malcolm 1988).

Ff:100dd ratios of 25-35 or higher are often identified by managers as desirable for harvested herds (Neff and Woolsey 1979, Menzel 1992, Durbin 1997). Where pronghorn numbers are at or above carrying capacity, managers should cautiously consider reducing population density to allow density dependent functions to operate. A more lasting effect on fawn survival could be accomplished through habitat alterations that increase carrying capacity of the rangeland.

Fawn survival can vary widely among biomes (Ellis 1970, Vriend and Barrett 1978). Consequently, care should be taken not to use characteristics of one biome to denote conditions in other biomes (O'Gara and Yoakum 1994, Lee et al. 1998). For 20 years of fawn survival data from prairie grassland, shrubsteppe and desert biomes, Vriend and Barrett (1978:360, 365) stated "We conclude that low recruitment is a reality for pronghorn populations throughout most of their North American range...Average production (survival) rates for the states west of the Great Divide are 33 percent lower than those for pronghorn in the Great Plains." Ff:100dd ratios for the Great Plains grasslands, and Great Basin shrub steppe biomes averaged 80-100ff:100dd and 30-50ff:100dd, respectively. Bright and Hervert (2005) provided additional evidence that recruitment is particularly low in the Sonoran Desert, Arizona (mean of 19ff:100dd for 1995 to 2002). They concluded that predator control was not warranted for years when inadequate nutritious forage was available to sustain pronghorn fawns. "Predator control may be useful in limited situations but likely would be prohibitively expensive with little chance of making a difference over the entire range of Sonoran pronghorn" (Bright and Hervert 2005:45).

Different biomes seem to have characteristic long-term ff:100dd ratios that can vary widely. This ratio can also vary widely within a biome in response to short-term weather and vegetation conditions. It is not necessarily correlated with population growth rate (Figure 3).

Perspectives on Pronghorn-Predator Relationships:
Numerous studies have been conducted on pronghorn neonate-predator interactions and most implicate predators as major causes for high mortality rates (Beale 1978 Utah, Barrett 1980 Alberta, Bodie 1979 Idaho, Tucker 1979 Texas, Corneli 1982 Montana, McNay 1980 Nevada, Firchow 1986 Colorado, Trainer et al. 1983 Oregon, and others). The literature also contains reports of herds thriving with little or no effort to control predators for pronghorn objectives (Hess 1986, 1999 California, Nevada and Oregon; Danvir 1999 Utah, and Pojar and Gill 1990 Colorado. Unfortunately, many wildlife agencies still support predator control for pronghorn (Table 5), instead of investing in needed habitat enhancements.

Surveys of public attitudes during the last 2 decades contend that the general public questions the need, and techniques used, for large-scale predator control programs (Gum et al. 1978, Arthur 1981, Messmer 1999, Reiter et al. 1999. These assessments are supported by the ecological investigations reported in this review. The use of extensive predator control programs to enhance the public's wildlife on the public's rangelands is generally not well supported by the public.

MANAGEMENT IMPLICATIONS

Field investigations conducted over more than 60 years have produced an abundance of evidence regarding the interactions of pronghorn, predators and predator control. This wealth of information is available and can be used to help assess the need for future control programs to enhance pronghorn neonate survival. From this review we conclude and recommend the following:

1. Native predators currently exist in all habitats occupied by pronghorn. Prey and predators have coevolved.
2. Pronghorn are prolific fawn producers – averaging 190 ff:100dd. Mortality of fawns is generally high – 50-80 percent of annual production. Predation averaged 53 percent of overall fawn mortality for the 12 studies using radio telemetry and is a common natural mortality factor.
3. Predation is highest during the first 30 days following parturition – the hiding period for fawns before they grow large and swift enough to evade predators. Chronically low fawn recruitment is not necessarily justification for a large-scale predator control program. Low fawn recruitment may be a symptom of low quality habitat or other predisposing factors.
4. For most habitats, coyotes are the main predator of pronghorn neonates. Bobcats and golden eagles take lower percentages. Cougar, badger and red fox predation rates are minimal and localized.
5. Rates of neonatal mortality are generally higher in marginal pronghorn habitats or when a population is at or above ecological carrying capacity. Mortality rates are likewise high for areas suffering from high density dependency functions.
6. Even when predation has been identified as a major limiting factor for pronghorn below management objectives, other important mortality factors affecting carrying capacity should be considered before initiating predator control. Chronically low fawn recruitment is rarely justification for a large-scale predator control program. Low fawn recruitment may be a symptom of low quality habitat or other predisposing factors. Predation rates are often increased by other ecological factors: e.g. low abundance of alternate prey, large numbers of predators, poor health of prey, inclement weather, or unhealthy vegetation condition. Predation rates generally vary temporally and geographically, and recommendations for predator control should be supported by long-term studies (generally more than 5 years) that assess which environmental factors are truly limiting.
7. Effects of predation are greatest where prey numbers are small and predators are many. Predation rates are generally higher for shrubsteppes and deserts than grasslands.
8. Numerous studies confirm that effective coyote control programs can increase initial fawn survival; however, it is rare that such practices result in increased pronghorn herd size in prime pronghorn habitats. Generally, the condition and health of vegetation influences rates of predation. Adequate plant abundance and structure are needed for neonate concealment cover. Quality, quantity, and diversity of preferred nutritious forage translate to healthy animals less predisposed to predation.
9. A ratio of 15 to 20 ff:100dd in summer surveys is probably needed to sustain herds for areas in healthy vegetation condition and not intensively hunted.
10. A predator control program to enhance pronghorn productivity may be justified if predation rates are high and the pronghorn population is well below ecological carrying capacity.

11. A short-term predator control program may be justified to assist the growth of a newly translocated population, or to protect a captive herd.

12. To be effective, a coyote control program must remove >70 percent of the predators annually for 2 consecutive years prior to the fawning season.

13. Any proposed predator control program needs to be preceded with adequately planned, science based, adaptive management including: biological studies, justification, identification of alternative control practices, population objectives, methods, time and location, date of project beginning and termination, financial obligations by source, procedures for monitoring progress, publication of final results, and documentation of public input. Final plans and results should be made available to all cooperators and interested parties. Where deemed necessary, the success of predator control can be enhanced by cooperation among management agencies, land owners, conservation and environmental organizations and interested public. Public support or hindrance can determine the success or failure of a control program. Managers should be aware of the value systems of relevant stakeholders.

14. As new biological and management information becomes available, these recommendations need to be reviewed and updated.

When the "father of wildlife management", Aldo Leopold, was a young, eager wildlife biologist, he thought every predator killed translated to more game (Flader 1974). Leopold's later field experiences proved this a myth, and that healthy ecosystems were more often the key factor influencing wildlife populations. It is time for wildlife managers to set new standards for implementing predator control programs purporting to increase pronghorn fawn recruitment and thereby enhancing pronghorn populations. We now know that: (1) large numbers of pronghorn fawns are commonly produced and taken by predators, (2) predators impact neonate populations differently for various areas and years, and (3) predation is rarely a limiting factor affecting pronghorn herds for ecosystems in healthy vegetative condition.

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Table l. Mortality studies of neonate and adult pronghorn from 1944 to 1997 - most conducted without the use of biotelemetry.

Reference Citation	Location	Predators Studied			Findings and Conclusions
		Coyote	Bobcat	Eagle	
Knipe (1944)	Arizona	X		X	Early report on predation and predator control.
Einarsen (1948)	Oregon	X	X	X	If coyotes are not controlled, they may be a limiting factor for fawns.
Jones (1949)	Texas	X			Regardless of control, coyotes prevented fawn increases.
Buechner (1950)	Texas	X		X	Fawns taken by eagles/ coyotes. Predator control for livestock helps fawns.
Arrington & Edwards (1951)	Arizona	X	X	X	Trapping and poisoning predators increased fawns.
Ackerly & Regier (1953)	California	X	X	X	Predation was not significant in total mortality.
Udy (1953)	Utah	X			Predation greater in small herds. Forage key to increasing numbers.
Hansen (1955)	Oregon	X	X	X	Fawn mortality studied including predation.
Folker (1956)	Idaho	X	X	X	Predation and other mortality reported.
Yoakum (1957)	Oregon	X	X	X	Predation reported not a major cause of mortality.
Compton (1958)	Oregon	X	X	X	Concluded predation not limiting herds.
Hinman (1959)	Utah	X			Golden eagles kill many fawns: forage biggest issue.
Larsen (1970)	New Mexico	X		X	Reported mortality factors including predation.
Neff and Woolsey (1979)	Arizona	X			Predation major factor: limits survival and herds.
Neff et al. (1985)	Arizona	X			Aerial gunning of coyotes increased fawn survival.
Menzel (1992)	Nebraska	X			Increased FF:DD ratios but not herds.
Fairbands (1993)	Colorado	X		X	Studies mainly of fawn behavior. Used telemetry.
Byers (1997)	Montana	X		X	Reported behavior and predation. Used telemetry.
TOTAL: 18 studies: Arizona 4, California l, Idaho l, Montana 1, Nebraska l, New Mexico 1, Oregon 4, Texas 2, Utah 3.					

Table 2. Radiotelemetry studies of predation on pronghorn fawns (modified from Linnell et al. 1995 and O'Gara and Shaw 2004). Predator codes are: C=coyote, B=bobcat, M=Mt. Lion, E=golden eagle, U=unknown.

Study Reference	Province or State	Number Fawns Radioed	Mortality Attributed to Predation		Number Mortalities Attributed to Predators				
			n	%	C	B	M	E	U
Beale (1978)	Utah	200	97	48	39	36	—	21	1
Bodie (1979)	Idaho	42	15	36	4	2	—	7	2
Tucker (1979)	Texas	18	9	50	6	3	—	—	—
Barrett (1982)	Alberta	62	27	44	14	13	—	—	—
McNay (1982)	Nevada	34	13	38	12	—	—	1	—
Autenrieth (1982)	Idaho	48	24	50	7	3	—	8	6
Trainer et al. (1983)	Oregon	131	83	63	55	7	—	8	13
Autenrieth (1984)	Idaho	67	13	19	3	7	—	3	—
Firchow (1986)	Colorado	26	12	46	12	—	—	—	—
Ockenfels et al. (1992)	Arizona	11	1	9	1	—	—	—	—
Canon (1993)	Texas	78	63	81	49	5	6	3	—
Rothchild (1993)	Kansas	43	25	58	25	—	—	—	—
Total 12 Studies	8 States 1 Province	760	382	53 (mean)	227	76	6	51	22

Table 3. Studies using telemetry to determine the cause of neonatal mortality in pronghorn at the National Bison Range, Montana.

Reference	n	Total Mortalities (%)	Predation Mortalities (%)	Predator Species (%)			% Predation by Species		
				Coyote	Bobcat	Golden Eagle	Coyote	Bobcat	Golden Eagle
Reichel (1976)	19	16(84)	5(26)	5(26)	—	—	100	—	—
Von Gunten (1978)	23	20(87)	20(87)	16(70)	3(13)	1(4)	80	15	5
Corneli (1980)	24	16(67)	14(58)	9(38)	3(13)	2(8)	64	21	14
Total	66	52(79)	39(59)	30(45)	6(9)	3(5)	77	15	8

Table 4. Mortality attributed to predation for radio-collared pronghorn neonates on the July 30 each year. Source: Hart Mountain National Antelope Refuge files, Lakeview, Oregon, USA. The number of mortalities is expressed as a percent of the annual sample.

Year	n	Total Mortalities (%)	Total Predation Mortality (%)	Mortality by Predator (%)				
				Coyote	Bobcat	Golden Eagle	Cougar	Unknown
1996	52	43(83)	37(44)	29(56)	—	1(2)	—	7(13)
1997	52	46(88)	38(43)	23(44)	—	2(4)	—	13(25)
1998	26	26(100)	21(81)	19(73)	1(4)	1(4)	—	—
1999	25	21(84)	17(81)	16(64)	—	1(4)	—	—
2000	39	27(69)	16(59)	11(28)	1(3)	4(10)	—	—
2001	50	18(36)	10(55)	8(16)	1(2)	1(2)	—	—
2002	32	15(47)	11(73)	9(28)	—	2(6)	—	—
2003	28	7(25)	5(71)	2(7)	—	1(4)	2(7)	—
2004	22	11(50)	7(63)	5(23)	—	1(5)	1(5)	—
2005	21	11(52)	7(33)	3(14)	4(19)	—	—	—
Total	347	225(65)	169(49)	125(36)	7(2)	14(4)	3(1)	20(6)

Table 5. Management agencies in the United States that contributed funds for predator control and their intended impact for pronghorn.

| State	1999		2001
	Dollars Contributed	% That May Benefit Pronghorn	Contributed Funds
Arizona	33,900	100	X
California	23,000	<1	
Idaho	100,000	<5	
Montana	100,000	66	X
New Mexico	50,000	0	
North Dakota	184,000	10	
Nevada	—	—	X
Oregon	80,000	15	X
Utah	100,000	unknown	X
Wyoming	100,000	unknown	X
TOTAL	779,400		
Source: 1999 — Wildlife Management Institute (2000). 2001 — Hacks and Menzel (2002). Contributed funds for pronghorn enhancement but amounts not specified.			
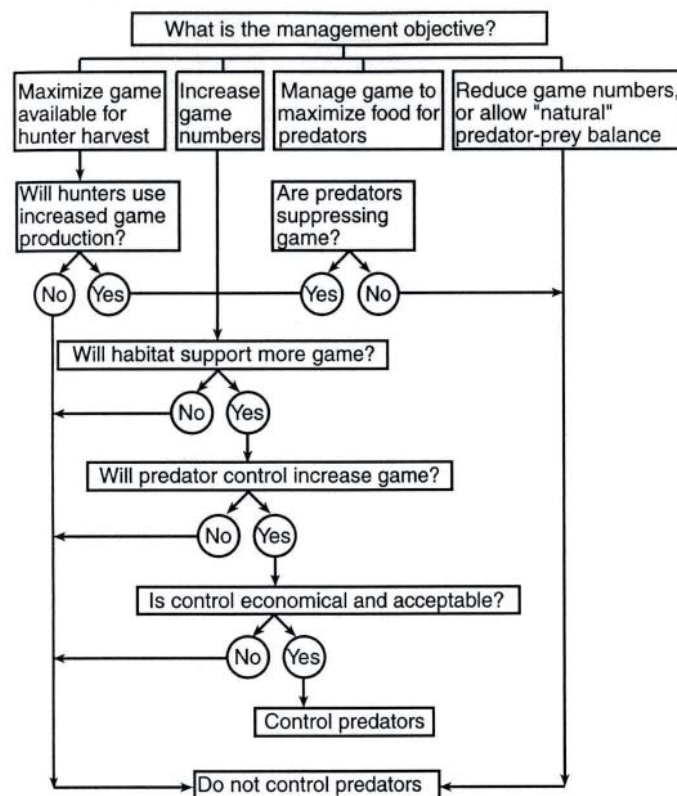
Fig. 1. Recommended decision matrix to determine whether proposed research projects or predator control programs are warranted (Connolly 1978b).
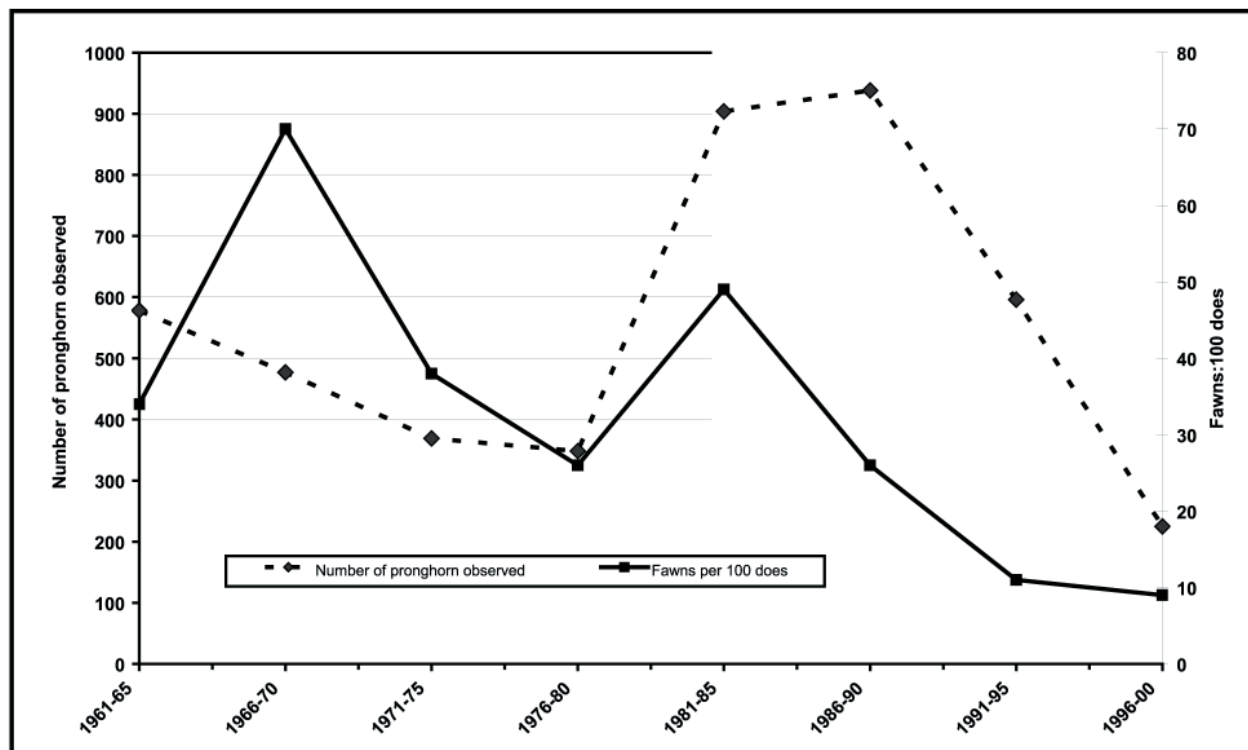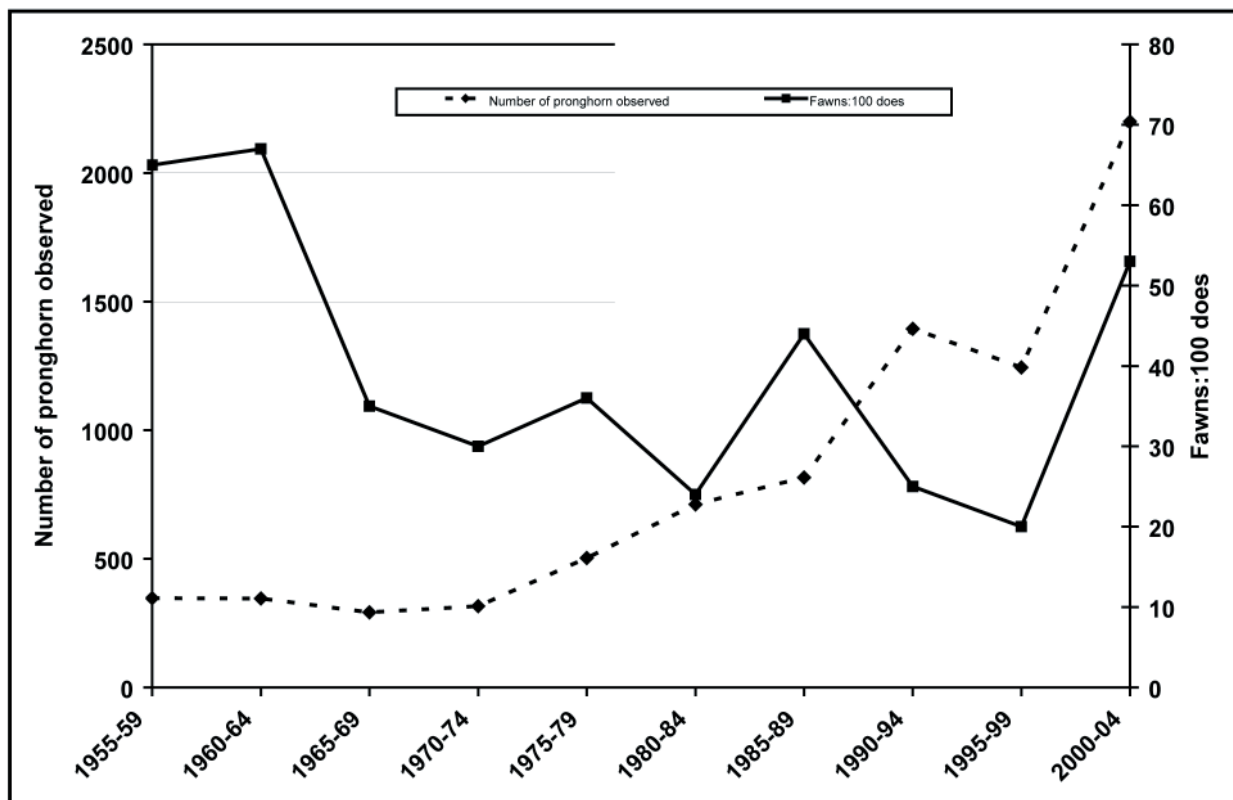

Fig. 2. Number of pronghorn observed and ff:100dd ratios during summer surveys in 5-yr increments from 1961 to 2000, Anderson Mesa, Arizona. Poisoning of coyotes was carried out until 1972. Trapping was carried out on private land until 1981. Trapping was banned on public land in 1974. Aerial gunning was carried out 1982-1983, 1987-1989, 1998, and 2000. (Source: Arizona Game & Fish Department 2002).

Fig. 3. Number of pronghorn observed and ff:100dd ratios during summer surveys in 5-yr increments from 1955 to 2004, Hart Mountain NWR Predator control was carried out through 1967, but not thereafter. (Source: U.S. Fish & Wildlife Service files, Lakeview, Oregon).

THE PENINSULAR PRONGHORN RECOVERY PLAN: 20 YEARS

JORGE CANCINO, Centro de Investigaciones Biológicas del Noroeste, S.C., Mar Ber-
meho 195. Col Playa Palo de Sta. Rita. La Paz, 23090, Baja California Sur, México.
jcancino@cibonor.mx

RAMON CASTELLANOS, Reserva de la Biosfera El Vizcaíno. Domicilio conocido "Casa de la
fauna", Guerrero Negro, 23940, Baja California Sur, México. berrendo@vizcaino.gob.mx

JEFF HOLLAND, Los Angeles Zoo. 5333 Zoo Drive, Los Angeles, CA 90027 U.S.A.
JHolland@zoo.lacity.org

FELIPE RAMÍREZ, Dirección General de Vida Silvestre. Av. Revolución 1425, col. Tlacopac
San Angel. México, 01040, D.F.

VICTOR SÁNCHEZ, Comisión Nacional de Áreas Naturales Protegidas. Camino al Ajusco 200
3er. Piso. Tlalpan. Col. Jardines en la Montaña, México, 14210, D.F.

Abstract: The peninsular pronghorn (*Antilocapra americana peninsulari*s) is critically endan-
gered. Contributing factors may include habitat modification, poaching, predation, drought and
inbreeding. The current working draft of the Peninsular Pronghorn Recovery Plan (PPRP) has
evolved substantially from the first draft, which was prepared in 1984. The PPRP prescribes 3
management strategies: a) Monitoring of the wild population b) Captive breeding, and c) Envi-
ronmental education. Monitoring of the wild population was the primary emphasis from 1984 to
1996 and is still a key element of the program, which includes monthly surveillance and annual
population estimates. However the primary focus shifted to captive breeding and management
in 1998 when 5 fawns were captured and used to establish a captive population. As a result
of additional captures and reproduction, the captive population has subsequently grown to 130
animals, which are held in a 259 ha enclosure that is part of the El Vizcaino Biosphere Reserve.
A visitor center associated with captive breeding facility is the most prominent component of the
environmental education program and has become a special-interest destination for visitors to the
reserve. The next new tasks in the PPRP are the future reintroductions. Population and Habitat
Viability Assessment workshops were held in 1994 and 2004. The PPRP includes programs,
projects and agreements among several Mexican and international institutions.

Key words: *Antilocapra americana peninsularis,* captive breeding, education, endangered
species, Mexico, peninsular pronghorn, recovery plan.

The International Union for the Conservation of Nature (IUCN) has classified the peninsular
pronghorn (*Antilocapra americana* peninsularis) as a subspecies at "critical risk" (IUCN 2003).
The species is also classified as endangered by the government of Mexico list NOM-059 2002
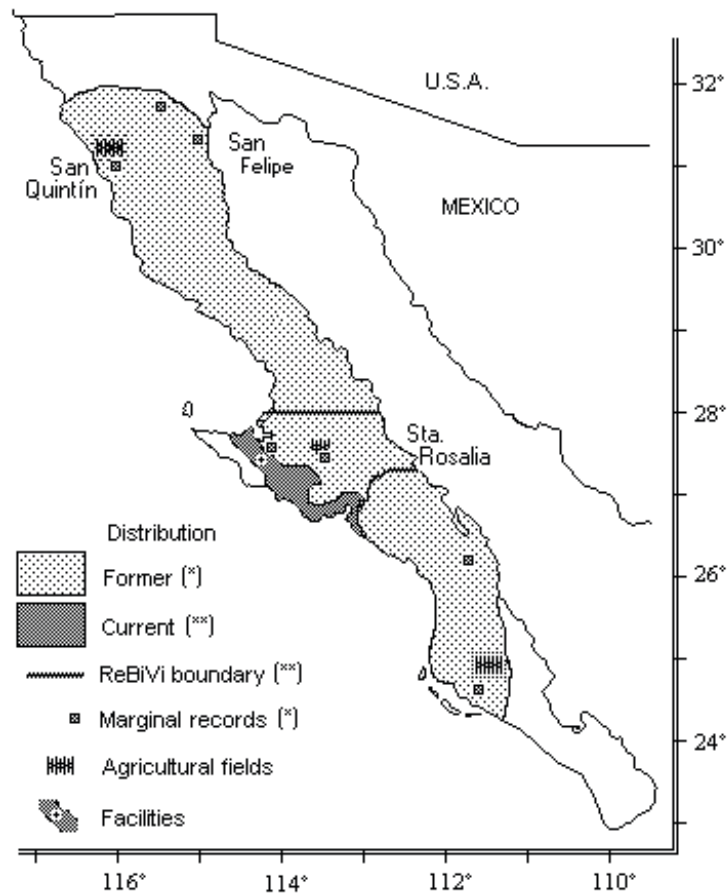(D.O.F. 2002). Figure 1 shows the historic range of the peninsular subspecies, marginal records

Fig. 1. Former and current distribution of the peninsular pronghorn, and other references. (*)(Hall 1981), and (**)(SEDUE 1988).

to estimate this range (Hall 1981), the current distribution in the "El Vizcaino" Biosphere Reserve (ReBiVi after its Spanish name) and the reserve boundaries (SEDUE 1988). This figure also shows the agricultural fields and some towns in the area, but not the extensive road network or other development (e.g. numeros small towns, ranches, and fishering camps).

Peninsular pronghorn population has decreased because of:

1. ***Habitat changes.*** The former range of peninsular pronghorn spanned 40,000 Km^2 and has been reduced in extent by 90%. The reduction has resulted from spread of agriculture, dirt roads, cattle ranching, settlement and tourist developments (*Cancin*o et al. 1994).

2. ***Poaching.*** Anecdotal reports describe the massive aerial shooting. At present poaching probably consist primarily of occasional shooting. We had found several traces (e.g. rifle cartridges), received local reports, and formal denounces also.

3. ***Predation.*** There are a couple of relevant studies on coyote (*Canis latrans*) diets (Sanabria et al. 1996, Grajales 1998). The first one reported the consumption of pronghorn fawns but not in the second one. Discussions about predation versus scavaging can be endless; however, it is a matter of fact that predation happens. Another potential predator in the Vizcaino Desert is the golden eagle (*Aquila chrysaetos*).

4. ***Drought.*** Peninsular pronghorn inhabit an arid desert environment. Droughts that span several years can have devastating effects on the population as has been reported for Sonoran pronghorn in Arizona (Hervert et al. 2001).

5. *Inbreeding.* Genetic diversity of the peninsular pronghorn has not been studied. However, the population is quit small and has been closed to immigration in over 100 years.

The first version of the Peninsular Pronghorn Recovery Plan (PPRP) was prepared in 1984 (Jaramillo 1989). Since then, some important changes have been incorporated. For instance, the initial draft did not consider captive management which is now a central theme. From 1984 until 1996 wild population monitoring was the main activity.

The first peer review of the PPRP occurred in 1994 as part of the Population and Habitat Viability Assessment Workshop (PHVA), a meeting developed in the format of the Conservation Breeding Specialist Group (Seal 1993, Cancino et al. 1995). The ReBiVi was decreed in 1988 (SEDUE 1988); however it didn't get implemented until 1994. The captive pronghorns at the ReBiVi are held in a 259 hectare enclosure that is subdivided with moveable fences. The enclosure also included an irrigation system, and two towers. Figure 2 shows a diagram of the facilities.
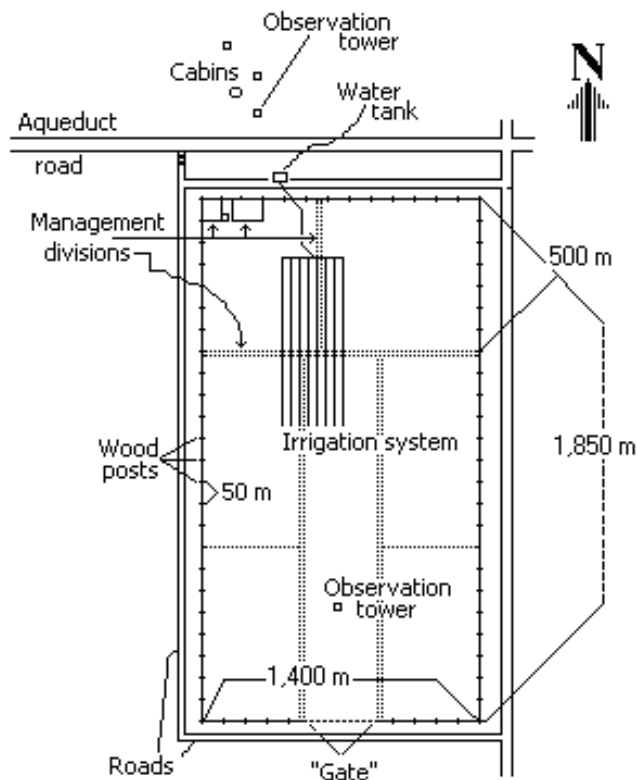

Fig. 2. Diagram of the facilities for the peninsular pronghorn captive management, located in the "El Vizcaino" Biosphere Reserve (modified from Cancino et al. 2002).

The ReBiVi captive pronghorn population originated with 5 fawns captured in 1998. Eleven more wild-captured fawns and 6 adults were added until 2000. Also, 9 births occurred in 2000 and represent the first births in captivity for this subspecies (Castellanos and Holland 2003).

As of 2004, there are 129 peninsular pronghorns in captivity. Table 1 includes a summary of pronghorn numbers for the past 7 years. SPARKS (v1.42) is the program used for the studbook (Scobie 1997). Staff from the Los Angeles Zoo have been assisting with the development of

reproductive strategies since 2001 (Castellanos and Holland 2003). One animal was released into the wild in 2004.

Table 1. Numbers of the peninsular pronghorn captive population (until April 2004).

	1998	1999	2000	2001	2002	2003	2004
Wild fawns captured	5	4	7	—	—	—	—
Wild adults captured	—	5	1	1	1	1	1
Births in captivity	—	—	9	17	25	34	49
Deaths	—	3	4	6	4	3	8
Releases	—	—	—	—	—	—	1
Subtotal	5	6	13	12	22	32	41
Total	5	11	24	36	58	90	130*
* Total excludes 1 animal collared released.							

Some fawns (n=12) were donated by the Wyoming Game and Fish Department and the F.E. Warren Air Force Base, in 2000 (Cancino and Guenzel 2002). They were transferred to Bioparque Estrella at Nuevo León and used for exhibit. The PPRP still consider some techniques for assisted reproduction. For that purpose, another 47 fawns were translocated from the same Base, in June 2005, and located at "El Bonito" ranch, in Coahuila (Zitek 2005).

Although pronghorn husbandry has become the primary focus of the conservation efforts, monitoring of the wild pronghorn population has continued. Monitoring efforts include monthly surveillance, and annual population surveys which combine the results of aerial and ground counts. Ground survey was possible because of the extensive dirt road network. Aerial survey has been carried out using a Cessna 182 of the Environmental Flying Services (a NGO based in Tucson, Arizona). Just the main Core Zone of the Reserve is aerial surveyed. Population esti-mates for 1977-2003 period are shown in the Fig. 3.

Environmental education is the primary focus of a visitor center located in the Vizcaino Des-ert and associated with the captive breeding facility. This center expanded the impact of the cap-tive management facilities by turning the place into a special destination in the Reserve. Outreach efforts undertaken to increase public awareness have been included, for instance a videotape made by Canal 11, from the National Polytechnic Institute. Posters, brochures, postal cards, and stickers are distributed for free in local and state schools during visits and chats. Chats at schools achieve different levels, from elementary school to some particular groups in the state university.

In 2004, the PHVA was revisited (Cancino 2003). This meeting had 47 attendants from Mex-ico and USA. Over 25 different institutions were represented. There were five working groups: (1) Pronghorn and society, (2) Captive management, (3) The wild population, (4) Habitat, and (5) Population modeling with Vortex. One of the more outstanding themes was the future trans-locations. The PPRP includes projects, programs, and agreements among several Mexican and international institutions such as Ford Motor Co., Espacios Naturales y Desarrollo Sustentable, the coauthors' institutions and other mentioned in this report. Efforts under the PPRP over the past 20 years are contributing to the recovery of the peninsular pronghorn. Much work remains, and depends upon the continued cooperation of national and international organizations.
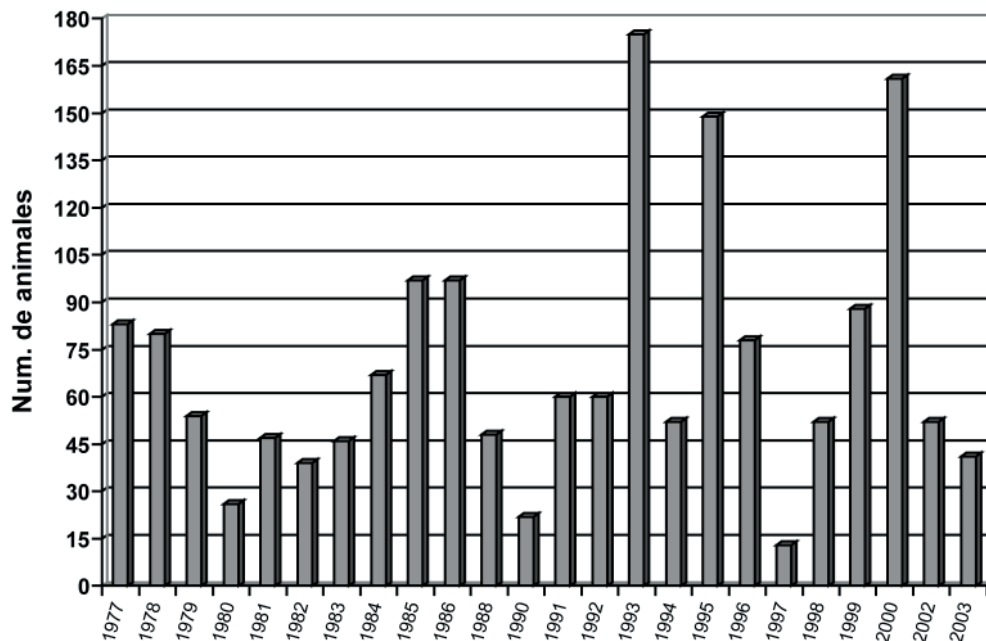
Fig. 3. Data surveys for the peninsular pronghorn for the 1977-2003 period and for the Core Zone of the ReBiVi

ACKNOWLEDGEMENT

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PRONGHORN RECRUITMENT STUDY: STATUS REPORT

SCOTT C. SPRAGUE, Arizona Game and Fish Department, 2221 W. Greenway Rd., Phoenix, AZ 85023

KIRBY D. BRISTOW, Arizona Game and Fish Department, 2221 W. Greenway Rd., Phoenix, AZ 85023

TIM ROGERS, Arizona Game and Fish Department, 2221 W. Greenway Rd., Phoenix, AZ 85023

SHELLI A. DUBAY, (Current address) Michigan Department of Natural Resources Waterloo Wildlife Office, 13578 Seymour Road, Grass Lake, MI 49240

STAN C. CUNNINGHAM, Arizona Game and Fish Department, 2221 W. Greenway Rd., Phoenix, AZ 85023

RICHARD A. OCKENFELS, Arizona Game and Fish Department, 2221 W. Greenway Rd., Phoenix, AZ 85023. E-mail: rockenfels@gf.state.az.us

Abstract: Arizona's American Pronghorn (*Antilocapra americana americana*) have suffered a significant decline. This project was initiated in 2001 to determine how 9 factors work in concert to affect fawn recruitment. Pairs of study sites, representing low and higher recruitment areas, were selected in different habitat types across the state. Samples are collected from hunter-harvested animals to test for disease exposure and mineral deficiencies. Fresh pellets and plants are collected for nutritional analysis of diets during 4 sample periods. Availability and quality of water is monitored through spring and summer. Relative abundance of predators is determined using scat deposition rates. Potential fawn bed site cover within 1 km of water is estimated using a line-intercept method and visibility board. Recreational use is measured using traffic counters. Tree/shrub densities have been recorded at random locations in each study site. Fence density and type will be observed. Soil samples are collected to observe health indices. Comparisons between and among sites will determine the distribution and significance of each factor. Analyses will also investigate correlations between variables to derive combinations that have compounded effects. After 2 years of data collection, disease, nutrition, water, hiding cover, and predator abundance seem to be having an impact. No preliminary analysis is available for the fence, tree, and soil components. Measurements of recreational use along major roads have shown no evidence of impact. Data collection will come to a close in August 2004, and the completion date for the final report is 30 June 2005.

FACTORS INFLUENCING A DECLINING PRONGHORN POPULATION IN WIND CAVE NATIONAL PARK, SOUTH DAKOTA

JARET D. SIEVERS, Box 2140B, NPB 138, South Dakota State University, Brookings, South Dakota 57007, jaretsievers@yahoo.com

J. A. JENKS, Box 2140B, NPB 138, South Dakota State University, Brookings, South Dakota 57007

C. N. JACQUES, Box 2140B, NPB 138, South Dakota State University, Brookings, South Dakota 57007

Abstract: Pronghorn (*Antilocapra americana*) were introduced into Wind Cave National Park in 1914 and have inhabited the park for almost a century. A decline in the population has raised concern for sustaining a stable population inside Wind Cave. Knowledge of diet quality, genetic variation, causes and extent of mortality, and information related to movement and dispersal are important in understanding the factors contributing to this decline. The primary objective of our study was to identify factors contributing to the decline of pronghorn in Wind Cave with regard to movement, mortality, genetic variation, and diet quality. Radio telemetry was used to monitor the movement and mortality of 8 adult (>1 year at capture) and 19 neonate (< 1 month at capture) pronghorn from 26 January 2002 to 31 December 2003. We obtained 407 visual locations on adult females (n=407) and 148 visual locations on neonates. Movement out of Wind Cave did not result in significant losses during our study. Survival of adult female pronghorn was 75% overall, and pooled survival of pronghorn neonates was 31% over a 2 year period. Predation accounted for all adult pronghorn deaths and 92% of neonate mortalities during the study. Twenty-seven plant species were identified in pronghorn annual diets through microhistological fecal analysis. Microsatellite DNA analysis showed that pronghorn in Wind Cave had slightly lower observed heterozygosity (HO=0.455) than free-ranging populations in South Dakota (HO=0.475, 0.677). We concluded that fawn mortality was a significant factor limiting population growth in pronghorn within Wind Cave National Park.

ROAD EFFECTS ON PRONGHORN IN SOUTHERN ALBERTA, CANADA

SHANNON D. GAVIN, Department of Biological Sciences, University of Calgary, Calgary, Alberta, Canada T2N 1N4

Abstract. Traffic along roads may be associated with mortality via vehicular collisions or indirectly by increased hunting access. The risk-disturbance hypothesis proposes that organisms will perceive human disturbances as a predation risk and exhibit risk avoidance behaviour. Traffic may disrupt the daily activities of wildlife such as foraging or cause habitat avoidance surrounding road networks. This paper reports results for the first year of a 2 year study on the effects of traffic level and distance from roads on the behaviour and habitat use of pronghorn (*Antilocapra americana*). There was a trend for pronghorn to increase vigilance and forage less along roads with higher traffic levels. Pronghorn also foraged more when they were further away from roads. Low traffic roads had a higher density of fecal pellet groups than the higher traffic roads suggesting pronghorn perceived a greater risk along these higher traveled roads. Distance from roads did not affect habitat use as measured by pellet group density. My results indicate that the intensity of road use affects pronghorn foraging behaviour and habitat use. Understanding how wildlife respond to these perturbations is important for maintaining populations especially those that occupy their most northern geographic range.

INTRODUCTION

Predation is a strong selective force on an organism's behaviour and habitat selection for foraging or reproductive opportunities (Lima and Dill 1990). Organisms may respond to stimuli that are not in their evolutionary history if these stimuli have similar characteristics to a natural predator such as fast and direct approach rate (Frid and Dill 2002). The risk- disturbance hypothesis proposes that organisms will perceive human disturbances as a predation risk and exhibit behaviour that will minimize this risk (Frid and Dill 2002). This can include increasing vigilance levels, higher flight probabilities, habitat avoidance or forming larger groups to dilute the predation risk. Organisms, therefore, face a trade-off between resource acquisition and the costs of increased energy expenditures from risk avoidance behaviour (Lima and Dill 1990; Elgar 1989). Risk perception towards human disturbances should also be stronger in populations that are under hunting pressure because this maintains a degree of danger towards humans (Verlhurst 2001).

Wide ranging species, such as the pronghorn (*Antilocapra american*a), are vulnerable to fragmentation because roads, fences, or competing human land uses can restrict animal movement and can alter the quality of the habitat for animal use. Roads can increase wildlife mortality risk either directly (vehicular collisions) or indirectly (increased hunter access) which may result in animals avoiding habitat adjacent to roads (Jalkotzy et al. 1997). Human disturbances that disrupt an animal's daily behavioural activities can affect energy expenditure during already energy draining periods such as winter or reproductive periods. Bighorn sheep (*Ovis canadensis*) were more likely to flee the area in response to hikers during the lambing and rut season which can have ramifications on reproductive fitness (Papouchis et al. 2001). If an individual perceives

risk towards the disturbance, it may have to reduce foraging to increase vigilance behaviour or expend energy in leaving the area (Jalkotzy et al. 1997). The strength of the behavioural response towards the human disturbance may be reflected in their habitat use near the disturbance. The greater the energy expended on risk avoidance behaviour may cause animals to avoid or shift away from the disturbed area (Frid and Dill 2002). If alternative habitat is available, potential consequences of shifting into new habitat include moving into areas with lower forage quality or fewer refuge areas. Caribou (*Rangifer tarandus*), for example, avoid linear features like seismic lines and roads due to the increase in traffic and predators (Curatolo and Murphy 1986; Dyer et al. 2001) which may impede the caribou's ability to avoid harsh weather and deep snow (Eide et al. 1986). These same linear features are used as conduits by wolves (*Canis lupus*) and provide increased access into caribou range. As a result, caribou that occupy habitat near a road suffer higher predation (James and Stuart-Smith 2000).

RESEARCH OBJECTIVES

Southern Alberta, Canada, is at the most northern and extreme range of the pronghorn where populations fluctuate due to severe weather (Glasgow 1990). Pronghorn still exhibit some migratory behaviour as they move from their summer to winter ranges (Glasgow 1990). Anthropogenic features such as roads and fences that impede movement away from deep snow, access to watering holes, thermal cover, and quality food resources may impact populations.

This paper reports the results from the first year of a two year study examining whether pronghorn exhibit behaviour and habitat use analogous to a natural predation hazard which would support the risk-disturbance hypothesis. I measured potential risk perception towards roads by recording responses across increasing traffic levels and proximity to roads which may be associated with increasing risk. My objectives were 1) to determine the time pronghorn allocate to specific behaviours along roads of various traffic levels and at different distances from the road and 2) to determine pronghorn habitat use along roads of various traffic levels and at different distances from the road. I predicted that roads with higher traffic levels would be perceived as a predation risk, which would be reflected in lower foraging, increased vigilance and reduced presence along these roads. If pronghorn perceive roads with a predation risk, then non-roaded areas should have higher density of pronghorns in these areas compared to those closer to roads.

METHODS

Study Area:

The pronghorn range in Alberta is categorized as a dry mixed grass which is the largest of the 4 grassland subregions in the province (Alberta Environmental Protection 1997). The common vegetation in this area includes wheat grass (*Agropyron smithii*), spear grass (*Stipa* species) and blue grama (*Bouteloua gracilis*). This subregion is the warmest and driest in Alberta with high rates of evaporation, low precipitation and high variation in seasonal temperatures (Alberta Environmental Protection 1997). Summer temperatures can reach above 40°C while low winter temperatures of -30°C are often offset by south-westerly Chinook winds that reduce snow cover (Mitchell 1980). Activities and habitat losses from agriculture, residential development, roads, and the petroleum industry have caused a 61% decline of prairie habitat (Alberta Environmental Protection 1997). As well, the dry mixed grass region of Alberta has one of the highest road den-

sities (1.07 km/km²) compared to the other three natural regions (Alberta Environmental Protection 1997).

Study Design:

Stratified sampling of pronghorn range was used to select survey areas that consisted of similar land use practices (rangeland only), habitat, road fencing, and pronghorn population densities (Patton 1992). Roads were categorized into traffic level ranges based on annual summer daily traffic counts for sections of that road for which 2002 traffic data were supplied by the Alberta Transportation Department. Two fenced roads were selected for each traffic level category of low (0-10 vehicles/day), medium (70-200 vehicles/day), and high (>300 vehicles/day). Traffic categories were chosen based on the roads available within pronghorn range. For habitat use surveys, a fourth category consisted of an area that was over 1 km away from any roads and was referred to as the "non-roaded" category. In this category, surveys were conducted perpendicular from fences that separated pastures to compare to the surveys along the fenced roads. Most ungulates, including pronghorn, have a visual acuity of 1 km (Nowak 1991) therefore; plots at distances beyond 1 km should be useful in comparing areas near roads and those away from roads. All plot and observation locations were recorded on GPS, to enable the application of a digital mapping analysis.

Behavioural Observations: Observations occurred within early morning and some evenings to avoid the mid-day heat waves that could obscure observations (Maher 1991). Each observation period lasted 3 hours on average. Behavioural observations were conducted when pronghorn were located from roads and within the field during pellet group surveys. I used a technique called the Russian Tank Maneuver for pronghorn observations near roads. This consisted of the observer using the vehicle as a blind to hide in the vegetation along the road and then the vehicle was driven out of sight to minimize influencing their behaviour. Pronghorns will normally flare the white hairs on their rump when alarmed and if they detect a human presence. Unless they exhibited this behaviour, I assumed that our presence did not affect their behaviour. Observations of animals in similar group compositions and sizes along the same roads were excluded from the analyses to minimize pseudo-replication. The animal was observed for 10 minutes using continuous recording, and focal animal sampling for recording time allotted to daily activities (Martin and Bateson 1986). When there were more than one animal, a focal animal was arbitrarily selected. For each focal observation, I recorded the size and herd composition (bachelor, mixed or female/fawn), position of the focal animal in the group (peripheral or centre), and its gender. I recorded all behaviours: foraging, vigilance, movement, resting and social interactions. Here I only present results on foraging and vigilance behaviours. The time allocated to these behaviours was analyzed based on the pronghorn's distance from the road and its traffic frequency. Distance from a road was estimated and categorized as 0-400m and >400m. Conducting pellet group surveys at designated distances along transects from roads to examine habitat use helped establish the accuracy in estimating the distances pronghorn were from roads for behavioural observations. Traffic level categories included low, medium and high traffic roads.

Habitat Use: Fecal pellet surveys were conducted in the summer of 2003 to estimate the presence of pronghorns along roads and their relative use of that area. Temporary 30m by 30m plots were placed along a transect at 0 m (along the fence), 200 m, 400 m and 600 m from the

fenced road. Pellet groups were compared across four categories of traffic (non-roaded, low, medium and high) where each traffic category had a total of 20 transects searched for pronghorn pellet groups. Fecal pellets were considered a group if they contained 5 or more individual pellets and were considered within the plot if more than half of the group was within the plot boundaries. Vegetation surveys were also conducted using the Daubenmire canopy coverage method which estimates the coverage of specific vegetation categories in each of the plots (Daubenmire 1959). These data are currently being analyzed to examine the interaction of habitat characteristics on pellet group distribution.

Analyses: Data were analyzed using the statistical software, JMP IN version 4.0 (SAS Institute, 2001). Two-way ANOVA's were used to examine whether the proportion of foraging or vigilance was different among three traffic levels (low, medium, and high), distances from roads (0-400m and >400m) and subsequent interactions. For analyses, I calculated the proportion of time of the behaviour for each focal observation by dividing it with the total observation time for that focal observation. This was done because some individuals moved out of sight before the 10 minute observation bout was completed.

A contingency test was used to analyze whether the presence/ absence of pellets (scored as 0 or 1) was independent of traffic level (non-roaded, low, medium, high), as well as distance from a road (0m, 200m, 400m, 600m).

RESULTS
Behaviour:
Traffic level did not affect the proportion of foraging and there was no interaction between traffic level and distance from roads (Whole model: $F_{5,40}$=1.9, p=0.1; Traffic: $F_{2,40}$=1.2, p=0.3; Traffic*Distance: $F_{2,40}$=0.3, p=0.8). However, there was a trend of pronghorn reducing their foraging proportions along high traffic level roads compared to the other two traffic level categories. Pronghorn foraging proportion was affected by the distance the focal animal was located from roads (Figure 1; $F_{1,40}$=4.3, p=0.0439). The proportion of time pronghorn spent foraging doubled at distances >400 m from a road compared to closer proximities to the roads.

The proportion of time pronghorn spent being vigilant was not affected by traffic level or distance from roads (Whole model $F_{5,40}$=0.6, p=0.7). However, pronghorn did show a trend of higher vigilance along higher traffic roads compared to lower traffic roads.

Habitat Use:
The data were not normally distributed so non-parametric statistical analyses were used. Traffic level had a significant affect on the density of pronghorn pellet groups located (Pearson's χ^2=23.7, d.f.=3, p<0.0001) with a higher proportion of pellet groups found along low traffic roads (Figure 2). Non-roaded areas had the lowest pronghorn presence recorded compared to all other traffic level categories. The distance from roads did not affect pronghorn pellet density (Pearson's χ^2=1.3, d.f.=3, p=0.6).
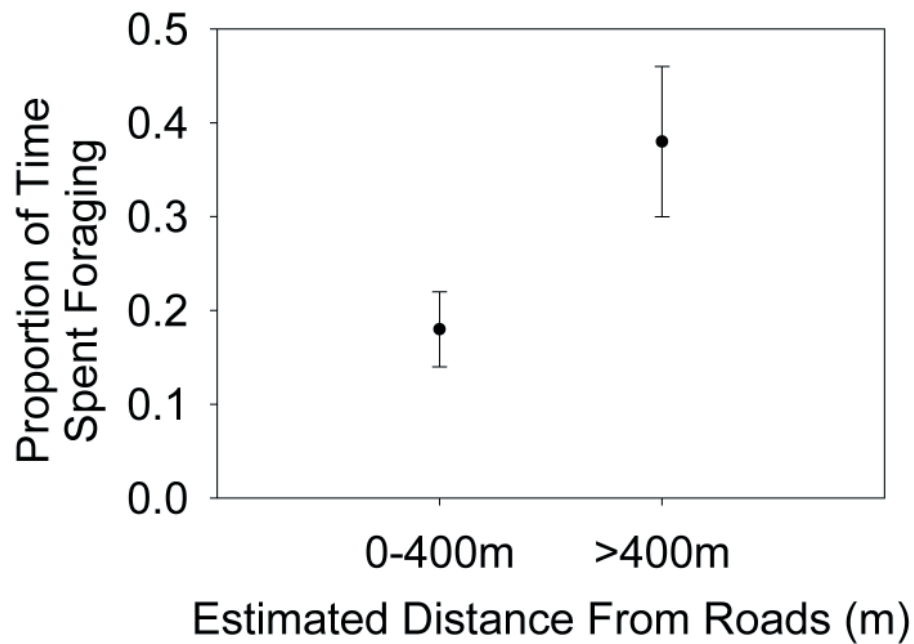
Fig. 1. The mean proportion of time pronghorn spent foraging across two estimated distance categories from roads, regardless of traffic level (N= 46). Foraging proportion was calculated by dividing each observed foraging time by the total time the observation bout lasted.
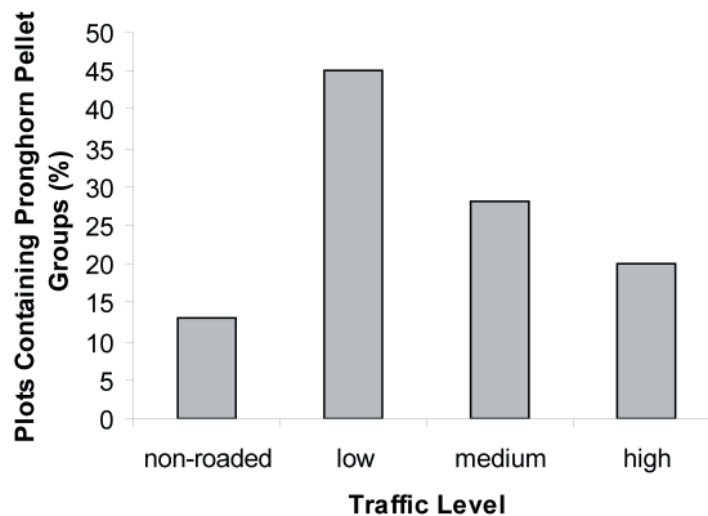

Fig. 2. The percentage of 30X30 m plots containing pronghorn fecal pellet groups out of all plots searched compared across three traffic level categories and non-roaded areas (N= 319).

DISCUSSION

Pronghorn did exhibit behaviour that was consistent with behaviour under a natural predation risk. The duration of pronghorn foraging was lower near roads than further away which suggest that roads of any traffic level act as a source of risk in the environment. The intensity of the response may be heightened by increasing traffic level because pronghorn showed a trend of reducing their foraging durations and increasing their vigilance levels along higher traffic roads. Because the data presented here are preliminary data, the sample size is low which can reduce the power of the statistical test even when there is a biological effect (Cohen 1969). The increased human activity along high traffic level roads may be associated with higher predator density and risk which can have ramifications on energy intake. Winter survival depends on conserving valuable energy reserves and allocating sufficient time to foraging. Individuals that are reducing their foraging or increasing their vigilance towards human disturbances, risk deleting their energy reserves more quickly which can lower their probability of survival during the winter. Bradshaw et al. (1998) modeled energetic losses in woodland caribou in response to multiple encounters with a disturbance from petroleum exploration. Caribou normally lose 10-15% of their autumn mass during the winter and 20-34 disturbance events would be required to exceed the normal winter loss. Caribou were exposed to five disturbance events in five years that could potentially lead to losses exceeding the normal winter loss. The birth and rut season are also very energy demanding time periods that can be confounded by the effects of human disturbances.

During rut in September, males reduce their foraging for reproduction and harem defense (Byers 1997). Therefore, individuals that reduce their foraging throughout the summer due to disruptions from traffic may enter rut and the winter with a lower fat reserve which can affect survival (Bobek 1977).

The preliminary analyses suggest that pronghorn may be perceiving road traffic as a predation risk which supports the risk-disturbance hypothesis. Increasing risk avoidance behaviour with increasing traffic may also cause individuals to adjust their habitat use near the disturbance. The higher risk avoidance behaviour exhibited within habitat near high traffic roads may have influenced the lower pronghorn presence along these roads. Pronghorn pellet densities were highest within habitat near lower traffic level roads which may be perceived with lower risk because of the infrequent vehicle use. I had expected that non-roaded areas would have the highest pellet density which would be associated with pronghorn preferring these areas because they have lowest risk but these areas actually had the lowest pellet density. It is possible that there may be habitat differences between the survey sites and future analyses of vegetation coverage will be examined. Pronghorn did not completely avoid areas near high traffic roads, although they were at lower densities in these areas. Under natural predation hazards, if safer areas have more individuals, intra-specific competition may reduce an individual's resource consumption resulting in some individuals accepting greater risk to achieve necessary energy requirements (Lima and Dill 1990). Individuals occupying areas near higher traffic roads may be trading safety for higher resource acquisition. It is also possible that suitable alternative habitat was not available for individuals to shift into to avoid high traffic roads.

This study suggests that pronghorn are exhibiting behaviour consistent with the risk-disturbance hypothesis. The cumulative effect of hunting and vehicular collisions on wildlife mortality may contribute to wildlife associating human presence with a predation risk. In Alberta, pronghorn are a game species that have few protected habitats in the province. This study contributes to the current knowledge because research into how pronghorn respond to perturbations in their northern range where they are not protected in National Parks is lacking.

MANAGEMENT IMPLICATIONS

In Alberta, pronghorns occupy much of the dry mixed grass region that makes up only 7 % of the area of Alberta (Alberta Environmental Protection 1997). Therefore, fragmentations causing habitat loss or barriers to this restricted range are critical components when considering management strategies, especially in their northern habitat. There is an increasing urgency to monitor the landscape effects of anthropogenic features on pronghorn behaviour and dynamics to create management practices that will maintain a viable population in all parts of their range.

ACKNOWLEDGMENTS

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MOVEMENT AND DISPERSION OF PRONGHORN IN SOUTHWESTERN WYOMING

DALY SHELDON, Zoology and Physiology Department, University of Wyoming, Box 3166 University Station, Laramie, WY 82071. email: sheldon2@uwyo.edu; phone: 307/766-2091.

FRED LINDZEY, Zoology and Physiology Department, University of Wyoming, Box 3166 University Station, Laramie, WY 82071.

Abstract: Pronghorn (*Antilocapra american*a) 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. Although it is generally recognized that fences can hinder or block the ability of pronghorn to move, the influence of fences on movement and dispersion patterns has not been quantified for pronghorn in their natural setting. Using global positioning system (GPS) collars and geographic information systems (GIS), we demonstrate how results of analyses can be used to characterize pronghorn home ranges within a population in southwestern Wyoming. Furthermore, this technology is used to evaluate the effect of fences on the movement and dispersion patterns of collared pronghorn. Results of this ongoing study should aid managers in evaluating the influence of existing fences and the possible consequences of proposed fences on pronghorn populations throughout their range.

PRONGHORN AND FENCES: A REVIEW AND NEW MANAGEMENT STRATEGIES

JIM D. YOAKUM, Western Wildlife, Post Office Box 369, Verdi, NV 89439-0369

Abstract: During the 1960s and 1970s, the influence of rangeland wire fences on pronghorn welfare was a major management issue. New fence configurations were researched and filed tested to allow pronghorn access through fences constructed to control livestock. Then the pronghorn/fence controversy subsided. Now, two decades later, this paper reviews, assesses and makes readily available to wildlife and range managers, the fence designs that have proven most effective in allowing pronghorn movements. In addition, certain fences that apparently limit pronghorn mobility have been identified and are not recommended. The need for disassembling dysfunctional rangeland fences warrants greater implementation emphasis. A new recommended smooth wire fence design has been developed to allow pronghorn movement on rangelands occupied by livestock. Field investigations are in progress by the Wyoming Cooperative Fish and Wildlife Research Unit regarding the relationships of electrical fences to pronghorn and wild/domestic ungulates.

HISTORY OF PRONGHORNS TRANSLOCATED FROM YELLOWSTONE NATIONAL PARK

M. DOUGLAS SCOTT,[1] National Science Foundation Rural Systemic Initiative, Chief Dull Knife College, Lame Deer, Montana 59043, USA

[1] Present address: 16257 Bridger Canyon, Bozeman, Montana 59715, USA

Abstract: At the beginning of the 20th Century many people feared that pronghorns (*Antilocapra americana*) would soon become extinct and Yellowstone National Park (YNP) trapped 12 animals intended for preservation in American and British zoos. By 1938, pronghorns were thought to be too abundant and damaging their range in the park. Fish and game agencies, national parks, and game preserves in the West were reintroducing pronghorns into empty historic range, and from 1947 to 1964, 888 live Yellowstone pronghorns were translocated for wild release in 6 states. The (former) Montana Fish and Game Department (MFG) provided most of the trapping materials and expertise, and nearly half of the captured pronghorns were released in south central Montana. The fenced National Bison Range (NBR), in northwestern Montana, received 31 of the animals in the 1950s. The NBR also received 20 pronghorns from other sources over the years, but their present herd gene pool still is likely to be about 72% derived from Yellowstone. This herd multiplied quickly, and many were translocated to other states during the 1960s. One pronghorn herd in far western Kansas may be the most genetically pure, unfenced descendants of Yellowstone animals, with possibly 44% of the gene pool derived from NBR/YNP animals. Pronghorn populations unaffected by translocated animals are a rarity in the U.S. today. Managers working with such populations should make efforts to manage them through manipulation of habitat, predation, and hunting, rather than stocking animals with dissimilar genetic makeup, so that adapted ecotypes might be preserved. Yellowstone's pronghorn herd is dwindling, and the park may have to supplement them with translocated animals carrying Yellowstone genes. Other management options for this herd are discussed.

PRONGHORN WORKSHOP PROCEEDINGS 114-133

Key words: *Antilocapra americana,* genetics, history, population size, pronghorns, translocations, Yellowstone National Park

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Yellowstone National Park was officially designated by an act of the United States Congress in 1872. Almost from the beginning the number of pronghorns in the park was of interest, and Yellowstone's second superintendent, P. W. Norris, estimated their population in the park to be in the "thousands" (Norris 1878). Even some 30 years later, two acting superintendents still thought YNP held about 2,000 antelope (Pitcher 1906, Young 1907, 1908). These early estimates were subject to error, but a thorough review of pronghorn sightings in and near the park from 1806 through 1881 (Schullery and Whittlesley 1992) confirmed that pronghorns were commonly seen in the northern half of YNP, as well as in nearby Paradise Valley, through which the Yellowstone River flows north for about 70 km (Fig. 1).

Fig. 1. Pronghorn range in YNP, and potential habitat in Paradise Valley to the north.

During the last 20 years of the 19th century, Paradise Valley quickly became settled by farmers and miners who immigrated from Europe and eastern states. These people often "lived off the land" during their startup years, and evidently unrestricted shooting, as well as land use changes, eradicated pronghorns from the valley. By 1905, Acting Superintendent Pitcher noted: "The valley of the Yellowstone north of the park is now completely taken up by ranchers, and their wire fences running in every direction have completely shut off the old winter range of the antelope, and they are now compelled to remain at all times entirely within the limits of the park or very close to its borders" (Pitcher 1905). In 1907, Acting Superintendent Young remarked that pronghorns "are rapidly being exterminated in the United States outside the park", and that the few park pronghorns that wandered out (to the north) were "slaughtered by hunters in Montana" (Young 1907).

Many conservationists of the day shared Young's concern that the pronghorn was headed for extinction (Nelson 1925). Nelson reported a Biological Survey (now the U.S. Fish and Wildlife Service, USFWS) census made during 1922-1924 found about 30,000 pronghorns in North America, a drastic decline from an estimated original population of 30-40 million animals. Hoover et al. (1959:11) surveyed western state agencies and concluded that, in 1918, only 13,000 pronghorns remained in the United States.

As a result of this fear of pronghorn extinction at the turn of the century, limited numbers of Yellowstone animals were sent to zoos or used for reintroductions to distant localities. At the same time, several states began restocking former range from their own remnant herds, followed by protection of the animals from illegal hunting. In terms of increasing pronghorn numbers, the reintroduction programs were successful (Kitchen and O'Gara 1982). The total U.S. herd was estimated at > 1 million animals in 1983 (Yoakum 1986) and they are currently hunted in most western states on a sustained yield basis.

Unfortunately, the YNP pronghorn herd, which in 1908 possibly contained 5-10% of the entire North American population, has not shared in the success story of the species recovery. As early as 1897, Acting Superintendent Young believed Yellowstone pronghorns were "suffering for lack of suitable winter range" (Young 1897). A Presidential Proclamation by Herbert Hoover in 1932 officially protected former ranchland that included 3077 ha of important pronghorn winter range by including it within the northern park boundary. In spite of this, an Assistant Chief Ranger (Barrows 1938) stated just 6 years later that "Signs of over-use by antelope are beginning to appear on portions of the winter range." The first written record that suggested controlling the YNP pronghorn population because of "overgrazing" by them and the abundant park elk *(Cervus elaphus)* came the very next year (Barrows 1939). No studies were done to accurately determine if signs of grazing were primarily caused by elk, pronghorns, or other ungulates.

Reports in YNP files of spring pronghorn counts suggest that the Yellowstone herd remained fairly stable at about 700-800 animals from 1932 to 1946. Nevertheless, in 1944 park officials encouraged the MFG to hold a pronghorn hunt on the park boundary to "relieve the pressure on the winter range by removing surplus animals and stabilizing the herd at optimum size" (Rogers 1944). The hunt was not held. In 1946, park officials obtained authority from the Secretary of the Interior to begin a live-trapping program within the park to eventually reduce the herd to about 400 animals (U.S. National Park Service 1946). This desired level was revised downward 3 more times until 1953, when the Region Two National Park Service office approved a recommended reduction to 100-125 animals (Rogers 1953). Apparently, however, no thorough ecological data were gathered during these years which supported pronghorn reductions of this magnitude.

Large reductions of YNP pronghorns began in January 1947, when 235 animals were captured for translocation from a herd of approximately 780 (Rogers 1947). Several other large and small removals occurred in the 1950s and early 1960s. In April, 1962 a helicopter survey indicated the herd had declined to 278 animals (Howe 1962). Reduction to the 100-125 level was still thought to be necessary, so a research project which required killing pronghorns inside the park was approved (Barmore and Meagher 1965). Between fall 1965 and fall 1967, 106 pronghorns, mostly pregnant females, were collected in the park (O'Gara 1968). Total population size continued to decline during this time, and a park biologist reconsidered the wisdom of removing animals from Yellowstone, suggesting collections might instead be made in Montana's NBR (Barmore 1967).

All pronghorn removals from YNP stopped in 1967, but spring counts continued to drop nearer to 100 animals over the next 6 years (M. D. Scott, YNP unpublished data). In 1973, a park Resource Management Specialist stated "Pronghorn numbers may have been reduced below a minimum threshold for survival and recommendations have been made to reintroduce these animals" (Bucknall 1973). Fortunately this was not done, but pronghorn numbers stayed low, between 100 and 200 animals, for the next decade. After 1981, spring counts suggested pronghorns increased, then decreased again (Table 1). The decrease may have been partly due to pronghorn "depredation" hunts authorized near the park border by the Montana Department of

Table 1. Spring counts[a] and harvest outside the park, YNP pronghorn herd, 1981-2003.

Year	No. counted[a]	Hunting loss[b]
1981	102	
1982	131	
1983	310	
1984	365	
1985	364	10–12[c]
1986	363	12–15[c]
1987	478	16
1988	495	51
1989	372	–
1990	472	–
1991	591	23[d]
1992	536	31
1993	439	37
1994	no count	26
1995	235	2
1996	272[e]	–[c]
1997	210	–[c]
1998	231	–[c]
1999	204	–[c]
2000	205	–[c]
2001	206	–[c]
2002	242	–
2003	246	–

[a]Counts vary in accuracy and were generally done from a single aircraft on a single day.
[b]The first hunt since 1907 was held in 1985. No hunts were held in 1989, 1990, 2002, or 2003. From 1985 to 1995, 25 rifle permits and unlimited archery permits were issued per year. From 1996 to 1999, 5 rifle permits and unlimited archery permits were issued annually. In 2000-2001, 5 rifle permits per year were issued.
[c]Careful records were not kept these years by the Montana agency that approved the hunt. In 1996 through 2001, less than 5 pronghorns were thought to have been killed per year.
[d]These values include estimated kill by survey non-respondents.
[e]March ground count by author.

Fish, Wildlife and Parks (MTFWP), at the insistence of an adjacent property owner called "The Church Universal and Triumphant". A dwindling winter food supply, caused by heavy use of big sagebrush (*Artemisia tridentata*) by > 1000 elk on pronghorn winter range (M. D. Scott, YNP unpublished data; Singer and Renkin 1995) may have been a major reason for pronghorn declines. Also, coyote (*Canis latrans*) predation was found to cause > 95% loss to pronghorn fawns each year in the early 1990s (M.D. Scott, YNP unpublished data).

Lee et al. (1994) measured mitochondrial DNA variation in 110 individuals representing most of the pronghorn range in North America. They found that YNP pronghorns possessed more genetic variation than any other herd they sampled, and also discovered the herd possessed 1 haplotype found nowhere else at that time. They theorized that Yellowstone, because it was a

refuge when many pronghorn herds were being decimated at the beginning of the 20th century, preserved genotypes that may have been originally found over a much larger area.

The current YNP pronghorn range is surrounded on all four sides by rugged mountains, which largely isolates the herd from all other herds. Seemingly, the most likely pronghorns those in Yellowstone might contact is a herd on the south edge of Livingston, Montana, about 70 km to the north, which would be reached through Paradise Valley. However, this route is mostly blocked by two narrow, rock-walled canyons – Yankee Jim Canyon on the south and Allenspur Canyon on the north. Pre-1882 historical accounts reviewed by Schullery and Whittlesey (1992) revealed that pronghorns were abundant in Paradise valley before homesteaders arrived in numbers. However, by 1905, park Superintendent Pitcher noted that pronghorns were absent from the valley – largely because of homesteading activity. Since that time, these geographic barriers, plus the unusual genetics of the herd, suggest the YNP pronghorn herd size is not buffered by immigration or emigration, which makes it more susceptible to wide variation in numbers.

OBJECTIVES

Since the YNP pronghorn herd is genetically unique, geographically isolated, and has fluctuated widely in size, it seems wise to explore all options that could be used to increase the herd if the population size falls dangerously low. One way is to supplant the herd by artificial stocking, as was first suggested in 1973. However, considering the unique genetic mixture in the herd and the Federal legal mandate to preserve biological diversity (Carlson 1988, U.S. National Park Service 1988, Doremus 1991), animals should only be obtained from populations of similar genetic composition.

One benefit of translocating Yellowstone pronghorns in the past is that there may have been genetically similar descendant populations established elsewhere that might be used to restock the park in an emergency. Finding such populations was the first objective of this study.

At the earliest stages of my search for YNP pronghorn descendants, I found several other states, parks, and refuges had received Yellowstone animals, but current managers had incomplete or no records as to how many were received, or whether herds included animals from other sources. A second goal was to help these agencies clarify, as much as possible, the early ancestry of current herds. The third objective was to help explain some of the unexpected genetic relationships Lee et al. (1994) found between YNP pronghorns and pronghorns living considerable distances away, possibly a result of past stocking of Yellowstone animals in those areas.

METHODS

All likely written material related to pronghorn translocations from YNP, totaling some 5,000 pages, was researched. Most Yellowstone records were in park archives, while some data were scattered in the files of the former Research Division. In most cases, I was able to find the original document which described a translocation activity. Major sources included Superintendent's annual reports, written almost yearly since the park was created, and population count records in research office files. Additionally, letters from superintendents to regional or Washington offices were reviewed, as well as internal letters and memos written by park rangers and biologists.

Letters and notes sent to, and received from, outside wildlife agencies and biologists rounded out park records. Details of some of the early Yellowstone translocations were published and these sources were reviewed. As a check on YNP records, I went to meetings of the Pronghorn Workshop, which is attended by biologists representing those states and Canadian provinces that manage pronghorns, and asked biologists to search their records to see if they had received pronghorns from Yellowstone. Some were also able to provide news clippings of YNP pronghorn releases in their area. If discrepancies occurred between park and outside records, I used original park data.

I also telephoned biologists in numerous parks and refuges in the West, to determine whether their management areas had obtained pronghorns from the park. Lastly, I was able to talk with James McLucas, retired big game trapper for the State of Montana. He kindly supplied written details of YNP trapping operations he was involved in since 1945, and provided additional data on other translocations to the NBR, Montana.

RESULTS
Removal of pronghorns from YNP got off to a shaky start in 1891, when a predator entered a pen and killed 2 individuals that were to be shipped to the National Zoological Gardens, Washington, D.C. (Anderson 1891). In 1907, 3 animals were successfully sent to the London, England Zoological Gardens (Young 1908) and removals from Yellowstone for zoos were made at irregular intervals through 1965 (Table 2). Zoos in the United States and England received ≥ 23 live Yellowstone pronghorns. A total of 888 Yellowstone pronghorns were directly shipped for release in 6 states, which included 2 wildlife refuges, a national monument, and a national park. Forty were lost during trapping operations. Of the 888 that were shipped, 20 died en route or shortly after arrival. Additionally, pronghorns which carried mostly YNP genes were sent from Montana's NBR for release in 4 states. The subsequent histories of all herds carrying Yellowstone genes were analyzed to determine likelihood that their genetics represented pure YNP stock.

Montana - NBR:
In 1911 the Boone and Crockett Club sponsored the first shipment of 12 YNP pronghorns to the fenced 7,500-ha NBR (Brett 1911). Survivors of this group multiplied to 64 animals, before being entirely destroyed by predators by 1922 (Nelson 1925). In spring 1924, the U.S. Biological Survey (now USFWS) captured 40 pronghorn fawns on the Washoe Antelope Reservation (now the Sheldon National Wildlife Refuge) in northwestern Nevada and raised them for release in several states. The NBR received 9 of these in autumn, 1924 (Nelson 1925). The fate of these Nevada pronghorns is unknown, although a Bison Range brochure (U.S. Fish and Wildlife Service 1990) stated "Pronghorns were first introduced in 1910 but apparently did not prosper; the last of these animals disappeared in 1926." These dates may be referring to the original 1911 stocking as well as the 1924 introduction. Evidently, the Nevada animals died because, on 14 February 1951, the MFG released 15 Yellowstone pronghorns on the NBR as part of a new university research project (J. McLucas, MTFWP, personal communication; National Bison Range 2004). In 1952 Mr. McLucas delivered 10 pronghorns to the NBR that were captured in the Winston Flats area, near Townsend, Montana (J. McLucas, MTFWP, unpublished data). During the 1952 breeding season, approximately 9 Yellowstone animals and their offspring survived. If all resi-

dent and newly-stocked animals contributed equally to the gene pool, the resultant average gene pool of this herd and their offspring would have been about 47% YNP and 53% Townsend in their genetics. In 1955, 2 more pronghorns from an unknown location in Montana were released on the Bison Range. With their genetic contributions to a pre-existing herd of 14, the new gene pool would have averaged about 41% Yellowstone genes. In 1957, 16 YNP pronghorns were added to an existing mixed breeding herd of 10. With equal contributions from all, the resulting gene pool would have carried about 77% Yellowstone genes and 23% mixed Montana genes. In 1966, 2 fawns from somewhere in Montana, and 1 buck from Malheur National Wildlife Refuge, Oregon, were stocked on the NBR. Combined with an existing herd of 111 animals, this resulted in a gene pool averaging 75% YNP genes and 25% other gene sources. Finally, in 1987, 5 prong-horns from the Helena area were stocked on the NBR. These blended with 140 existing animals on the refuge, and the resultant gene pool averaged 72% Yellowstone and 28% other pronghorn genes. (All of the above herd population data and pronghorn stocking events were obtained from the NBR (2004). O'Gara (1999) stated that he released 9 does from "central Montana" on the Bison Range in 1986, whereas the NBR report stated he stocked 4 does and 1 buck in 1987.)

Animals stocked on the Bison Range, of which 31 of 51 were from YNP, multiplied well, and from the early 1960s through 1971 some had to be translocated or culled to keep the herd in balance with food supplies (NBR 2004). Records indicate the following states received pronghorns containing at least some Yellowstone genes:

Transplants From the NBR:

Arizona: The Arizona Game and Fish Department (Swank 1964) sent a request in 1964 to YNP and the MFG for 100-150 pronghorns to be released in "northwestern Arizona on state and federal public lands." Yellowstone was unsuccessful in making large pronghorn removals that winter (Howe 1965), and McLucas (MTFWP, personal communication) stated that, instead, NBR animals were sent to Arizona's north rim of the Grand Canyon. The NBR shipped 55 animals to Arizona in October 1965, with 2 dying in the trapping operation (National Bison Range 2004). Whitaker (1966) noted 54 animals reached Arizona alive. Alexander (2000) reported that these animals were released at June Tank, in Game Management Unit (GMU) 13A, on the Arizona Strip in the northwest corner of the state. In November 1971 the NBR sent another 37 prong-horns to "northern Arizona", with 2 dying during trapping (National Bison Range 2004). The pronghorns were released at Upper Clayhole RCA, in GMU 13B of the Arizona Strip (Alexander 2000). Nelson (1925) stated that there were still a few native pronghorns in the Grand Canyon area in the early 1920s, and he also reported that 12 of 40 fawns raised in northwestern Nevada in 1924 were released in Hermit Basin of Grand Canyon National Park. Alexander (2000) reported 34 antelope from central Arizona were released in GMU 13A in 1961. Between 1979 and 2000, Arizona's GMU 13B received pronghorns from Lyman, Wyoming; Limon, Colorado; Crestone, Colorado; and central Arizona (Alexander 2000). Thus, the Arizona Strip pronghorn population likely contains a mixture of YNP, central Montana, Colorado, Wyoming, and native Arizona genes.

Kansas: Nelson (1925) reported only 8 pronghorns remained in extreme southwestern Kansas by 1924, and they often crossed into Oklahoma. The NBR shipped 84 pronghorns to Kansas in 1964 (National Bison Range 2004). Nine of these were dead on arrival, so 75 were stocked (Hlavachick 1970). At that time, the Bison Range animals averaged roughly 77% YNP genes. These were released in Wallace County, in extreme west central Kansas, which was still populated by at least 56 native animals (Hlavachick 1970). Thus, if the native herd total count was reasonably accurate, my calculations indicate that about 44% of the gene pool carried by the approximately 250 pronghorns living in this part of Kansas (Funk 1988) is derived from YNP animals.

Montana: In November 1988, NBR personnel trapped 41 of their pronghorns and translocated them to a site some 30 miles (48 km) west and across the Flathead River, on the reservation of the Confederated Salish and Kootenai Tribes (National Bison Range 2004). In April of 1989 14 of them returned to the Bison Range area, and 20 more returned in September. They ran up and down the fence until gates were opened to let them back in the enclosure. The fate of the other 7 animals was unknown. Evidently no wild herd was established from the release.

Nebraska: McLucas (MTFWP, personal communication) stated pronghorns from the NBR were sent to Nebraska. I have been unable to verify this elsewhere, but the National Bison Range Narrative Report (2004) noted an unsuccessful attempt in 1987 to use chemical restraints to capture 6 pronghorns for delivery to Fort Niobrara, Nebraska.

Nelson (1925) reported 10 small bands, totaling 187 animals, survived in Nebraska, mostly in the western panhandle. Ten of these animals came from 40 fawns raised in northwestern Nevada in 1924. These were released on the "Niobrara Federal Game Refuge" near Valentine, Nebraska (Nelson 1925). Suetsugu (Nebraska Game and Parks Commission, personal communication) reported that native Nebraska pronghorns increased enough in the 1940s and 1950s so that a hunting season was opened in western counties. In 1958, 27 pronghorns from the Pueblo, Colorado Army Depot were transplanted to the Sioux Army Depot near Sidney, Nebraska (Suetsugu and Menzel 1966). These multiplied rapidly and were later the source of animals for transplants elsewhere in Nebraska, and 85 also were sent to Kansas in 1967 (Hlavachick 1970). It appears that there was little, if any, YNP-NBR influence on Nebraska pronghorn genetics.

Utah: Utah received some pronghorns directly from YNP in 1964, which will be covered later. In 1967 the NBR sent 51 animals to Utah (National Bison Range 2004). Evidently, 2 pronghorns died in transit to Utah. Once there, 28 were kept in captivity in Logan for research purposes, and 21 were shipped to Beaver County, in southwestern Utah, with 4 dying before release (Smith and Beale 1980). Nelson (1925) reported that native pronghorns survived in Beaver County in 1923, and Smith and Beale (1980) noted that numerous pronghorns from eastern Utah and western Wyoming were translocated to the western part of Utah. They also stated that native herds survived in many parts of Utah. The presence of YNP-NBR genes is likely to be moderate, at most, in Utah.

Table 2. Pronghorns moved from Yellowstone National Park, Wyoming, 1892 to 1965.

| | Pronghorns Trapped | | | | | | | Pronghorns Released or Exhibited | | | | |
| | Number Handled | | | Trap | | Trap-ping Agency | Date Shipped | Number Arriving | | Location | Agency | Reference |
Date Caught	Live	Dead	Escaped	Type	Loca-tion			Live	Dead			
1891		2		unk	unk	YNP	–					Anderson 1891
1892	1			unk	unk	YNP	unk	unk		Wash. D.C.	Nat. Zoo	Anderson 1892
Jun 1896	6			unk	Yancy's Hole	YNP	11 Jan. 1897	unk		Wash. D.C.	Nat. Zoo	Anderson 1896
Jun 1907	3			unk	unk	YNP	30 Dec 1907	3		London, U.K.	Zoo. Gard.	Young 1908
1909	2			unk	unk	YNP	19 March 1909		2[a]	Wash. D.C.	Nat. Zoo	Benson 1909
Dec 1910 Jan 1911	23	3		unk	Gardiner	YNP	Jan 1911	8	3[a]	Commanche Co., OK	Wichita Mtn. Natl. Game Pres.	Brett 1911
							unk	12		Moiese Lake Co., MT	NBR	
23 and 27 1947	216	19	5	Corral	Stephens Creek	MFG YNP	23 Jan 1947	33	1	Horseshoe Hills Gallatin Co., MT	MFG	Couey 1947 Jan Rogers 1947
							27 Jan 1947	43	2	Ringling Meagher Co., MT	MFG	
							27 Jan 1947	48		Mission Creek Park Co., MT	MFG	
							27 Jan 1947	46		Potter Basin Park Col, MT	MFG	
							27 Jan 1947	43		Goat Mtn. Park Co., MT	MFG	

Table 2. (continued).

	Pronghorns Trapped								Pronghorns Released or Exhibited				
	Number Handled			Trap		Trap-ping Agency	Date Shipped		Number Arriving		Location	Agency	Reference
Date Caught	Live	Dead	Escaped	Type	Loca-tion				Live	Dead			
20 Dec 1947	247	57	1	Corral	Stephens Creek	MFG YNP	unk		56	1	Rattlesnake area Beaverhead Co., MT	MFG	Rogers 1948
Jan-Feb 1951		11[b]		unk	unk	MFG YNP	unk		75		T. Roosevelt Nat. Mem. Park Bowman Co., ND	NPS[d]	Rogers 1951
Jan-Feb 1951							unk		12		Wind Cave Natl. Park, SD	NPS[d]	
							unk		15		Moiese Lake Co., MT	NBR	
							unk		36		Irving Flats Lake Co., MT	NPS[d]	
							unk		31		Hot Springs Lake Co., MT	MFG	
							unk		17		Spring Creek Madison Co., MT	MFG	
							unk		30		Wigwam Creek Madison Co., MT	MT	
							unk		31		St. Joseph Creek Madison Co., MT	MFG	

Table 2. (continued).

	Pronghorns Trapped						Pronghorns Released or Exhibited				
Date Caught	Number Handled			Trap		Trapping Agency	Date Shipped	Number Arriving		Location	Agency	Reference
	Live	Dead	Escaped	Type	Location			Live	Dead			
Jan 1954	207			unk	unk	MFG NPS	13 Jan 1954	60	1	Smith Valley Lander Co., NV	NDOW[e]	Rogers 1956 NDOW 1957
							13 Jan 1954	71		Pine Valley Eureka Co., NV	NDOW[e]	
							Jan 1954	75[c]		North Dakota	NDGF[f]	Hamilton 1953
Feb 1957	116	4[b]		Corral	Stephens Creek	MFG NPS	14 Feb 1957	46	4	Majuba Mtn. Pershing Co. NV	NDOW[e]	Garrison 1957 Teske (Pers comm.) 2004 Garrison 1958
							14 Feb 1957	44	6	Nine-Mile Flat Mineral Co. NV	NDOW[e]	
							15 Feb 1957	16		Moiese Lake Co., MT	NBR	
19 Dec 1963	15	3		corral (elk)	Stephens Creek	MFG NPS	unk	6[c]		Arizona	Disney Productions	Howe 1965
							unk	6[c]		Great Bend, KS	City zoo	
							unk	3[c]		Bismarck, ND	Dakota Zoo	
16 Dec 1964	22	2	1	Corral	Stephens Creek	MFG NPS	unk	20	2	Awapa plateau Wayne Co. UT	UDWR[g]	Barmore 1965
06 Jan 1965	5	2		Corral	Stephens Creek	MFG NPS	unk	5[c]		Bismarck, ND	Dakota Zoo	Barmore 1965

[a] Died from injuries by unknown causes soon after arrival.
[b] Incomplete records as to how many died during shipping.
[c] Unaccounted for in trapping or release records.
[d] National Park Service

[e] Nevada Department of Wildlife
[f] North Dakota Game and Fish Department
[g] Utah Division of Wildlife Resources

Translocations Directly From YNP :

   Montana: In 1947 273 pronghorns were removed from Yellowstone and distributed among 6 sites in southwestern Montana (Table 2). Beer's (1944) survey of 1941 distribution of pronghorns in Montana, before intensive translocations took place, suggested pronghorn herds were present and growing in all counties where YNP pronghorns were sent. Released Yellowstone pronghorns generally were not marked, so their long-term contribution to resident herds was not known. Animals were translocated from 60 to 100 miles (96-160 km) away from the park, and it was possible that some returned to YNP. Goldsmith (1984) reported pronghorns translocated to southeastern California dispersed primarily in the direction of their original home in northern California. As indicated previously, most of 41 NBR pronghorns translocated 30 miles away swam a major river and returned to their home range within a few months (National Bison Range 2004).

   During January and February, 1951 another 160 pronghorns were taken from YNP and released at 6 sites in Montana (including the NBR). Madison County releases again supplemented native herds. The 2 releases in northwest Montana's Lake County were isolated from other herds (Beer 1944). However, McLucas (MTFWP, personal communication) reported that local residents soon exterminated the stocked animals in Lake County.

   Nevada: On 13 January, 1954, 60 YNP pronghorns were released in Smith Creek Valley in Lander County, and 71 were released in Pine Valley, Eureka County, Nevada (L. J. Teske, NDOW, personal communication). Much earlier, Nelson (1925) reported no pronghorn herds survived within 100 miles (160 km), of the release areas. Teske (NDOW, personal communication) noted that the Smith Creek Valley herd received 49 pronghorns translocated from Pueblo, Colorado in 2001. He also reported that Pine Valley and nearby areas (Eureka County) received 104 pronghorns in December 1984 from Douglas, Wyoming, and 40 more from Oregon's Umatilla Army Depot in October 1985. Originally, these 2 herds may have been pure descendants of Yellowstone animals, but it is likely that they now derive $\geq 50\%$ of their genes from other introduced animals.

   Another 100 YNP pronghorns were shipped to western Nevada in February 1957 (Garrison 1957). Ninety survived the trip and 46 were released near Majuba Mountain and Lovelock in Pershing County. The other 44 were released on Nine Mile Flat, near Hawthorne in Mineral County (L. J. Teske, NDOW, personal communication). Earlier, Nelson (1925) reported no pronghorns in Mineral or Pershing Counties, but Pershing county adjoins Washoe County, which had 2000-2500 native pronghorns in the 1920s (Nelson 1925). It is probable that pronghorns from YNP and Washoe County intermingled. The Nine Mile Flat animals in far western Nevada were supplemented by later releases of other pronghorns from unknown locations (M. Cox, NDOW, personal communication).   It is unknown if this herd still contains a significant percentage of Yellowstone genes.

   North Dakota: Theodore Roosevelt National Memorial Park (TRNMP), in western North Dakota, became home for 75 YNP pronghorns in early 1951 (Rogers 1951). The animals were released in the south park unit only, and also just outside the park boundary, but they are now common in both the south and north park units (J. Norland, YNP, personal communication). Yel-

lowstone records indicate another 75 pronghorns were shipped to North Dakota in January, 1954 (Hamilton 1953, Hamilton 1955). The NDGF was said to be the receiving agency, but I have no data on the fate of these animals, if they actually existed.

Nelson (1925) reported that western North Dakota still had 5 native herds, totaling 225 animals, in 1924. Most of the herds lived in counties near TRNMP, so it is likely those herds, if they survived, blended with Yellowstone animals. By 1964, pronghorn numbers peaked at 15,000 head in North Dakota (Samuelson 1982), possibly diluting YNP genes. Severe winters reduced the herd to 1,200 by 1979 (Samuelson 1982). The current amount of genetic material derived from YNP in western North Dakota is likely to be moderate at most.

Oklahoma: In January 1911, the Boone and Crockett Club financed the shipment of 9-12 Yellowstone pronghorns to the Wichita National Game Preserve (now the Wichita Mountain National Wildlife Refuge - WMNWR) in southwestern Oklahoma (Brett 1911, Halloran and Glass 1959, Nelson 1925). However, Nelson (1925) stated "Of the antelope sent to Oklahoma, some reached their destination dead and others badly injured, and eventually all died." In the fall of 1921 the American Bison Society stocked the preserve with 10 pronghorns from Brooks, Alberta, and 6 from the same source were released in fall 1922. The pronghorns slowly increased in following years. This part of Oklahoma had almost no remaining native pronghorns (Nelson 1925). In 1938 an unknown number of pronghorns from east-central New Mexico were stocked in the Wichita Mountains National Wildlife Refuge (Howard et al. 1984). It is unlikely there are any YNP pronghorn genes present in Oklahoma.

South Dakota: The Boone and Crockett Club sent 13 young pronghorns from Brooks, Alberta to Wind Cave National Park (WCNP) in October 1914. Nine more animals from Brooks were sent in October 1916 (Nelson 1925). These animals increased moderately then declined to 6 does in 1924. In July of that year a young buck from northwestern Nevada was stocked (Nelson 1925). The WCNP herd grew to approximately 150 head by 1948 (Cahalane 1948). In early 1951, 12 YNP pronghorns were added (Rogers 1951). All 12 were thought to be bucks (U.S. National Park Service 1950).

Nelson (1925) reported that several native herds of pronghorns lived in the counties surrounding WCNP. Even after this preserve was fenced, a biologist noted that pronghorns were able to get in and out (R. Klukas, NPS, Omaha Regional Office, personal communication). At present, Yellowstone genes must have a very minor influence in the Wind Cave herd.

Utah: Utah received 20 YNP pronghorns in December of 1964 (Barmore 1965). They were released on the Awapa Plateau (Parker Mountain) Wayne County, south central Utah (Smith and Beale 1980). In 1965, 109 pronghorns from Chinook, in northern Montana, were stocked in the same area (Smith and Beale 1980). Eastern Wayne county was within the range of Utah's largest pronghorn herd in 1923 (Nelson 1925). It is likely that Yellowstone animals, if they survived, interbred with the Chinook pronghorns and the native herd. Lately some of the pronghorn herds in Utah have increased greatly (Yoakum 2004).

DISCUSSION AND MANAGEMENT IMPLICATIONS

Locations of herds closely related to YNP animals:

Since stocking of the pronghorn-vacant NBR began in 1951, 31 YNP pronghorns, and 20 pronghorns mostly from other parts of Montana, were stocked there until 1987. As a result of various stocking events, the average proportion of Yellowstone genes in the herd has ranged from a high of 100% in 1951 to a low of 41% in 1954. Currently, the herd averages roughly 72% Yellowstone genes. This herd likely contains the highest percentage of YNP pronghorn genes of any herd influenced by Yellowstone translocations and it may be the best source of animals if YNP ever has to do restocking to supplement its depleted herd.

NBR pronghorns were translocated for release in the Arizona Strip – area to the north of Grand Canyon, Arizona; Wallace County, Kansas; Lake County, Montana, and Beaver County, Utah. Of the survivors from these translocations, the Wallace County herd, in western Kansas, with possibly 44% Yellowstone genes, is apparently the most closely related to YNP animals.

Pronghorns were translocated from YNP to 12 sites in Montana, including the NBR. In the sites where free-ranging translocations remained, they likely interbred freely with remaining resident pronghorns.

Of the 4 general areas in Nevada that received YNP pronghorns, only 1, Nine Mile Flat in Mineral County, may still hold animals moderately related to Yellowstone ancestors, but only if the herd has not mingled with other Nevada (or California) pronghorns. Tissue samples should be procured from this herd and their mitochondrial DNA compared to that from YNP animals.

North Dakota's TRNMP, Oklahoma's WMNWR, WCNP in South Dakota, and Wayne County, Utah all received YNP pronghorns. Records indicate that introduced Yellowstone animals extensively mingled with native survivors or introduced pronghorns in those areas, generally causing a dilution of YNP genes.

Correlation with Results of Pronghorn Genetics Studies:

Table 3 summarizes some unexpected genetic relationships between YNP animals and distant herds. Lee et al.'s (1994) analysis of allozyme data found that southwestern North Dakota pronghorns are closely related to those from western Kansas. Both areas have NBR/YNP ancestors, but it is surprising that Yellowstone stock in North Dakota was not diluted more by interbreeding with remnant native herds.

YNP pronghorns shared 1 rare haplotype (D) with pronghorns in Island Park, Idaho, even though the herds are separated by 80 km of nearly continuous mountains and forest. It is possible that some Island Park pronghorns worked their way north through open forest over Targhee Pass, then east up the Madison River and Nez Perce Creek into Yellowstone's centrally-located Hayden Valley. Part of the resident Yellowstone herd regularly migrates east up the Lamar Valley, and old records indicate some then went south up Antelope Creek. My observations in 1988 through 1994 (Scott and Geisser 1996) found some animals can then pass over Mt. Washburn, travel south through Canyon Junction, and into Hayden Valley. Thus, at one time, when pronghorns were much more abundant, Hayden Valley was probably where members of these herds mingled.

Table 3. Rare haplotypes shared by YNP pronghorns and other distant herds (from Lee et al. 1994 and Reat et al. 1999).

Rare haplotypes	Source	Explanation for presence
D, F, J	YNP	NP refuge – may have preserved once-widespread genes
D, F	Garfield Co. MT	Isolated remote area – also may have preserved rare types
H (Closely related to haplotype I)	Bowman Co. ND	Part of herd genes came from stocked YNP animals
I (Closely related to haplotype J)	Wallace Co. KS	Kansas herd came partly from NBR animals which contain mostly YNP genes
D	Island Park, ID	Live 80 km sw of the YNP herd - may mingle in Yellowstone's Hayden Valley
J	Northeastern AZ	Received Wyoming transplants. Translocations may have carried rare genes preserved mostly in YNP

In a survey of many North American herds (but none from Arizona), Lee et al. (1994) found haplotype J only in YNP. Since then, Reat et al. (1999) found 15 animals from "northeast" (actually east-central) Arizona that carried the J haplotype. Unpublished data indicated this part of Arizona had received translocations from Wyoming (Rhodes et al. 1999), but no YNP or NBR records indicate shipments to this area. It may be that Yellowstone preserved some rare haplotypes that were originally present over larger areas of Wyoming, and are now preserved in small isolated locales. One of these locations may have been the source of translocations to east-central Arizona, or the pronghorns with haplotype J may have been native to that part of Arizona.

The lack of a close genetic relationship between YNP pronghorns and others surrounding the park (Lee et al. 1994) seems to confirm that Yellowstone pronghorns are reproductively isolated. It is especially surprising that YNP pronghorns were not closely related to an animal collected from the Mission Creek area 70 km north and on the other side of Allenspur and Yankee Jim canyon barriers. In 1947 48 Yellowstone animals were stocked there, and 132 more were released in contiguous areas to the north of this in the Shields River valley and near Ringling, Montana. Either all of these animals died before they could cross with the herds already living there, which is unlikely, or else they somehow found a way through the Allenspur and Yankee Jim canyons and returned to Yellowstone. I have seen a few Yellowstone pronghorns use an old railroad right-of-way to traverse Yankee Jim Canyon, so returning pronghorns probably could have negotiated that barrier.

Recommendations For Further Translocating Efforts In Pronghorn Management:
Keep better records: I found that many translocations were not well documented, or what few records were kept were not saved in an organized fashion. If animals are translocated ≤ 300 km from their home range, biologists should clearly mark all released animals to determine whether any return to the source herd. Ungulates move surprising distances. Survival and breeding activity of released pronghorns should be monitored, to identify actual contributions toward recovery of a herd.

Genetic history of herd(s) that are being considered for receiving translocations should be evaluated. If the native herds are genetically unique, outside animals should not be introduced unless the unique herd is on the verge of becoming extinct. Because such herds are rare, they are of great scientific value, and should not be contaminated by other gene pools. Both Rhodes et al. (1999) and Rhodes et al. (2001) noted that before future translocations are made into existing Arizona pronghorn populations managers should take into consideration potential negative genetic impacts. Other methods, such as habitat management, predator control, or even captive breeding should be used to increase numbers within such herds. Restoration of pronghorn herds is thought to be largely the result of translocation efforts (Cadieux 1987). Contributions of changing land use and human population loss in the rural West have not generally been given similar credit. Nevertheless, the era of unrestricted translocation of common ungulates is fast drawing to a close, largely because most habitats are filled. These past efforts have had a disastrous, permanent effect on our ability to decipher the genetics of animal populations adapted to local conditions, i.e. "ecotypes". The closure of this era should be speeded up.

Preserving The YNP Pronghorn Herd:

At present, the relative effects of coyote predation, elk competition for sage (Singer and Renkin 1995), past management mistakes, and residential developments on winter range, on YNP pronghorn population dynamics is not known. We do know, however, that the herd has very low survival rates due to coyote predation (M. D. Scott, YNP, unpublished data), and that it has fluctuated greatly in size. The best insurance against loss of this unique herd is to establish another population in a place where it would not be genetically contaminated by other herds. A good location to do this is the Paradise Valley, which extends north from Yellowstone for approximately 70 km. It has remained largely devoid of pronghorns since they were exterminated at the turn of the 20th century, and it is isolated from pronghorn herds farther north by the Allenspur Canyon barrier on the north end of the valley. An important added benefit of this location is that it adjoins the current YNP pronghorn range on the south and, if the narrow route through Yankee Jim Canyon can be kept open, some of the Paradise Valley animals might move into Yellowstone, as they probably did 100 years ago. This could provide a population buffer if YNP animals suffer any more large declines.

YNP officials should work with MTFWP personnel, and private landowners in Paradise Valley, to secure added range for the Yellowstone pronghorns by restocking them in Paradise Valley. Possibly 10-15 adults could be kept in fenced pastures for 2-3 years if predators were controlled. Once 1 or 2 generations of offspring were produced, the herd could be released from the pastures and, hopefully, the offspring would not follow the adults back into the park if they should try to do so. With citizen help, the new resident herd could be protected, and possibly increase to 100-200 head in the 50,000-acre (20,243 ha) valley.

An important component to creating such a buffer population would be keeping the Yankee Jim Canyon barrier as open as possible, to allow interchange between the new Paradise Valley herd and the YNP herd. In the last 2 decades, several houses with horse pastures have been built at the north mouth of Yankee Jim Canyon, and new fences cross the narrow pronghorn migration route on the west side of the canyon. Montana State wildlife officials need to work with

those landowners to encourage them to construct and maintain fences that meet guidelines for pronghorn passage requirements (Lee et al. 1998). Even now, when winter weather is severe, a few Yellowstone pronghorns occasionally pass through Yankee Jim Canyon when migrating to warmer, drier, more vegetated range than is found nearer the park.

Regardless of whether a buffer Yellowstone population can be established in Paradise Valley, positive management steps should be taken in and near YNP to ensure preservation of this unique, dwindling herd, which was calculated to have an 18% chance of extinction in 100 years (Goodman 1995). These include:

1. Intensively control coyotes every 3-4 years in the Boundary Line Area (BLA) of YNP where they appear to be abnormally abundant. This is caused, at least partly, by the unnaturally large, winterkilled supply of elk carrion to carry them through the winter. Crabtree and Sheldon (1999) have shown that YNP coyotes mainly feed on plentiful elk carrion in winter. Most pronghorn does use the BLA to give birth in summer and a majority of the herd winters there as well. Managing the coyote numbers would allow much higher fawn survival in control years, producing more recruitment to the adult population, which is much more resistant to predation (M.D. Scott, YNP, unpublished data). Only periodic replenishment of adults would be required, which means coyotes would not have to be continuously controlled. Coyote control for the benefit of pronghorns inside Yellowstone would require a moderate public education program on the part of the NPS.

2. Harvest of pronghorns adjacent to the northern border of YNP should remain closed. The Montana pronghorn "depredation" hunting season on land north of the park border was closed in 2002 after 17 years. The monetary value of pronghorn depredation on crops in this area was negligible (Scott 1991), and there are tens of thousands of pronghorns elsewhere in Montana that may be hunted.

3. Revegetation with native plants should be done in the BLA to improve the forage quality for pronghorns. Shrubs in the BLA have been severely depleted (Singer and Renkin 1995), and native grasses and forbs have been largely replaced by weedy exotic plants of inferior nutritional value (M. D. Scott and S. A. Scott, YNP, unpublished data).

4. Increase forage availability on the BLA. Reduction of the elk herd to a size that no longer extensively competes for feed with other ungulate species is desirable. Elk are unnaturally concentrated in Yellowstone during fall and winter by hunting pressure along the entire park perimeter. This has led to over utilization of forage in the BLA. The MT-FWP needs to devise changeable open-hunting zones on the YNP boundary, so the elk will be less able to determine the hunting area boundaries. This should encourage more elk to leave the park during these seasons.

5. Anthropocentric structures should be removed from the BLA. Even though it is the most important winter range for ungulates in YNP, it is a NPS "sacrifice area". The ranger target range, buildings, drift fences, bison capture facilities, horse corral, junk, excess vehicles, and old railroad bed all need to be removed.

6. More extensive population monitoring is needed. Rather than the current practice of doing just 1 spring survey, ≥ 3 spring census counts should be conducted. Single counts are unreliable (M. D. Scott, YNP, unpublished data), and multiple surveys will give an idea of the errors encountered.

7. NPS managers should work with the USFWS to have the YNP pronghorn designated as

a threatened, unique population. With such a designation, the NPS might actually take action on some of the management actions listed above.

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MORPHOLOGICAL CHARACTERS OF THE LIMB BONES OF *ANTILOCAPRA AMERICANA* AND OTHER UNGULATES

ANDREA M.F. VALLI, Istituto Italiano di Paleontologia Umana, Rome, Italy and Conseil Général de l'Allier, DJECS 1, avenue Victor Hugo - BP 1669 - 03016 Moulins sur Allier Cedex, France e-mail: andrea_vallifr@yahoo.fr

Abstract: The main characters of the limb bones of the pronghorn "antelope" (*Antilocapra americana*) are described and compared with the bones of some bovid and cervid taxa. Its peculiar features are pointed out: they form a mix of bovid and cervid characters, and a few unique to the family. The particular combination of such features allows the differentiation of antilocaprid limb bones from those of other ruminants. The abylity to identify postcranial pronghorn limb bones may aid in archeological and biological (e.g., predator food habits) research; as well as foresnsic work on enforcement cases.

Key words: *Antilocapra americana*, Antilocapridae, Bovidae, Cervidae, limb bones.

INTRODUCTION

Antilocapridae is a family of horned ruminants that is only found in North America, from late early Miocene to the Recent (Janis and Manning 1998; Janis 2000). Following McKenna and Bell (1997), the group includes two subfamilies, Cosorycinae and Antilocaprinae. Janis and Manning (1998) prefer to retain the original nomenclature for the first subfamily, Merycodontinae.

The earliest known species which could belong to the Antilocapridae was found in the Upper Harrison beds, 4 miles north of Agate (Sioux County, Nebraska), and it was described by Cook (1934) as *Merycodus prodromus*. These layers date to the late Arikareean (early Miocene; Tedford et al. 1987). The subfamily Merycodontinae flourished during the middle Miocene and the beginning of the late Miocene, and vanished at the end of the late Clarendonian (Janis and Manning 1998). The second subfamily only appeared during the late Barstovian, with the genus *Plioceros*, and spread throughout North America during the late Miocene- Pleistocene. Nevertheless, at present only one species, *Antilocapra americana*, the pronghorn "antelope", survives in several states of the U.S.A. and Canada. This species is also known from several Quaternary localities (Chorn et al. 1988; Kurtén and Anderson 1980). The remains from Bautista Pleistocene Beds could be the first record for the genus (Richards and McCrossin 1991). Such levels are considered to be of Irvingtonian age (Savage and Russell 1983). At least one other fossil species, *A. pacifica*, is known from the Big Break Locality (Contra Costa County, California; Richards and McCrossin 1991). *A. pacifica*, as with all the substantiated remains of *A. americana* dates to the Rancholabrean land mammal age.

The Antilocapridae appear to be adapted to life in grasslands, based on the relatively hypsodont molar teeth. Despite this character, the extant species does not feed extensively on grass (Janis 1988; Hofmann 1989; Fortelius and Solounias 2000). Grass generally comprises no more

than around 12 percent of its diet on a year-round basis (Hansen and Clark 1977). Nevertheless, *A. americana* is a typical inhabitant of the grasslands, where it is the fastest running animal in North America (Byers 1997). Based on their present day-life style and anatomical characters, antilocaprines are considered very good environmental markers (Janis and Manning 1998; Janis 2000). So detecting their presence in a local fossil fauna is therefore important for reconstructing paleoenvironments.

The last major study of this family was the Frick's 1937 monograph on the horned ruminants of North America. Frick's study on the description and analysis of antilocaprid crania (including the diagnostic frontal horns) and teeth, based on the extensive collections in the American Museum of Natural History of New York (AMNH), but lacked detail concerning the postcranial skeleton. Very few papers deal with post-cranial features in spite of the wide literature on antilocaprids (e.g., Colbert and Chaffee 1939; Hibbard and Dalquest 1960; Voorhies 1969; Webb 1973; Munthe 1988; Leite 1990; Richards and McCrossin 1991; Morgan and Morgan 1995).

The main goal of this paper is to present the morphological characters of certain limb bones of the skeleton of *A. americana*.

MATERIALS AND METHODS

I analysed characters on skeletons of *A. americana* in the mammalogy collection of the American Museum of Natural History (AMNH). Typical morphological features of *A. americana* are defined on the basis of different shape of postcranial skeleton. These features are inferred from comparison with taxa of cervids (mainly the white-tailed deer *Odocoileus virginianus*) and bovids selected for size and/or environment adaptation. Such characteristics, that are enough to recognize bones of *A. americana* simply by visual recognition, are showed by narrative descriptions and figures found in this manuscript or from the cited literature.

Anatomical characters included some of those selected by Heintz (1970) to distinguish cervid bones from bovid bones, and those detected by Lister (1996) and by Pfeiffer (1999) on cervid limb bones, mainly red deer, *Cervus elaphus*, and fallow deer, *Dama dama*. In addition, I found a few more characters not recognized by the previous authors.

Antilocaprid characters are compared to those of several bovids and cervids in the collection of the AMNH. A full list of the analyzed specimens is reported in the Appendix A. Sex and geographical origin are also indicated. I examined the postcranial elements for all adult specimens available (where adult is an individual with long bones having fused epiphyses). I do not include in my analysis carpian or tarsian bones (except astragal, calcaneus and cubo-navicular) or cubitus, because of the lack of available specimens for the study (such elements are often missing or connected in the preserved skeletons). In the geographic range of fossil and extant antilocaprids (North America) there is no other ruminant of similar size, except *O. virginianus* and *O. hemionus*. Postcranial bones of North American bovids (e.g. *Oreamnos americana*) are totally different in sizes and/or proportions. The other bovids (and their relatives and ancestor) whose bones are described in the article, never reached North America. However, they have been included in the analysis in order to obtain a larger morphological variability. Limb bones of *O. virginianus* (*O. hemionus* are enough similar in morphology to these of the congeneric species for avoiding com-

parison) are dimensionally close to those of *A. americana*. Nevertheless, the combination of the features figured here is enough to recognize them from the remains of *Antilocapra*.

In the present work, the word "specimen" is not synonymous of "individual", because unfortunately not all the skeletons preserved in the museum collections are complete. Concenring limb elements, one individual normally has two specimens (the right one and the left one), but sometimes one can be missing or broken, so it will not available for analysis. In addition, the features of the limb bones on one side of animals may differ from the ones on the other side. For this reason, I prefer to use "specimens" instead of "individuals".

The measurements of antilocaprid and cervid limb bones discussed in this paper are available by contacting the author. Bone measurements of bovids are available in the literature, e.g. Scott 1985.

RESULTS

Humerus: (Fig. 1) The humerus is a fairly long bone. The ratio (radius maximum length/humerus maximum length) x100 is 109.21 (22 specimens, minimum 103.65; maximum 115.97; *SD* 3.15). On the proximal end, the lateral profile of the *tuberculum majus* is not indented (Fig. 1.A.1, a), whereas the *caput humeri* has a very sharp ridge (Fig. 1.A.2, b). Distally, above the trochlea, there is only one pit, triangular in shape and generally deep (see Lister 1996, page 126, Fig. 2 , char. 1). The shape of the trochlea, in distal view, is rather bovid-like, with the exterior condyle higher or at the same level as the medial groove and the lateral ridge, between the tow (exterior condyle and medial groove), rounded (Fig. 1.D.2). The lateral ridge of the trochlea ranges from symmetrical to asymmetrical, even if the first feature is more frequent. On the lateral side, the epicondyle can have a marked bulge (7 specimens), a small one (10 specimens) or nothing at all (11 specimens; for the shape of this character see Lister 1996, page 126, Fig. 2, char. 2). On the posterior side, the edge of the pulley inside the *fossa olecrani* can be horizontal (12 specimens) or oblique (16 specimens, 12 out of them show a little triangular nick on the edge; Fig 1.D.1, a).

The *tuberculum majus* of the bovid humerus can be either indented (as in *O. oreotragus*, *A. melampus*, *C. taurinus* and *O. ammon*; but in the two last species it is weakly indented, Fig. 1.C, a; in *Kobus* spp., in contrast it is greatly indented) or not indented (as it is in *Tragelaphus*, *B. tragocamelus*, *Cephalophus*, *Gazella* spp., *A. marsupialis* and *O. americanus*). Above the trochlea, on the distal end, *T. buxtoni*, *B. tragocamelus*, *Kobus* spp., *O. oreotragus*, *A. melampus* and *O. ammon* have two cranial holes, variously shaped. *T. imberbis*, *Cephalophus*, *A. marsupialis* and *O. americanus* have only one hole. *Gazella* can have one or two holes, depending on the individual. *C. taurinus* has not a true hole but only a shallow surface. The shape of the trochlea in distal view is always bovid-like, as far as the level of the condyle is concerned, but the lateral ridge is asymmetrical and cervid-like, in *Tragelaphus* ssp., *B. tragocamelus*, *Cephalophus*, *Kobus* and *O. oreotragus*. In *O. virginianus*, the lateral profile of the *tuberculum majus* is different-shaped from that of *A. americana* and it is more indented (Fig. 1.B, a). On the distal end, the shape of the trochlea is rather cervid-like (Fig. 1.E, a; see also Heintz 1970, vol. 2, page 31, Fig 23). The edge of the pulley inside the *fossa olecrani* is generally oblique (6 specimens out of 8; Fig. 1.E, arrow).

Radius: (Fig. 1) On the proximal end, the lateral edge is either truncated (25 specimens; Fig. 1.F, a) or has a mild projection (5 specimens) with a gentle slope that ends half way up the projection. In proximal view, the lateral side is marked with a straight line perpendicular to the main axis of the articular surface. Medially, on 3 specimens out of 30, the border of the proximal end makes a thick ledge projecting out of the proximal end. On one specimen this edge is incipient but on all the others it is small and not projecting (Fig. 1.F, b). The posterior side is not greatly raised above the anterior one (28 specimens out of 30; see Lister 1996, page 127, Fig. 2 , char. 6). *O. virginianus* has a radius which is quite different in its proximal end, because of the presence of a thick ledge projecting on the medial side and because of the shape of the lateral side (Fig. 1.G, a and b respectively).

On the distal end, the difference in height between the posterior part of the scaphoid articular facet and lunar articular facet is similar to the difference in these features found on some cervid radii (e.g., *M. muntjak* and *O. virginianus*; in *M. gouazopira* it is smaller). The medial edge of the scaphoid facet is only slightly indented and smooth (23 specimens out of 27; Fig. 1.I, a); the edge of the lunar is indented on almost half of the bones recorded (12 out of 27; Fig. 1.I, b; see also Lister 1996, page 128, Fig. 2, char. 2 and 3). The carpal cuneiform articular facet on the radius is as large as that on the ulna (as it is found in *M. muntjak* and *O. virginianus*; in *M. gouazopira*, the radial surface is larger). Finally, on the dorsal side, the bordering crestsof the groove for the extensor tendon are fairly sharp and long, similar to the radius of the Cervidae (Fig. 1.I, c).

Proximally on the lateral side, *Kobus* spp., *O. ammon*, *A. marsupialis*, and *Tragelaphus* spp. have a small, weakly-projecting process. The latter 2 taxa have the process at almost the same level as the articular surface. *B. tragocamelus*, *Cephalophus* spp. and *C. taurinus* have a larger, more projecting process, whereas in the *O. oreotragus* and *O. americanus* the lateral side is truncated (Fig. 1.H, a). *Gazella* spp. show a more variable shape: the *G. gazella* has a strongly-developed process, whereas *G. granti* can have either a large process or a short one. On the medial side, a thick ledge is present in *Tragelaphus* spp., *B. tragocamelus*, *A. melampus* and *O. americanus* (Fig. 1.H, b). Only a thin ledge can be detected on the bones of *Cephalophus* spp., *O. oreotragus* and *O. ammon*. *Kobus* spp. is rather pronghorn-like, with a ledge that does not project. *C. taurinus* and *A. marsupialis* have no ledge at all. Also *G. gazella* shows no ledge, but *G. granti* can have either a strong or a weakly projecting one.

At the distal end the difference between the levels of the scaphoid and lunar facets in *C. taurinus*, *B. tragocamelus*, *Tragelaphus* spp., *A. melampus* is the same as in *A. americana*. In *Gazella* spp., *Cephalophus*, *Kobus* spp., *O. oreotragus*, *A. marsupialis*, *O. americanus* and *O. ammon* the difference in high is more pronounced. The carpal cuneiform articular facet of the bovid radius is smaller than that of *A. americana*, except on 4 individuals of *C. taurinus* (but the other four individuals have the typical bovid shape). *O. oreotragus* and *O. americanus* have no facet on the distal end of their radius (Fig. 1.J, b). Finally, bordering crests of the groove for the extensor tendon are either short and blunt (*Tragelaphus* spp., *B. tragocamelus*, *Kobus* spp., *A. melampus*, *A. marsupialis* and *O. oreotragus*) or almost erased (*C. taurinus*, *O. ammon* and *O. americanus*; Fig. 1.J, c). Only *Cephalophus* spp. and *Gazella* spp. can have ridges that are short but also sharp, almost cervid-like in appearance.

Metacarpal III + IV: (Fig. 2) The metacarpal of *A. americana* is very long and slender, like that of *Gazella* spp., and straight in lateral view. The articular keels for proximal phalanges are parallel, sharp and continued posteriorly to the palmar side (this last feature can be found in ruminants that run on hard ground; Caloi and Palombo 1991; Köhler 1993). They are dorsally separated from the shaft by grooves (Fig. 2.A.1, a). Generally, a slight split can be found between the two trochleae (12 specimens have one, 6 have nothing and 4 have just an incipient split). On the distal end, the dorsal foramen is small and oval (Fig. 2.A.1, b). The dorsal gully is almost obliterated and it is very difficult to detect. On the plantar side, in contrast, the gully is clearly visible, but it is shallower than in American or Eurasian cervids (e.g. *O. virginianus*).

On the proximal end, the edge dividing the two articular facets is short and ends on the proximal foramen, which is cervid-like (Fig. 2.A.2, c). The palmar side of the foramen is usually closed (Fig. 2.A.2, d); it is open only on 3 specimens out of 24 (also the metacarpals of *O. virginianus* has a posterior side usually closed; 8 specimens out of 12). On all of the specimens a non-articular surface (fossa) exists on the proximal end, on the capitato-trapezoidal surface (Fig. 2.A.2, e): on 24 specimens it is relatively large, on 4 it is small. It is always connected with the proximal foramen. On the dorsal edge, the tuberosity can be smooth or rough, but is never bordered by a clear rim (see Lister 1996, page 129, Fig. 2, char. 5). Posteriorly, on the medial part of the proximal end, 1 or 2 small pores can be detected near a shallow oval fossa (see Lister 1996, page 129, Fig. 2, char. 3 and 4).

A fossa can be found on the proximal end of *O. virginianus* metacarpals (9 specimens out of 12) but it is clearly smaller than that of *A. americana*. The distal end of *O. virginianus* metacarpals differs from those of *A. americana* for the articular keels more blunt in their dorsal side, and by the presence of a clear split between keels (for the shape of this feature see Lister, 1996, page 129, Fig. 2, char. 6).

On the bovid metacarpal the palmar side is always flat or only slightly concave (*C. taurinus* and *O. ammon*). On the proximal end, the ridge which divides the two articular facets is quite long, reaching the posterior edge (Fig. 2.B, c). Again on the proximal end, the capitato-trapezoidal articular facet is larger than that of the magnum, generally more than twice the size (*Tragelaphus*, *B. tragocamelus*, *Cephalophus* spp., *C. taurinus*, *Gazella*, *A. melampus* and *A. marsupialis*, Fig. 2.B). It is smaller than this in the climbing bovids, *O. americanus*, *O. ammon* and *O. oreotragus*. A fossa on the proximal end is found in *O. ammon*, *C. taurinus* (a large one) and *Kobus* (variable in size). It is absent in *Tragelaphus*, *B. tragocamelus*, *Cephalophus* spp. and *O. oreotragus*. It is variably present in *Gazella* spp., *A. melampus* (when it exists it is not connected with the proximal foramen), *O. americanus* and *A. marsupialis* (on the last two species the size can be variable).

The distal keels on the metapodials of bovids are continued through the trochlea, except in *Tragelaphus* spp., *Cephalophus* spp. and *O. americanus*, where the dorsal side is blunt, and in *C. taurinus* where the dorsal side is not as sharp as in *A. americana* but it is sharper than in cervids. *O. oreotragus* has the distal trochleae for the phalanges articulation widely separated. A split on the palmar side, between the trochleae, can be found in *Tragelaphus* spp., *C. taurinus*, *Gazella* spp., *A. melampus*, *A. marsupialis* and *O. ammon*.

Only the metacarpals of *Gazella* spp., *A. melampus* and *A. marsupialis* are as slender as those of *A. americana*. In three individuals of *Cephalophus*, metapodial shafts are not straight but "S"-shaped. The metapodials of *M. gouazopira* have a very slender shaft but the distal end is fairly stocky and strong.

Femur: The ratio (tibia maximum length/femur maximum length) x100 is 117.38 (19 specimens; minimum 114.29; maximum 119.70; *SD* 1.66). In proximal view, the *fossa trochanteri* is oblique with a large ansa between the femoral head and the *trochanter major* (see Pfeiffer 1999, page 81, Fig. 65.A). The top of the *trochanter major* is flat and horizontal; its rear part has a well pronounced process. In cranial view, the line linking the base of the femoral head and the rear part of the *trochanter major* is continued and similar in shape to the fig. 67.C of Pfeiffer's paper (1999, page 82).

On the distal end, the ridges bordering the distal trochlea are either divergent (12 specimens) or parallel (11 specimens). The fossa between the 2 condyles is deep.

Tibia: (Fig. 3) The tibia is long and slender: it is the longest limb bone in *A. americana*. On the proximal end, the tibia of *A. americana* has the medial peak slightly higher than the lateral one (Fig. 3.A.1, a). In proximal view, the shape of the tibial ansa is varying: it can be "U" or "V"-shaped, and in the latter case the angle of the "V" ranges from either 70° to 80° or 90°. This feature is often variable within a single individual. The tibial tuberosity is rather square-shaped (Fig. 3.A.1, b). On 12 specimens it is more proximally oriented and on another 12 specimens it is more posteriorly oriented (see Lister 1996, page 130, Fig. 2, char. 2). Both shapes can be found on the same individual. The foramen on the shaft (Fig. 3.A.1, c) is in a very lateral position and almost not visible in caudal view. It is also high positioned, located in the proximal third of the shaft. The cranial crest is generally shorter than the cervid one.

On the distal end, the two malleolar articular facets are different in size: the cranial facet is little larger antero-posteriorly than the caudal one. They are widely spaced (Fig. 3.A.2, d). The middle of the distal epiphysis, is square-shaped in cranial view (Fig. 3.A.3, e). In lateral view, the distal edge is rather "L"-shaped (see Lister 1996, page 130, Fig. 2, char. 5, and Pfeiffer, 1999, page 87, Fig. 72).

The cranial crest of the bovid tibia is generally short, but *Gazella* spp., *A. melampus*, *O. oreotragus*, *Cephalophus* spp. and *O. americanus* have a relatively long crest. In *Cephalophus* spp. it is rectangular in shape. In *O. americanus* its outline is quite rounded. The tibial crest of *Tragelaphus* spp. and *Kobus* spp. is also rounded. In contrast, that of *B. tragocamelus*, *C. taurinus* and *A. marsupialis* is rectangular in outline. The foramen on the shaft is visible in caudal view, except for a few individuals of *A. marsupialis* and *O. ammon*.

On the distal end, the cranial malleolar articular facet is either slightly smaller than the posterior one (*O. ammon*, *C. taurinus*) or clearly smaller (*Tragelaphus* spp., *Kobus* spp., *B. tragocamelus*, *O. oreotragus*, *O. americanus*, *Gazella* spp., *A. melampus* and *A. marsupialis*; Fig. 3.B, f). The malleolar articular facets of *Cephalophus* spp. are equal in size. In *C. taurinus* and *O. americanus* the two facets can be fused. In lateral view, the distal edge is rather "U"-shaped

(all bovids except *B. tragocamelus*, *O. americanus* and *O. ammon*, which have an "L"-shaped outline). All the bovid tibia are straight except *B. tragocamelus* and *Cephalophus* spp., where the shaft is fairly "S"-shaped.

The dorsal crest of *O. virginianus* tibia is longer than that of *A. americana*, more cervid-like (see Heintz, 1970, vol. 2, page 35, Fig. 30). On the proximal end, the tibial tuberosity is clearly square-shaped, but generally (14 specimens out of 16) is more posteriorly oriented (see Lister 1996, page 130, Fig. 2, char. 2). On the distal end, the two malleolar articular facets are slightly different in size and little spaced (14 specimens out of 16). In lateral view, the distal edge is rather "L"-shaped than "U"-shaped (9 specimens against 5).

Astragalus: (Fig. 4) The distal trochlea is generally bovid-like in that the two halves are of the same width (but on several specimens the lateral side may be slightly wider) and the outline of the notch is symmetrical (that is true on all the specimens). The lateral half of the trochlea is flat in its distal part (where it is articulating with cubo-navicular). The longitudinal axis is straight on its distal and proximal halves. The bulge on the medial side (dorsal view) above the distal trochlea is always well pronounced (Fig. 4.A.1, c).

The proximo-medial ridge has a "V"-shaped nick (Fig. 4.A.1, a) between its distal and proximal parts and the two parts are equally laterally extended. The whole of the ridge can be more or less developed (generally more) but the nick is always present. It improves the contact of the articular surface with the medial part of the distal epiphysis of the tibia, which has no possibility of any lateral movement. The transverse axis of the proximal trochlea (Fig. 4.A.2, b), which is very narrow, also strengthens the tibia-astragalus articulation.

A proximal-medial ridge such as that of *A. americana* can be found in bovids. *Gazella* spp. also show a little "V"-shaped nick. However, the proximal part of the ridge extends further laterally than does the distal part. On the whole the development of the ridge is quite variable: generally, it is less than in *A. americana*. The medial ridge in the astragali of *O. ammon* and *C. taurinus* looks similar to those of *Gazella* spp. It is wider in all the *O. ammon* and half of the specimens of *C. taurinus* studied. The astragal medial ridge of *A. marsupialis* is pronghorn-like but is relatively less developed. *O. oreotragus* shows a little nick, but the distal part of the medial ridge is much wider and more developed than the proximal one. *Cephalophus* spp., in contrast, have a proximal part that is more developed than the distal one, but they lack the nick. The whole of the ridge is narrower than that of *A. americana*. *Kobus* spp. show a very narrow medial ridge, and in *Tragelaphus* spp., *B. tragocamelus* and *O. americanus* it is almost absent (Fig. 4.C, a).

The transverse axis of the proximal trochlea of the bovid astragalus is wider than that of *A. americana*, except in *C. taurinus*, *A. marsupialis*, *A. melampus*, and *G. gazella*.

In cervids the shape of the medial ridge varies: one can recognise the condition *C. elaphus*, with the the proximal part more laterally extended than the distal one, and the condition found in *D. dama*, which is the opposite or with equal extension of the two parts (Lister 1996; Pfeiffer 1999). The "V"-shaped nick is absent (Fig. 4.B.1, a) and the transverse axis of the proximal trochlea is wider than that of *A. americana* (Fig. 4.B.2, b).

Calcaneus: (Fig. 4) Some characters on the calcaneus of *A. americana* are bovid-like, and others are cervid-like. On the plantar side of the calcaneal head the *musculum perforatum* sulcus is very large and shallow, a bovid-like feature (Fig. 4.D.1, a). A cervid would have a deeper groove (see Heintz, 1970, vol. 2, page 36, Fig. 32). In contrast, the back of the body of the calcaneus is almost straight, only very slightly concave. This is less concave than in bovids and more similar to the condition in cervids. The dorsal edge of the astragalar facet is showed in Fig. 4.D.2, b: the inner part of the proximal process is almost as straight as in cervids (e.g., *O. virginianus*, *M. gouazopira*). According to Heintz (1970), in most bovids the dorsal edge of the astragalar facet is oblique relative to the dorsal border of the calcaneal body (vol. 2, page 36, Fig. 33). Nevertheless, on 3 out of 5 individuals of *O. ammon*, this edge is rather pronghorn-like.

On the calcaneus of *A. americana* most proximal part of the tuberosity is on the medial side (Fig. 4.D.1, c). In *O. americanus* and *O. ammon* it is in the middle. In medial view, the *sustentaculum tali* is in the middle of the calcaneal body and its rear part never projects beyond the dorsal surface of the calcaneus (Fig. 4.D.2). The anterior part of the *sustentaculum tali* may be a little indented (8 specimens out of 25), but generally it is smooth.

Cubo-navicular: (Fig. 2) Its distal part looks like that of a bovid. The medial edges of the endo and ecto-cuneiform articular facets (Fig. 2.E.1, a) are not on the same line; the first is more laterally placed (for differences between cervid and bovid shapes of the distal side of cubo-navicular see Heintz, 1970, vol. 2, page 37, Fig. 34). Moreover, the articular facet for the ento-cuneiform steeply slopes backward: the plantar edge is almost at the same level as the ecto-cuneiform facet (which is fairly flat), but the dorsal edge is higher, making a step with the other articular facet. An articular surface can be found on the vertical wall below the anterior metatarsal facet. It is generally small (21 specimens), but a few specimens (4) have a larger one. This surface articulates with a small facet on the lateral side of the ecto-cuneiform. The plantar metatarsal facet is usually missing (Fig. 2.E.1, b). It is only present on 6 specimens out of 19. It is bovid-like, slopeing steeply inward and forward. The absence of the plantar metatarsal facet gives a triangular shape to the latero-distal corner in posterior view (Fig. 2.E.2, b). On the plantar side, the inner tendon edge is large and smooth, and its axis is quite oblique (Fig. 2.E.2, d; compare with the cubo-navicular of *O. virginianus*; Fig. 2.F, d).

On the proximal side, the calcaneal articular facet and the top of the median tendon area reach almost the same level: sometimes the former is higher, sometimes the latter. In proximal view, the part between the inner tendon and the calcaneal facet shows a large and shallow groove on all specimens, except for in three where there is a small medial bump that divides the groove in two.

On the distal part of the cubo-navicular, in the alignment of the medial edges of ento and ecto-cuneiform facets, all of the cervids and bovids studied are typical for their respective families, except for *Tragelaphus* spp. which is cervid-like. The ento-cuneiform facet is higher than that the ecto-cuneiform on *A. marsupialis*, *Gazella* spp., *M. gouazopira* and *O. virginianus*. In bovids this facet is almost horizontal; in cervids it is almost horizontal or steeply sloping back-

ward. *C. taurinus* has an ento-cuneiform facet that is pronghorn-like, with its posterior edge almost at the same level as the ecto-cuneiform facet, but the anterior edge is higher. The facet for the lateral side of the ecto-cuneiform, below the dorsal metatarsal facet, is present on all the taxa studied, except in half of the specimens of *O. virginianus*. This facet is small in *Cervus* spp., *Gazella* spp., *A. marsupialis*, *Tragelaphus* spp., *C. leucogaster* (in contrast to *C. dorsalis*) and *O. ammon*. It is larger in *A. melampus*, *C. taurinus*, *C. dorsalis* and *O. americanus*.

Metatarsal III + IV: (Fig. 2) The metatarsal is long and slender, like the metacarpal (Fig. 2. C.1). The articular keels for the proximal phalanges are sharp, and extend backward onto the plantar side without split between the two trochleae (a split is present in 5 specimens out of 23). The plantar foramen on the distal part of the bone is relatively as large as that found on red deer (17 specimens; for the shape of these two characters see Lister 1996, page 133, Fig. 2, char. 4 and 5). The plantar gully is not very deep, unlike cervids, but the distal part of the dorsal gully is closed, which is cervid-like (Janis and Scott 1987).

On the proximal end, the articular facets for the cubo-navicular and ecto-cuneiform meet one another on their dorsal part. In 8 specimens the join is along a line (Fig. 2.C.2, a), in 5 it is only at the most anterior point and on 8 specimens they do not join, but their edges are parallel and very close.

On the pronghorn metatarsal, the spur on the inner side (see Pfeiffer 1999, page 94, Fig. 77) can be either absent (10 specimens) or present (12 specimens); in the latter case, it is very small. The nick on the inner side of the ecto-cuneiform articular facet is generally absent, but on 4 out of 21 specimens it is present (Fig. 2.C.2, b), and on 4 other specimens it is incipient.

Generally the proximal end lacks the plantar articular facet for the cubo-navicular (12 speci-mens; Fig. 2.C.2, c), and in its place there is a high blade, which is triangular in shape and takes part in the formation of the diarthoidal facet. This surface articulates with a small bone, interpret-ed on the bovid metatarsal III + IV as the rudimentary metatarsal I (Heintz 1970). Moreover, on 9 specimens a facet exists on the top of the blade; it is small and rounded as in bovids. On only 3 specimens the shape is more similar to cervids.

In the general outline of the proximal end, in proximal view, the dorsal part is rounded and different from in the plantar one. The plantar-medial corner is more developed than the plantar-lateral one, which lacks the plantar tuberosity found in cervids and dromomerycids (Fig. 2.C.2; Janis and Manning 1998).

Proximally the bovid metatarsal has a plantar facet for the cubo-navicular which is quite short (Fig. 2.D, c) and usually rounded. It is flat in all taxa except *Tragelaphus* spp., *B. tragocam-elus*, *Kobus* spp., *C. taurinus* and 3 specimens of the *G. gazella*. The spur recognized by Pfeiffer (1999) on the inner side of certain cervid metatarsal (e.g., *D. dama* and *Axis axis*, the chital) was not found in any bovids except for 2 specimens of *T. buxtoni*, where it is very small. The nick on the side of the ecto-cuneiform is found in *O. oreotragus*, *Gazella* spp., *A. melampus* (where it is star-like), in a few specimens of *Tragelaphus* spp. and *B. tragocamelus*, and is very rare in *Cephalophus* spp. (found in only 2 specimens) and *O. americanus* (3 specimens) where it is very

small. All bovids have a diarthoidal facet, which is absent from the metatarsals of all extant cervids (Heintz 1963). The plantar outline, in proximal view, is more pronghorn-like.

In bovids the dorsal gully is not distally closed, in contrast to the condition in cervids. The lateral ridges may form small bumps at their distal limit in *T. buxtoni* (but not in *T. imberbis*), *O. americanus* and 2 individuals of *G. gazella*. The plantar gully, unlike the condition in *O. virginianus*, *M. gouazopira*, *M. muntjak* and the other cervids, is flat or poorly excavated. The gully of *Gazella* spp. and *A. melampus* is deeper than that of *A. americana* but not as deep as that of the cervids. The distal keels have the general shape seen on metacarpals.

A small spur is generally present (14 specimen out of 16) on the inner side of the proximal end of *O. virginianus* metatarsal, and there is a flat surface on top of four of such spurs (see for the shape of this character Pfeiffer 1999, page 94, Fig. 77). The caudal articular facet for the cubo-navicular is always present: it is a long and narrow articular surface. Whereas, the surface for the rudimentary metatarsal I always lacks.

Phalanges: (Fig. 1 and 4) On the same individual, the manual proximal phalanx is easily recognizable from the pedal one; but it is more difficult to recognize them from a field sample, because the differences are slight and the variation among individuals is large. Indeed, in proximal view, the outline of the manual phalanx is more rectangular (Fig. 4.E.2), while the pedal one has a more rounded lateral outline (Fig. 4.E.1). The muscular insertions are longer on the plantar side of the pedal phalanx than in the manual one (Fig. 4.E.3 and 4, a). This last character is rather variable and some pedal phalanges have shorter muscular insertions than the manual phalanges of other individuals. The length of manual and pedal phalanges is similar. An interesting character on the proximal phalanx of *A. americana* is the presence of rounded or oval marks close to the proximal end of the muscular insertion in palmo-plantar view (Fig. 4.E.3 and 4, b).

All the ruminants studied may sometimes have marks in the same position, but they differ from *A. americana* in shape and size. Only *O. americanus* shows some marks similar in shape to those of *A. americana*.

Manual and pedal medial phalanges are more difficult to separate. I was not able to separate them even in the same individual. The characters of the phalanges of *A. americana* are as follows: the presence of a little plateau on the proximal end behind the articular surface, which is smaller than those of cervid phalanges (Fig. 4.F, a; and 4.G, a); the strength of the ventral muscular insertions on the middle part of the bone (palmo-plantar view); and the presence of a little nick between the 2 lips of the distal end (palmo-plantar view).

The ungual phalanges are strong but slender. The plantar edge is almost horizontal with a small concavity in the middle. The rear part of the articular surface is horizontal in lateral view (Fig. 1.K). In proximal view, it is divided by a ridge that is oblique to the vertical axis. A little spur can be found at the top of the articular surface, where it meets the dorsal edge. It variably developed and more or less advanced from the posterior limit of the dorsal edge. Two small foramina are found at each side of the spur. The ungual phalanx lacks sesamoid articular facets.

A. americana has lost all traces of the lateral digits and their accompanying splints, the vestigial metapodials (O'Gara 1990; Janis and Manning 1998).

DISCUSSION

Antilocaprids present a mix of bovid and cervid characters on their limb bones. The main cervid-like features are:

1. The long and sharp ridges delimiting the medial gully on the dorsal side of the distal end of the radius;
2. The shape of the ridge between the articular facets of the capitato-trapezoidal and magnum, on the proximal end of the metacarpal cannon bone;
3. The plateau on the proximal end of the medial phalanges (both manual and pedal) behind the articular surface;
4. The dorsal gully of the metatarsal, which is closed distally (in fact, some merycodontine specimens and the fossil genus *Meryceros*, have an open metatarsal gully, although the closed condition appears to be the primitive one; Janis and Scott, 1987);
5. The dorsal edge of the astragalar facet on the distal part of the calcaneus.

Bovid-like characters include some ones probably related to their adaptative evolution, which parallels that of *Gazella* spp., and other which seem to be devoid of any adaptative significance. The main first features are as follows:

1. The length and slenderness of the metapodials, the shape of their distal end and articular keels (see Köhler 1993);
2. The strong tibia-astragalus contact and the shape of the distal trochlea of the astragalus;
3. The shape of the distal part of the cubo-navicular, the ento and ecto-cuneiform facets and the cubo-navicular-metatarsal contact;
4. The general shape and slenderness of the proximal phalanges.

In particular the features at the point 2 are interesting because they have as effect (like the fusion of limbs elements) to limit all the movements except those in the vertical plane. This improves running speed, and is advantageous for fast-running animals even if it reduces the possibility of zigzag escape strategies (Leinders and Sondaar 1974; Leinders 1976; Van Der Geer 1999).

The bovid-like characters without apparent adaptative evolution are:

1. The shape of the humerus distal trochlea;
2. The shallow gully on the palmo-plantar side of the metapodials;
3. The shape of the sulcus for the *musculum perforatum*, on the planter side of the calcaneal head;
4. The presence of the diarthoidal facet on the proximal end of the metapodial (which it is probably a primitive ruminant character, as it is also retained on the bones of Miocene cervids but not in more recent ones; Heintz 1963).

In addition, antilocaprids do have some own peculiar characters, which are not on found on other ruminant limb bones or which are very rare on them:

1. The shape of the proximal-medial ridge of the astragalus (its developement equal in its proximal and distal part, the presence of the 'V' nick);

2. The presence of oval marks on the proximal phalanges;
3. The mixing of the oblique edge of the pulley inside the *fossa olecrani* with a little triangular nick over it (however this is variable and not seen in all specimens).

The last two features, especially the second one, are very uncommon on antilocaprid bones until very recently (Pleistocene) and could be only typical of the extant species.

Limb bones of *A. americana* differ, for size and proportions, from those of all the others ruminants in the same geographical area, except from those of *O. virginianus* and *O. hemionus*. However, the analysis of the morphological characters of antilocaprid limb bones shows that they present a mixture of bovid and cervid features, with a few ones peculiar to the family. This particular combination makes antilocaprid bones recognizable from those of other ruminants, bovids or cervids, *Odocoileus* included. This is true at least for the end of the Pleistocene period, when the extant species is present in fossil accumulations (Kurtén and Anderson 1980). The most primitive taxa, the Merycodontinae (sensu Janis and Manning 1998), and the late Miocene/Pliocene Antilocaprinae need a more detailed analysis in order to understand when the features of the extant species appeared.

Many of the characters of the limb bones of *A. americana* may have no phylogenetic significance, but rather an adaptative one; e.g. its metapodials are similar to those of *Gazella* spp., because of functional convergence. In fact, *A. americana* occupy the same niche in North America as the different species of *Gazella* do in the Old World and it is considered an excellent enviromental marker (Janis and Manning 1998; Janis 2000).

Finally, the characters described here may show a large amount of individual variation within species. While the sample of *A. americana* is reasonably large, those for many others are quite small, and therefore must be used with caution.

Hopefully, these finds will be of value to archeology and field biologists, as well as enforcement divisions of agencies conducting forensis investigations.

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Appendix A. *Specimens examined.* – All the specimens are housed in AMNH of New York.

Taxon	Specimen no.	Sex	Geograp. area
Antilocapra americana	139766, 239122 75243, 100353, 100354, 130196 130197, 237994 130198 10419, 142361, 143498 19350 16139, 21529 5036 130201	female male male unknown male female male unknown unknown	Wyoming Wyoming Wyoming Wyoming Nebraska Zoo Zoo Zoo unknown
Boselaphus tragocamelus	54476 10265 10266, 10267 21511	male female male unknown	India Zoo Zoo Zoo
Tragelaphus buxtoni	81003, 81020 81002, 81016	female male	Ethiopia Ethiopia
T. imberbis	82019	male	Tanzania
Cephalophus dorsalis	52928 52924	female male	tropical Africa tropical Africa
C. leucogaster	52775, 52824, 52836, 52861 52778, 52788, 52830, 52926 119194	female male male	tropical Africa tropical Africa tropical Africa
Kobus ellipsiprymnus	53494, 53515 82126 53492 216377	female male unknown male	Zaire Zaire Zaire Mozambique
K. kob	53353 53347	female unknown	Belgian Congo Belgian Congo
Oreotragus oreotragus	33327, 80553	male	East Africa
Antidorcas marsupialis	83549, 83550	male	South Africa
Gazella gazella	54506, 54998 54997	female male	India India
G. granti	85152 82052, 85151, 85153	female male	Kenya Kenya
Connochaetes taurinus	27824, 54137 54133 80493 82026, 82029 6230 81789	female male male male female unknown	Kenya Kenya Angola Tanzania Zoo unknown
Aepyceros melampus	81690	male	unknown
Oreamnos americanus	122670 130223 35286 35492	female female female male	Canada Alaska Zoo unknown

Appendix A. (continued).

| Taxon	Specimen no.	Sex	Geograp. area
Ovis ammon	45490, 45492 54869, 54870	male male	China Russian Pamir
Odocoileus virginianus	91099, 245629 130302, 130397 14085 8363, 14084 70047	male male female male unknown	Georgia, USA New York State Zoo Zoo unknown
Mazama gouazopira	23481 130459 214752	female female male	Colombia Venezuela Bolivia
Muntiacus muntjak	54562 50002150 22830 22833, 35095	male male male male	Burma Vietnam Zoo unknown
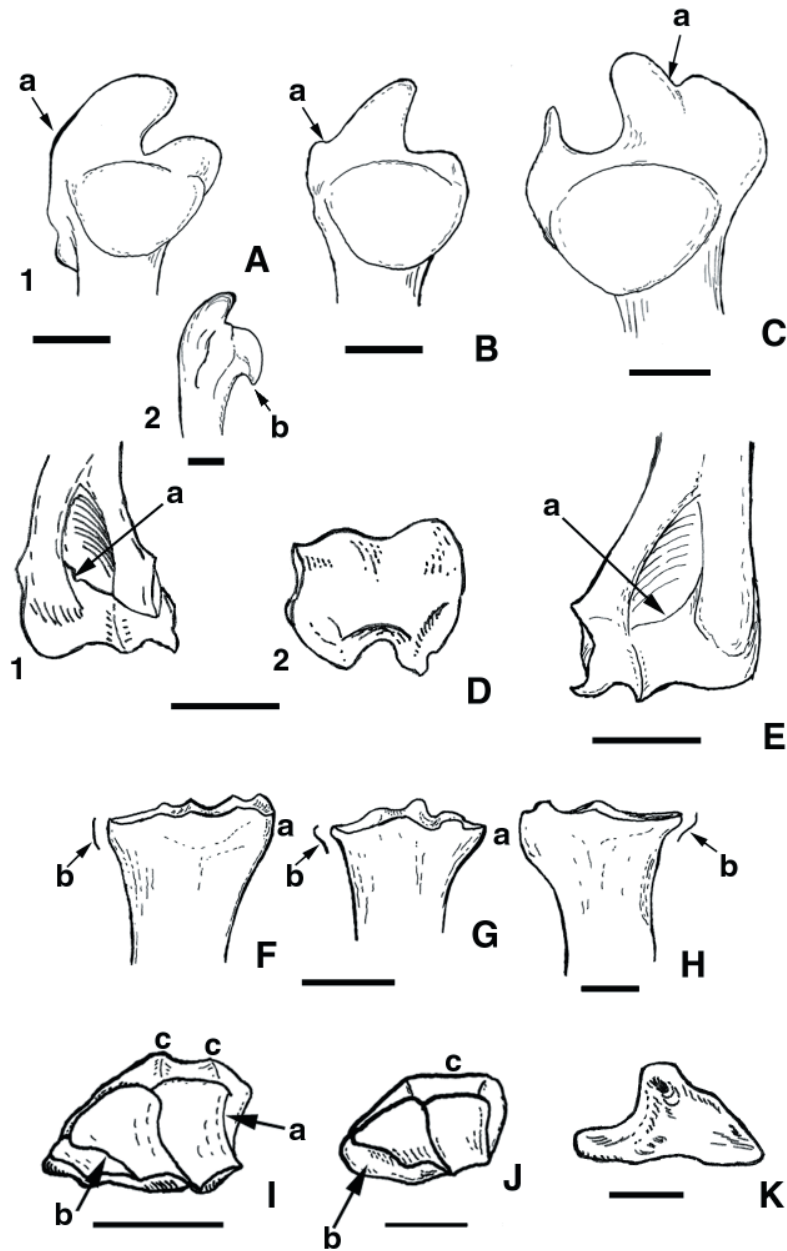
Fig. 1. A) Right humerus of A. americana: caudal (1) and lateral (2) views of the proximal end. B) Right humerus of O. virginianus: caudal view of the proximal end. C) Left humerus of C. taurinus: caudal view of the proximal end. D) Right humerus of A. americana: caudal (1) and distal (2) views of the distal end. E) Left humerus of O. virginianus: caudal view of the distal end. F) Left radius of A. americana: cranial view of the proximal end. G) Left radius of O. virginianus: cranial view of the proximal end. H) Right radius of O. americanus: cranial view of the proximal end. I) Right radius of A. americana: distal view of the distal end. J) Right radius of O. americanus: distal view of the distal end. Scale bars 2 cm. K) Ungual phalanx of A. americana in lateral view. Scale bar 1 cm.
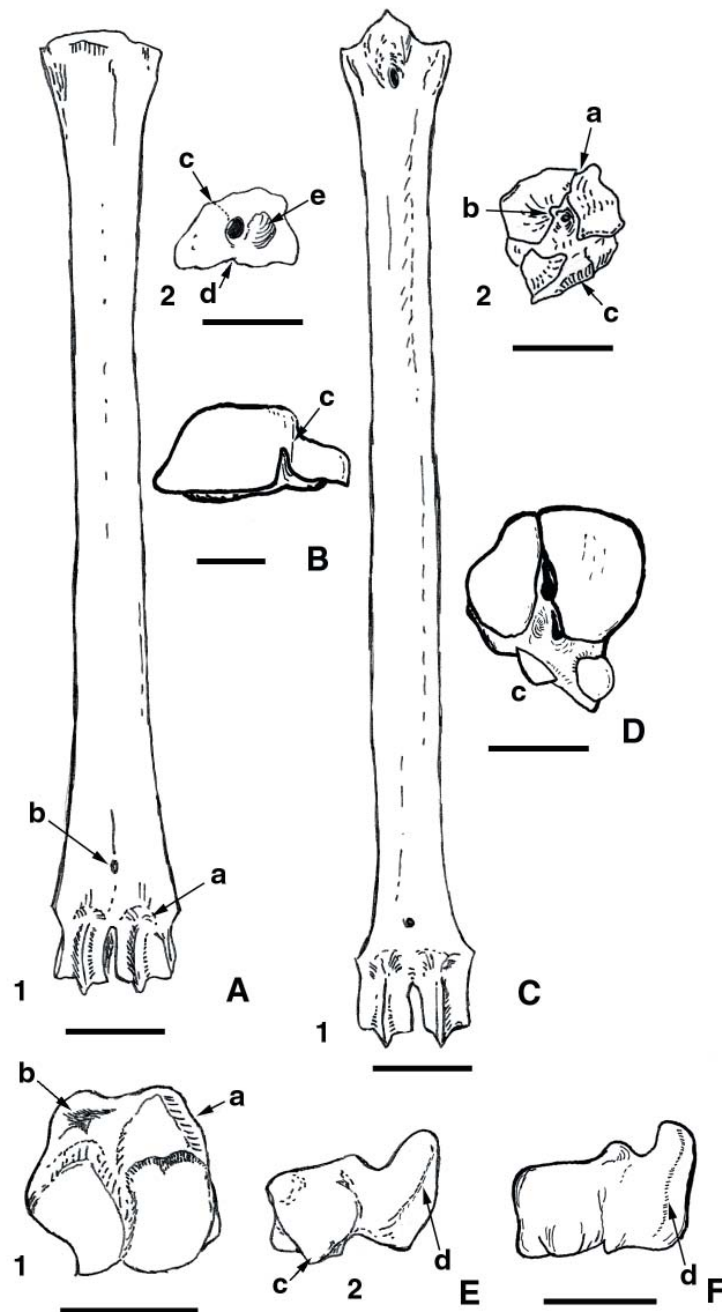
Fig. 2. A) Left metacarpal III+IV of A. americana: dorsal (1) and proximal (2) views. B) Right metacarpal III+IV of B. tragocamelus: proximal view. C) Right metatarsal III+IV of A. americana: plantar (1) and proximal (2) views. D) Left metatarsal III+IV of C. taurinus: proximal view. E) Left cubo-navicular of A. americana: distal (1) and (2) plantar views. F) Left cubo-navicular of O. americanus: plantar view. Scale bars 2 cm.
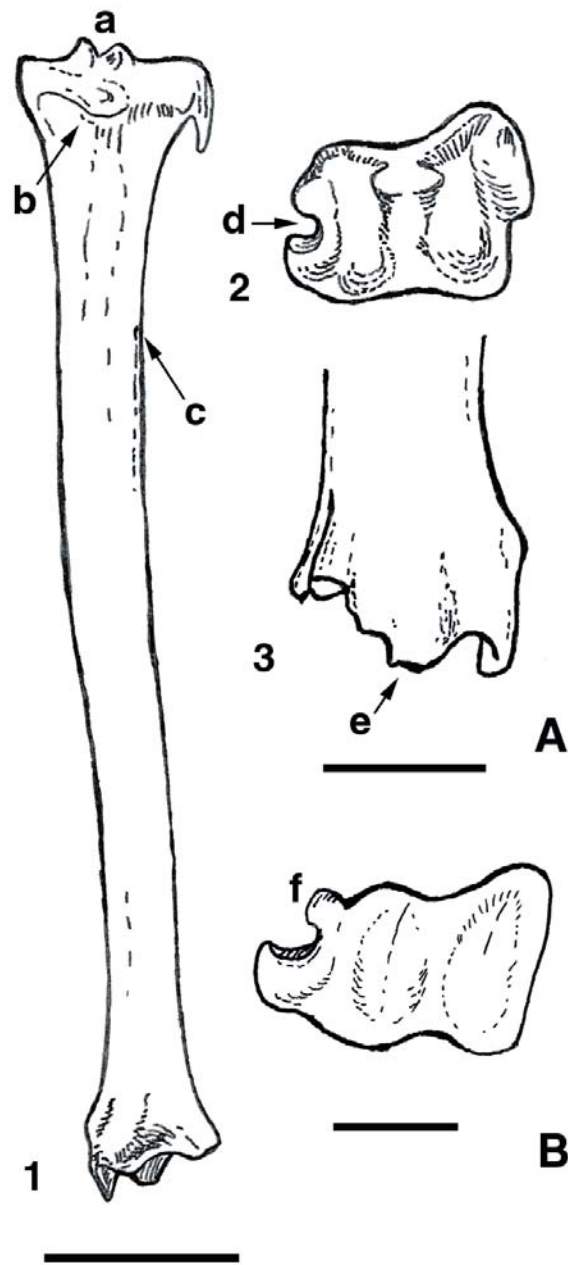
Fig. 3. A) Right tibia of A. americana: caudal view (1) of the whole bone, distal (2) and (3) cranial views of the distal end. Scale bars 5 and 2 cm respectively. B) Right tibia of K. ellipsiprymnus: distal view of the distal end. Scale bar 2 cm.
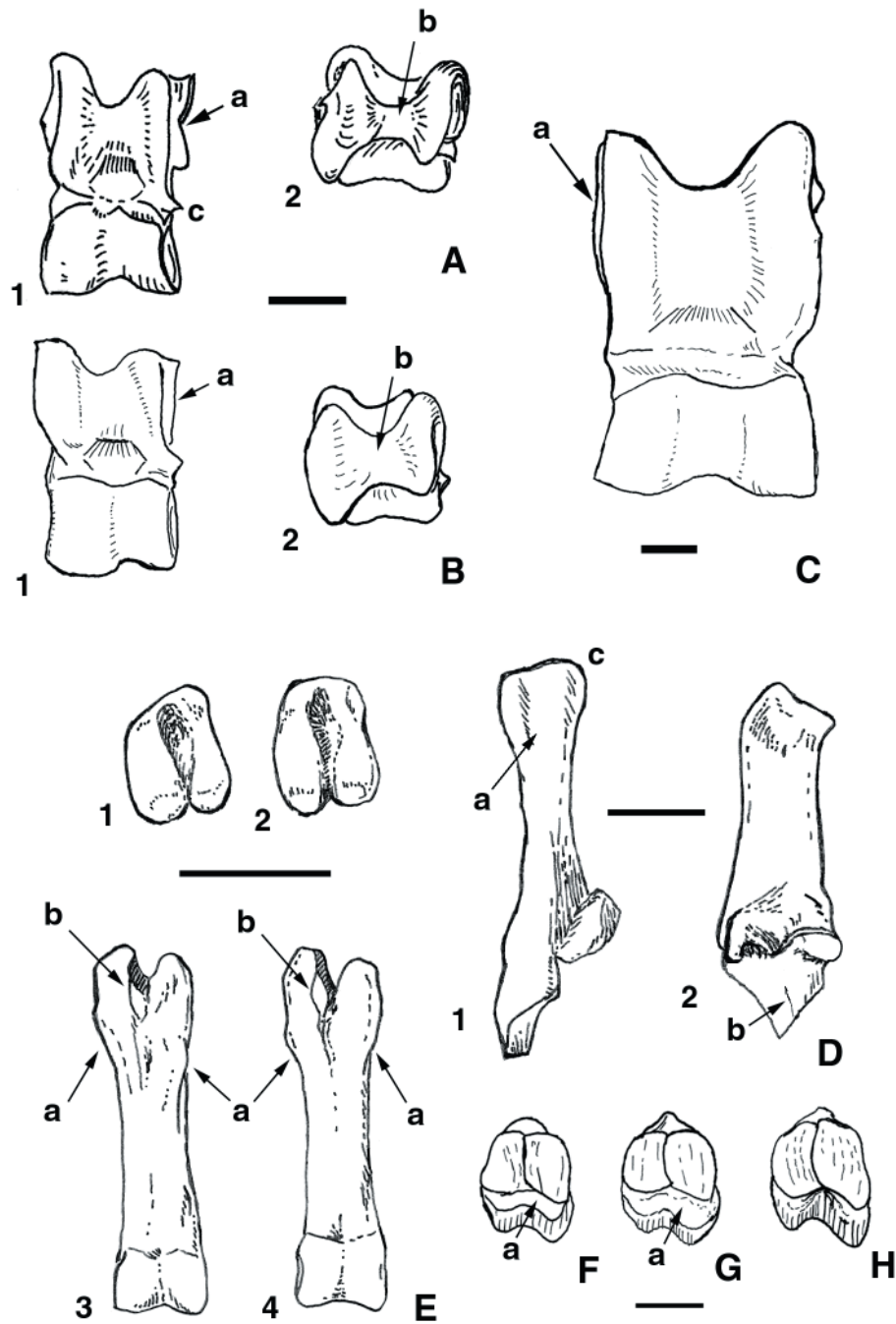
Fig. 4. A) Right astragalus of A. americana: dorsal (1) and proximal (2) views. B) Right astragalus of O. americanus: dorsal (1) and proximal (2) views. C) Left astragalus of T. buxtoni: dorsal view. Scale bars 1 cm. D) Left calcaneum of A. americana: plantar (1) and medial (2) views. E) Pedal (1 and 3) and manual (2 and 4) proximal phalanxes of A. americana: proximal (1 and 2) and palmo-plantar (3 and 4) views. Scale bars 2 cm. Proximal view of mesial phalanxes of F) A. americana, G) cervid, and H) bovid. Scale bar 1 cm.

Section IV.

List of Presenters

David Brown, Arizona State University, 3118 W McLellan Blvd, Phoenix, AZ 85017; debrown@imap3.asu

Jorge Cancino Hernandez, Centro de Investigatciones Biologicas del Noro Est, Sarapicos 225 Col Las Garzas, La Paz, Baja CS, Mexico,23070; jcancino@cibnor.mx

Shannon Gavin, University of Calgary, 2747 Cochrane Rd NW, Calgary, AB,Canada T2M4J1; sdgavin@ucalgary.ca

Chris Jacques, South Dakota State University, Box 2140B, NPB Rm 138 Dept, Brookings, SD 57007; jacques@rushmore.com

William F. Jensen, North Dakota Game & Fish Dept, 100 N Bismarck Expwy, Bismarck, ND 58501; bjensen@state.nd.us

Randy Kreil, ND Game & Fish Department, 100 N Bismarck Expry, Bismarck, ND 58501; rkreil@state.nd.us

Cal McCluskey, Bureau of Land Management, 1387 S Vinnell Way, Boise, ID 83719; cal_mccluskey@blm.gov

Carl Mitchell, U.S. Fish & Wildlife Service, 74 Grays Lake Rd, Wayan, ID 83285; carl_mitchell @fws.gov

Richard Ockenfels, Arizona Game & Fish Dept, 2221 W Greenway Rd, Phoenix, AZ 85023; rockenfels@gf.state.az.us

Bill Rudd, Wyoming Game & Fish, 351 Astle, Green River, WY 82935 Bill.Rudd@wgf.state.wy.us

Daly Sheldon, University of Wyoming, Dept 3166 1000 E Univ Ave, Laramie, WY 82071; sheldon2@uwyo.edu

Patricia Stastny, University of NE - Omaha, 6001 Dodge St, Biology Dept, Omaha, NE 68182; pstastny@hotmail.com

Bruce Stillings, North Dakota Game & Fish Dept, 225 30th Ave SW, Dickinson, ND 58601; bstillin@state.nd.us

Dan Svingen, U.S. Forest Service, 1141 S Highland Rd, Bismarck, ND 58501

Brian Wakeling, Arizona Game & Fish Dept, 2221 W Greenway Rd, Phoenix, AZ 85023; bwakeling@gf.state.az.us

Don Whittaker, Oregon Dept of Fish and Wildlife, 3406 Cherry Ave, Salem, OR 97302; don.whittaker@state.or.us

Jim Yoakum, Western Wildlife Consultants, PO Box 369, Verdi, NV 89439

Section V.

Business Meeting

21ST BIENNIAL PRONGHORN WORKSHOP
BUSINESS MEETING AGENDA

May 3, 2004 11:55 AM – 1:30 PM

- Website/CD for Proceedings (Richard Ockenfels)

- Management Guidelines (David Brown)

- Awards (Richard Ockenfels)

- Hall of Fame (Richard Ockenfels)

- Special edition of Wildlife Society Bulletin Regarding Pronghorn (William Rudd or Richard Ockenfels)

- Next Meeting Location (William Jensen)

- What to do with surplus funds from the workshop (William Jensen)

- Other Items

CALL TO ORDER

Meeting was called to order by Bill Jensen (ND) at 12:40 PM on 5/3/04. Richard Ockenfels (AZ) assisted by conducting the meeting.

APPOINTMENT OF RECORDER

Janel Kolar, ND Game and Fish Department, was asked to record the minutes.

ROLL CALL

Present – Al Arsenault, Alice Koch, Andy Lindbloom, Anis Aoude, Ben Rutten, Bill Rudd, Brad Compton, Brad Holliday, Brandon Mason, Brian Wakeling, Bruce Renhowe, Bruce Stillings, Bruce Trindle, Cal McClusky, Chris Kochanny, Chuck Berdan, Jack Clark, Daly Sheldon, Dan Halstead, David E. Brown, Don Whittaker, Fred Lindzey, Gary Schlichtenmeier, Glen Sargeant, Jerry Kobriger, Jesse Kolar, Jim D. Yoakum, John Wrede, Jorge Cancino, Kent Luttschwager, Kim Brinkley, Matt Peek, Michael Catanach, Mike Oehler, Nate Harling, Pat Mathis, Rich Guenzel, Robb Hitchcock, Roger Bredehoft, Roger Johnson, Shannon Gavin, Sue Fairbanks, Tim Smyser, Tim Woolley, Tom Becker, Tom Pojar, Ben Rutten

IDENTIFICATION OF VOTING MEMBERS

Arizona – Brian Wakeling; Baja CA – Jorge Cancino; ID – Brad Compton; KS – Matt Peek; NE – Bruce Trindle; – Pat Mathis, ND – Bruce Stillings; OR – Don Whittaker; SK – Al Arsenault; SD – John Wrede; UT - Tom Becker; WY – Bill Rudd; BLM – Cal McClusky; USFS – Dan Svingen; NPS – Mike Oehler; USGS – Glen Sargeant; University Representatives: Iowa State University - Sue Fairbanks; Arizona State University - Dave Brown; University of Wyoming -Fred Lindzey.

DISCUSSION

1. Proceedings – Available for 2002 and may sign up for 1998 and 2000. We have been looking for a way to distribute proceedings or at least make them available. Only a couple of people have complete sets which they are willing to lend to people (Jim Yoakum, Rich Ockenfels). Proposal to create portable document format (pdf) files to distribute on CD or on the internet. Action: Will continue to pursue various avenues. TWS Students working with Pat Mathis will work on preparing materials.

2. Update of Pronghorn Management Guidelines – Dave Brown reported on progress to date. Anyone who would like to take a look at the new guidelines can e-mail Dave. Next step – get together and hire a copy editor to clean up – either a volunteer or paid person. After that document will be published and distributed. Jim Yoakum recommended a commitment to distributing the Management Guidelines to every biologist. Jorge has translated 1998 version into Spanish. Action: Will continue trying to move forward.

3. Awards – Rich Ockenfels requested nominations for awards and received multiple nominations. *Action:* Will be given out at banquet tomorrow. Awards information should be printed in proceedings.

4. Hall of Fame – Rich Ockenfels proposed a Hall of Fame for special pronghorn awards. Discussion followed. Recommended that a committee be set up to identify Hall of Fame award recipients and publish in each proceedings. Motion: Motion to create a five-person committee co-chaired by Dave Brown & Robb Hitchcock. Bill Rudd seconded. Motion passed. Jorge will get the name of a representative from the association in Mexico that should be involved.

5. Pronghorn Book – Jim Yoakum announced that the Wildlife Management Institute has produced two books, both published by University Press of Colorado, on pronghorn this year: *Pronghorn Ecology and Management* by Bart W. O'Gara and Jim D. Yoakum, will be available this fall, and *Prairie Ghost Pronghorn and Human Interaction in Early America* by Richard E. McCabe, Bart W. O'Gara and Henry M. Reeves, which will be out any day now. A discount has been offered through the Wildlife Management Institute for participants of the 21st Biennial Pronghorn Workshop.

6. Special edition of The Wildlife Society Bulletin regarding pronghorn – Rich Ockenfels reported on special meeting May 7, on Sonoran pronghorn, which will be published as a special edition of The Wildlife Society Bulletin. Discussion will take place regarding another special edition of The Wildlife Society Bulletin on pronghorn subjects. Some subjects may include fences, roads, railroads, etc. Suggestion that we look at needs for research when reviewing subject options as well. Jim Yoakum notified attendees The Wildlife Society does not favor re-publication of materials. *Action:* Continue to pursue.

7. Next Meeting Location – Requested volunteers to host the 22nd Biennial Pronghorn Workshop in 2006. Brad Compton suggested Idaho is interested in pursuing. New Mexico may pursue for 2008.

8. Surplus funds from workshop – Bill Jensen explained that thanks to grants provided by the USFS and BLM, we should have surplus funds. Bill envisioned acknowledging the participation of the four students who are presenting papers by giving them an honorarium not to exceed $200 and using any additional money as seed money for the next host state. Discussion on using excess funding for publication of proceedings on internet or pronghorn management guides. Action: Bill will pay bills, distribute honorariums, and then let Idaho and New Mexico know what is left over for possible use.

There being no further business, Bruce Stillings moved to adjourn. Second by Jorge Cancino. Passed.

Respectfully submitted,
Janel Kolar, Recorder
North Dakota Game & Fish Department

Awards

**AWARDS PRESENTED AT THE 21ST BIENNIAL PRONGHORN WORKSHOP
BISMARCK, NORTH DAKOTA**

BERRENDO AWARD

Dr. Bart O'Gara (deceased, USFWS), Professor Emeritus and Past Leader, Montana Cooperative Fish and Wildlife Research Unit.

Bart, who passed away in 2003, was considered one of the premier pronghorn biologists in the world, having worked on the species since the 1960s. Co-author of the newest tome on pronghorn with Jim Yoakum, much of Bart's life was dedicated to the research and management of the species. Bart was the author of the pronghorn for Mammalian Species. He was a charter member of the Pronghorn Workshops, and he never missed a meeting.

2002 (20TH BIENNIAL; 1ST YEAR AWARDED)
James D. Yoakum (retired BLM), Western Wildlife, Verdi, Nevada

THE PRONGHORN WORKSHOP SPECIAL RECOGNITION AWARD
Alice Koch, Wildlife Biologist, California Department of Fish and Game

Recognized for more than a decade of management activities and habitat enhancement projects that benefit pronghorn herds in California. Alice has worked on the reintroduced herd in the Carrizo Plains, California. She is known as "missy pronghorn" for her dedication to the management of one of the few herds in California.

Rich Guenzel, Wildlife Biologist. Wyoming Game and Fish Department

Recognized for his census work and development of the Line Transect Methodology to improve census accuracy of pronghorn herds. Rich started his wildlife career studying pronghorn ecology in Wyoming, and he has retained that keen interest in pronghorn biology and management over several decades.

Arizona Antelope Foundation, Arizona not-for-profit 501-3(C): organization

Founded in 1992 solely dedicated to the conservation and proper management of pronghorn in Arizona and across the Southwest. They are the sole state organization dedicated only the purpose of conserving pronghorn.

John J. Hervert, Wildlife Program Manager, Arizona Game and Fish Department

Recognized for a decade of dedication management and research of the Endangered Sonoran Pronghorn. John manages the wildlife program in the Yuma Region, which contains all the currently occupied Sonoran pronghorn habitat in the United States. He is also actively involved in the management of the subspecies in Mexico.

2004 Workshop Attendees

Name	Affiliation	City	State	Email Address
Anis Aoude	Utah Division of Wildlife Resources	Hyrum	UT	anisaoude@utah.gov
Al Arsenault	Saskatchewan Environment	Saskatoon	SK Canada	aarsenault@serm.gov.sk.ca
Tom Becker	Utah Division of Wildlife Resources	Tooele	UT	beckert@sisna.com
Chuck Berdan	Bureau of Land Management	Belle Fourche	SD	cberdan@blm.gov
Rober Bredehoft	WY Game & Fish Dept	Laramie	WY	rbredeho@wyoming.com
Clay Brewer	Texas Parks & Wildlife Dept	Fort Davis	TX	cbrewer@overland.net
Kim Brinkley	Los Angeles Zoo	Glendale	CA	
David Brown	Arizona State University	Phoenix	AZ	debrown@imap3.asu
Jorge Cancino Hernandez	Centro de Investigatciones Biologicas del Noro Est	La Paz	Baja CS Mexico	jcancino04@cibnor.mx
Michael Catanach	New Mexico Dept of Game & Fish	Raton	NM	mcatanach@state.nm.us
W. Jack Clark	Clark & Associates	Centennial	CO	jackclark@earthlink.net
Michael Coffeen	USFWS	Phoenix	AZ	mike_coffeen@fws.gov
Brad Compton	Idaho Fish & Game	Boise	ID	bcompton@idfg.state.id.us
Todd Cornia	Desert Land & Livestock Ranch	Woodruff	UT	tcornia@fmc-slc.com
Rick Danvir	Desert Land & Livestock	Woodruff	UT	rdanvira@fmc-slc.com
Jacquie Ermer	ND Game & Fish Department	Riverdale	ND	jermer@state.nd.us
Sue Fairbanks	DNR Iowa State University	Ames	IA	suef@ia.state.edu
Jeff Faught	ND Game & Fish Department	Bismarck	ND	jfaught@state.nd.us
Shannon Gavin	University of Calgary	Calgary	AB Canada	sdgavin@ucalgary.ca
Rich Guenzel	Wyoming Game and Fish Dept	Laramie	WY	rich.guenzel@wgf.state.wy.us
Jerry Gulke	ND Game & Fish Department	Bismarck	ND	jgulke@state.nd.us
Dan Halstead	ND Game and Fish Department	Riverdale	ND	dhalstead@state.nd.us
Nate Harling	ND Game and Fish Dept	Dickinson	ND	nharling@state.nd.us
Robb Hitchcock	N AM Pronghorn Foundation	Casper	WY	rhitch@trib.com
Brad Holliday	Nebraska Game & Parks Commission	Gering	NE	brad.holliday@rmbo.org
Doug Howie	ND Game & Fish Department	Bismarck	ND	dhowie@state.nd.us
Chris Jacques	South Dakota State University	Brookings	SD	jacques@rushmore.com
Bill Jensen	North Dakota Game & Fish Dept	Bismarck	ND	bjensen@state.nd.us
Michael Johnson	ND Game & Fish Department	Bismarck	ND	mjohnson@state.nd.us
Roger Johnson	ND Game & Fish Department	Devils Lake	ND	rejohnso@state.nd.us
Thomas Keegan	Idaho Dept of Fish and Game	Salmon	IS	tkeegan@idfg.state.id.us
Jerry Kobriger	ND Game & Fish Department	Dickinson	ND	gkobrige@state.nd.us
Alice Koch	California Dept of Fish & Game	Templeton	CA	akoch@charter.net
Chris Kochanny	Advanced Telemetry Systems	Isanti	MN	ckochanny@atstrack.com
Jesse Kolar	ND Game & Fish Department	Dickinson	ND	jekolar@state.nd.us
Randy Kreil	ND Game & Fish Department	Bismarck	ND	rkreil@state.nd.us
Andy Lindbloom	SD Game, Fish & Parks	Ft Pierre	SD	andy.lindbloom@state.sd.us
Fred Lindzey	Wyoming Coop Research Unit	Laramie	WY	flindzey@uwyo.edu
Kent Luttschwager	ND Game & Fish Department	Williston	ND	kluttsch@state.nd.us
Cindy Maier	NRCS	Dickinson	ND	cindy-maier@nd.usda.gov
Jim Maskey	University of North Dakota	Grand Forks	ND	james.maskey@und.nodak.edu
Brandon Mason	ND Game & Fish Department	Bismarck	ND	bmason@state.nd.us

2004 Workshop Attendees (continued).

Name	Affiliation	City	State	Email Address
Phil Mastrangelo	USDA Wildlife Services	Bismarck	ND	p.mastrangelo@usda.gov
Pat Mathis	New Mexico Dept of Game & Fish	Las Crusces	NM	pmathis@state.nm.us
Cal McCluskey	Bureau of Land Management	Boise	ID	cal_mccluskey@blm.gov
Carl Mitchell	U.S. Fish & Wildlife Service	Wayan	ID	carl_mitchell@fws.gov
Richard Ockenfels	Arizona Game & Fish Dept	Phoenix	AZ	rockenfels@gf.state.az.us
Michael Oehler	National Park Service	Medora	ND	michael_oehler@nps.gov
Ray Parsons	ND Game and Fish Department	Bismarck	ND	rparsons@state.nd.us
John Paulson	USDA Wildlife Services	Bismarck	ND	john.d.paulson@aphis.usda.gov
Matt Peek	Kansas Wildlife and Parks	Emporia	KS	mattp@wp.state.ks.us
Tom Pojar	Colorado Division of Wildlife	Kremmling	CO	tom.pojar@state.co.us
Ryan Powers	USDA Wildlife Services	Bismarck	ND	ryan.a.powers@aphis.usda.gov
Bruce Renhowe	ND Game and Fish Department	Bismarck	ND	brenhowe@state.nd.us
Bill Rudd	Wyoming Game & Fish	Green River	WY	Bill.Rudd@wgf.state.wy.us
Ben Rutten	Nebraska Game & Parks Commission	Bassett	NE	brutten@ngpc.state.ne.us
Glen Sargeant	USGS	Jamestown	ND	glen_sargeant@usgs.gov
Gary Schlichtemeier	Nebraska Game & Parks Commission	Alliance	NE	gschlich@ngpc.state.ne.us
Daly Sheldon	University of Wyoming	Laramie	WY	sheldon2@uwyo.edu
Larry Sickerson	Montana Dept of Transportation	Helena	MT	lsickerson@state.mt.us
Jason Smith	University of North Dakota	Grand Forks	ND	jason.smith@und.nodak.edu
Tim Smyser	Idaho Fish & Game, UI	Moscow	ID	smys9459@uidaho.edu
Patricia Stastny	University of NE - Omaha	Omaha	NE	pstastny@hotmail.com
Bruce Stillings	North Dakota Game & Fish Dept	Dickinson	ND	bstillin@state.nd.us
Dan Svingen	U.S. Forest Service	Bismarck	ND	
Bruce Trindle	Nebraska Game & Parks Commission	Norfolk	NE	btrindle@ngpc.state.ne.us
Brian Wakeling	Arizona Game & Fish Dept	Phoenix	AZ	bwakeling@gf.state.az.us
Don Whittaker	Oregon Dept of Fish and Wildlife	Salem	OR	don.whittaker@state.or.us
Jeb Williams	ND Game & Fish Department	Bismarck	ND	jwilliam@state.nd.us
Tim Woolley	WY Game & Fish Dept	Savery	WY	tim.woolley@wgf.state.wy.us
John Wrede	SD Dept of Game Fish & Parks	Rapid City	SD	john.wrede@state.sd.us
Jim Yoakum	Western Wildlife Consultants	Verdi	NV	
Tim Zachmeier	Bureau of Land Management	Dickinson	ND	N/A