

Diet, Nutrients, and Free Water Requirements of Pronghorn

Antelope on Perry Mesa, Arizona

by

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ABSTRACT

For the past 30 years wildlife biologists have debated the need of pronghorn antelope (*Antilocapra americana*) to drink freestanding water (free water). Some have suggested that pronghorn may feed at night to increase preformed water (plant moisture) intake, thus decreasing their dependence on free water. Pronghorn diet composition and nutrient intake is integral to understanding water available to pronghorn through preformed and metabolic sources. The dual purpose of this study was to determine plant composition of pronghorn diets, and to examine whether night feeding provides a water allocation advantage by testing for differences between day and night and modeling free water requirements during biologically critical seasons and years of different precipitation. I determined species composition, selected nutrients, and moisture content of American pronghorn diets on Perry Mesa, Arizona in March, May, June and August of 2008 and 2009. I used microhistological analysis of fecal samples to determine percent plant composition of pronghorn diets. I used forage samples to evaluate the nutrient composition of those diets for moisture, crude protein and structural carbohydrates, and to calculate metabolic water. I used calculations proposed by Fox et al. (2000) to model free water requirements and modified the equations to reflect increased requirements for lactation. Diet analysis revealed that pronghorn used between 67% and 99% forbs and suggested fair range conditions. Preformed water was not significantly different between night and day. Night feeding appeared to be of marginal advantage, providing an average

potential 9% preformed water increase in 2008, and 3% in 2009. The model indicated that neither male nor female pronghorn could meet their water requirements from preformed and metabolic water during any time period, season or year. The average free water requirements for females ranged from 0.67 L/animal/day (SE 0.06) in March, 2008 to 3.12 L/animal/day (SE 0.02) in June, 2009. The model showed that American pronghorn on Perry Mesa require access to free water during biological stress periods.

DEDICATION

To my mother and father, for picking up the pieces.

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Chapter 1

INTRODUCTION

American pronghorn antelope (*Antilocapra americana*) are a species of management concern in Arizona. Over the past century once abundant populations declined, rebounding only after aggressive measures were implemented (Yoakum and O’Gara, 2000, Brown and Ockenfels 2007). Despite the historic recovery, many Arizona populations struggle to remain stable. Factors include urban development, habitat fragmentation, drought, intensive grazing, restricted access to water, and increases of woody vegetation (Ockenfels et al. 1994b, Autenrith et al. 2006, Warnecke and Brunner 2006). Although pronghorn have historically withstood natural boom-and-bust cycles common among desert animals, the trend toward small, fragmented populations necessitates careful monitoring and evaluation of current management strategies in order to maintain stability.

Provisioning water in the form of tanks and catchments has been one of the most popular and widespread management strategies over the last 70 years (Krausman et al. 2006, O’Brian et al. 2006). In 1946 the first Arizona Game and Fish Department (AZGFD) water catchment was constructed (AZGFD 2004) and since then wildlife managers, conservation groups and sportsman’s groups have spent >\$1 million installing hundreds of tanks and catchments across the west (Broyles 1998, Rosenstock et al. 1999). Over 700 water developments have been constructed in Arizona alone (AZGFD 2004).

It is commonly held that water is a limiting factor for wildlife in desert environments, thus game animal numbers would increase with the introduction of provisioned water (Leopold 1933, Sundstrom 1968, Yoakum 1994, Marshall et al. 2006). However, the failure of water developments to produce the expected, sustained population increases led to questions about the effectiveness of this practice (Robbins 1993, Brown 1998, Krausman et al. 2006). Several researchers voiced concern that provisioned water may have negative consequences for wildlife by serving as vectors of disease, harboring poor quality water, habituating wildlife to human intervention, or increasing predation on game species (Boyd et al. 1986, Broyles 1995, Brown 1998, Broyles 1998, Broyles and Cutler 1999). Although subsequent studies have found no relationship between anthropogenic waters and disease (AZGFD 2004) or poor water quality (AZGFD 2004, Bleich et al. 2006), the effects on predator prey relationships and game animal behavior have yet to be determined and the potential costs of anthropogenic waters to pronghorn are unknown.

There is considerable disagreement as to the necessity of freestanding water (free water) for pronghorn antelope (Krausman et al. 2006). Some studies have suggested that pronghorn can survive in the absence of freestanding water (Hoover et al. 1959, Monson 1968, AZGFD 1981, Cancino 1994). Many early claims to this effect were speculative or antidotal (Morgart et al. 2005). Others have found that free water needs are seasonal (Sundstrom 1968, Beale and Smith 1970, Whisler 1984, Fox et al. 2000, Wilson 2009). Still others have maintained

that consistent access to free water is necessary in order to sustain healthy pronghorn herds (Yoakum 1994, Morgart et al. 2005). Most studies have been done using observation or measurement of water consumed, leaving questions about whether pronghorn need water or simply drink when it is provided.

Researchers have suggested that pronghorn may meet their water requirements through behavioral adaptations, such as feeding at night and early in the morning when plant moisture is at its highest (Sundstrom 1968, AZGFD 1981, Yoakum 1994, Brown and Ockenfels 2007). This behavior has been documented as a water allocation strategy for several other desert ruminant species (Schmidt-Nelsen 1964, Grenot 1991, Nagy and Knight 1994, Cain et al. 2006). Pronghorn have been observed feeding during the early morning hours in southern California (Cancino 1994, D. E. Brown, Arizona State University, personal communications) and at night in southwestern Arizona (Wilson et al. 2009). Fox et al. (2000) conducted a study on Sonoran pronghorn in which they quantified the availability of preformed and metabolic water, then subtracted it from total water requirements calculated using known scaling equations. I used this as a basis for examining whether feeding at night allows American pronghorn to meet their water requirements.

The main question of my research was whether American pronghorn on central Arizona's semi-desert grasslands (Perry Mesa) could meet their daily water requirements through a combination of metabolic water and preformed water, as influenced by night time feeding, during 4 reproductively stressful

periods in 2008 and 2009. In order to accomplish this I established the following specific objectives:

1. Determine plant species composition, forage class composition and species richness of the diets through microhistological analysis.
2. Determine nutrient parameters of pronghorn diets as indicators of forage quality and to model metabolic water production.
3. Examine preformed water content of pronghorn diets.
4. Using metabolic and preformed water data, model pronghorn free water requirements to determine if night feeding would provide a water allocation advantage.
5. Examine whether pronghorn can meet water requirements through preformed and metabolic water during biologically stressful seasons and years of different precipitation.

Chapter 2

BACKGROUND

Pronghorn Water Economy

Water is necessary to mammalian life, enabling almost every physiological function including temperature control, movement of joints, metabolic processes, vision, and hearing. An organism's requirements change with exposure to solar radiation, temperature, metabolic rates, dry matter intake, reproductive status, activity levels and specific water conservation strategies (Robbins 1993). Animals obtain water from 3 basic sources 1) free water from streams, lakes, dew, ephemeral pools and snow, 2) preformed water, or the moisture content in foodstuff, and 3) metabolic, or oxidative water produced in the breakdown of nutrients (Leopold 1933, Squires 1988, Robbins 1993, Yoakum 1994).

Pronghorn exhibit numerous physical, physiological, and behavioral adaptations that interact to help conserve water and reduce water loss in times of heat and water stress. Understanding how these interact with various water sources from diet and nutrients facilitates a better understanding of water availability to pronghorn through dietary sources at critical biological periods and assess the need for free water.

Water loss. – Water loss poses particular challenges for animals in hot desert environments, including pronghorn. The majority of water loss occurs through respiration, cutaneous evaporation, urine and feces (Schmidt-Nielson

1964, Whisler 1984, Squires 1988, Robbins 1993, Cain et al. 2006). Lactation presents an additional water loss for females (Squires 1988, Olsson 2005, Cain et al. 2006). The amount of evaporative water loss is a function of ambient temperature, relative humidity, and body temperature. Due to their small size relative to other North American ungulates, pronghorn have larger surface area and thus greater potential evaporative water loss (Whisler 1984).

Physical adaptations. –American pronghorn have resided in Arizona's arid environment for nearly 1.8 million years (Brown and Ockenfels 2007) and have adapted numerous water conservation strategies (Wesley et al. 1970, Yoakum 1994). Large kidneys allow pronghorn to concentrate water by increasing the ability to process larger amounts of Antidiuretic hormone (Whisler 1984, Yoakum and O'Gara 2004, Brown and Ockenfels 2007). Long, curved nasal passages retain moisture particles as air is exhaled, and trap moisture from cold, dry air that is inhaled and warmed (Yoakum and O'Gara 2004). Light colored, long pelage and a unique hollow hair configuration allow pronghorn to deflect heat and provide insulation to help maintain body temperature (Cain et al. 2006, Brown and Ockenfels 2007). The thicker horn cores and thinner keratin sheaths (Cain et al. 2006), along with a large artery extending through the suborbital foreman adjacent to the horn, help to dissipate heat from the head (Brown and Ockenfels 2007). An extensive network of small blood vessels in the horn cores called intracranial carotid retia help cool the brain and allow pronghorn to continue functioning at higher body temperatures (Yoakum and O'Gara 2004,

Lust et al. 2007). Lastly, pronghorn have low body fat, allowing them to disperse heat more quickly (Yoakum and O’Gara 2004, Cain et al. 2006, Brown and Ockenfels 2007).

Ruminants as a group are able to store water in a unique way in the rumen. The rumen is roughly 20% of an animal’s body weight and can provide a short term water supply in times of deprivation. It serves a dual function of allowing dehydrated animals to quickly rehydrate by consuming large amounts of water without risk of osmotic shock by storing the water while it is more gradually incorporated into the body system (Whisler 1984, Cain et al. 2006).

Physiological adaptations. – Many animals decrease water loss by decreasing urine output, fecal output, and cutaneous evaporation (Nagy and Knight 1974, Cain et al. 2006). Whisler (1984) found these to be the most important physiological mechanisms for the pronghorn. Other researchers studying pronghorn have noted similar decreases in fecal and urine output in response to water stress (Wesley 1971, Beale and Holmgren 1974).

Pronghorn are reported to have body temperatures slightly higher than other ruminants, which can be both a benefit and a drawback in water economy. Excessively high temperatures produce increased cutaneous evaporation, but slight, incremental raises in temperature can balance body and air temperature and reduce evaporation (Whistler 1984, Robbins 1993). Pronghorn body temperature averages around 37.8 °C but fluctuates drastically in response to stimuli such as

fear and excitement (Yoakum and O’Gara 2004). Lust et al. (2007) reported an average body temperature of 38.6 ± 0.3 °C for 4 free living pronghorn. Whistler (1984) measured pronghorn body temperature under different conditions and found that they did in fact respond to high ambient temperatures with hyperthermia. Lust et al. (2007) found that carotid artery temperatures of 4 captive pronghorn in Wyoming were weakly correlated with hourly ambient temperature, suggesting evidence of longer-term, but not daily heterothermic adaptation to heat load.

Other physiological considerations. – Pronghorn metabolic rate may play a role in water economy. Desert ungulates typically have lower metabolic rates than ungulates of similar body size from temperate zones, allowing them to survive with less water and food (Cain et al. 2006). Pronghorn, the smallest of North American ungulates, are reported to have higher metabolism than most domestic animals (Wesley et al. 1970, Wesley et al. 1973, Yoakum and O’Gara 2004). There is a well-documented positive correlation between metabolic rates and water turnover rates (Richmond et al. 1962, Wesley et al. 1970, Whisler 1984, Robbins 1993). However, lower metabolic rate is not always linked to water economy (Williams et al. 2001), and for pronghorn this relationship remains a matter of speculation.

Behavioral adaptations. – Pronghorn employ numerous behavioral strategies to conserve water. By reducing energy expenditure and food intake animals decrease the water necessary for physiological functions (Robbins 1993).

Whisler (1984) found a 54% decrease in forage consumption in winter and 74% decrease in summer in response to water deprivation experiments. Use of shade is common among desert ungulates (Cain et al. 2006) and pronghorn have been documented reclining in shaded areas to decrease body temperature and evaporative water loss (personal observation, Beale and Holmgren 1974, Whisler 1984, Yoakum 2002, Wilson 2009). Increase in panting helps to dissipate heat, but also leads to water loss, and this behavior ceases when animals reach a certain level of water stress (Whisler 1984). Pronghorn select diets higher in moisture content when available (Wesley 1971, Beale and Holmgren 1974, Fox et al. 2000) and migrate to areas with greater water supply or lower temperatures (Cain et al. 2006). Many desert ungulates increase foraging and other activity at cooler times of day and although pronghorn move throughout the day, they primarily forage near sunrise and sunset (Reynolds 1984, Yoakum and O’Gara 2004, Cain et al. 2006, Wilson et al. 2009).

Effects of water deprivation. – Observing the effects of water deprivation can shed light on how water conservation strategies interact and aid in assessing water need. Several researchers have reported the effects of temporary, experimental water deprivation on pronghorn. Beale and Holmgren (1974) noted that pronghorn in Utah lost weight and became weak as the experimental deprivation period progressed. Whisler (1984) found that when water was reduced by 2/3 for captive pronghorn, they decreased activity and forage consumption and increased time spent in the shade. They lost 23% of body moisture, exhaled air

temperature dropped, and panting ceased. The amount of body water lost through evaporation declined 68% in the summer dehydration periods, and 51% in the winter dehydration periods. In addition pronghorn reduced metabolic rates, thus decreasing demands for oxygen consumption, heat production and forage intake while reducing overall body mass and thus maintenance requirements. Water turnover rates decreased during dehydration, suggesting physiological water conservation.

Beale and Holmgren (1974) reported that animals recovered from dehydration in a matter of hours after they were allowed to drink. Whisler (1984) made similar observations, stating that 1 pronghorn regained pre-dehydration forage intake by 1 day after the dehydration period was ended. She attributed this quick recovery to the rumen buffering effect, as evidenced by the pronghorn's plasma osmolality remaining consistent despite the rapid water intake of a large volume of water after the period of dehydration.

Diet Composition

Modeling pronghorn free water requirements must begin with detailed, up to date information on the species composition of pronghorn diets. Pronghorn are opportunistic feeders and exploit a wide variety of plants depending on availability and palatability (Yoakum and O'Gara 2004, Autenrith et al. 2006, Brown and Ockenfels 2007). On the gradient of ruminant feeding habits pronghorn are intermediate concentrate selectors, meaning their anatomy and

physiology are specially adapted to exploit high quality, low fiber diets when available and subsist on lower quality forage such as browse when necessary (Hofmann 1988, Yoakum and O’Gara 2004, Brown and Ockenfels 2007, Drake 2009).

Pronghorn exhibit the morphological and physiological adaptations that are characteristic of this group (Yoakum and O’Gara 2004). Their narrow, tapered muzzle and thin, flexible tongue and lips allow them to select small, nutritious plant parts such as leaves and flowers. Narrow jaw muscles and gracile skulls are evidence of limited need for chewing due to their more succulent and easily digestible diets. Their small body size and simply structured rumen are the result of high quality diets that require less fermentation than animals feeding on primarily grass and browse. Their smaller omasum and larger abomasum reflect the decreased requirement for extracting water from rough forage and a higher need for gastric digestion as food particles ferment for shorter periods of time. Their shorter mid gut and longer hind gut indicate less enzymatic digestion and increased water recovery prior to excretion of waste material (Hofmann 1988, Yoakum and O’Gara 2004).

Digestibility decreases as plants advance in phenology (Holechek and Valdez 1985) and pronghorn diets often change drastically with the seasons to take advantage of higher nutrient content of emerging plants (Yoakum and O’Gara 2004). Diet selection studies for pronghorn in desert grasslands have shown a clear pattern of preference for highly digestible, nutritious forbs

(Yoakum and O’Gara 2004, Autenrith et al. 2006, Brown and Ockenfels 2007, Brown et al. 2008, Drake 2009). Yoakum and O’Gara (2004) compiled the results of 14 pronghorn food habit studies on grasslands across North America and found that forbs made up an average of 62% of the diets, and were given a preference rating nearly 3 times higher than shrubs and grasses.

Shrubs are often consumed throughout the year in lower quantities, but increase in fall, winter, and dry seasons when forbs are less available and shrub nutritional values are higher (Beale and Smith 1970, Stephenson et al. 1985, Yoakum and O’Gara 2004, Autenrith et al. 2006, Brown et al. 2008). Shrub use also increases during drought periods (Stephenson et al. 1985, Brown et al. 2008) and Autenrith et al. (2006) referred to shrubs were referred to as “survival food.” In areas dominated by shrubs, such as the northern shrub steppes, they are utilized to a greater degree (Yoakum and O’Gara 2004).

Grasses, which are high in indigestible structural constituents such as lignin, occur in the diets in low quantities and are generally avoided if other forage is available (Yoakum and O’Gara 2004, Brown and Ockenfels 2007). This forage class was consistently utilized the least in the 14 grassland diet studies reviewed by Yoakum and O’Gara (2004), despite differences in methodology, years, seasons, locations and climactic conditions in the various studies. When grasses are utilized, it is most often in the early spring when they are younger, more digestible, and higher in nutrients. Pronghorn consume small quantities of dry grasses at other times of the year, most often shorter, finer bunch grasses

(Autenrith et al. 2006). Grasses most often found in Arizona pronghorn diets are blue grama (*Bouteloua gracilis*), Arizona fescue (*Festuca arizonicus*) and June grass (*Koeleria pyramidata*) in northern Arizona (Drake 2009), Brome (*Bromus spp*), three-awn (*Aristida spp.*) and barley (*Hordeum spp.*) in central Arizona (Brown et al. 2008), and three-awn and needle grama (*Bouteloua aristidoies*) in southwestern Arizona (AZGFD 1981).

Cacti and other succulents have been found inconsistently in pronghorn diets. Brown et al. (2008) found that prickly pear (*Opuntia sp.*) comprised up to 21% of the diet during dry winter periods, but during spring and summer when forbs were abundant it was either present in small amounts or absent. In Kansas, Sexton et al. (1981) found prickly pear to be >15% of February diets, but absent in January and March. Smith et al. (1998) found cactus in high levels during the cool/dry season in New Mexico, but <4% during the wet season. Sonoran pronghorn diets between 1974 and 1978 had 27% jumping cholla (*Cylindropuntia fulgida*) in June but <1% in February and March (AZGFD 1981). Stephenson et al. (1985) found only trace amounts of cactus in pronghorn diets in New Mexico, although it was available. In Utah Beale and Smith (1970) found <1% yearly from 1961 to 1965, 28% in 1966, and none in 1967. Other diets did not report cactus (Bayless 1969, Smith and Malechek 1974, Drake 2009).

Nutrient Requirements

Pronghorn diets are influenced by succulence, palatability, and nutrient contents (Koerth et al. 1984, Fox et al. 2000, Yoakum and O’Gara 2004). Understanding nutrient parameters in pronghorn diets is helpful in evaluating diet quality. It can also be used to model physiological processes such as metabolic water in order to understand pronghorn water balance. The bulk of metabolic water is produced through oxidation of protein, carbohydrates and lipids. Each gram of protein oxidized yields approximately 0.4 ml of metabolic water, anhydrous carbohydrates yield 0.56 ml, and lipids yield 1.7 ml (Robbins 1993).

Crude protein. – Actual amounts of protein required by pronghorn for growth and reproduction are not well understood, although studies suggest that pronghorn select plants based in part on protein content (Yoakum and O’Gara 2004). Crude protein is highest in young and growing plants and lowest in mature plants, and this phenotypic progression is reflected in pronghorn diets (Robbins 1993, Yoakum and O’Gara 2004). Yoakum and O’Gara (2004) reported on several studies that investigated the crude protein content of pronghorn forage plants and found it to vary between 7.3% and 38.0%, depending on the plant species, location, and time of year.

Carbohydrates. – Carbohydrates can be divided into 2 categories, soluble carbohydrates, which include monosaccharides and storage polysaccharides, and structural carbohydrates such as cellulose, hemicellulose and pectin (Fahey and

Berger 1988, Robbins 1993). Soluble carbohydrates are determined by measuring Nitrogen Free Extract (NFE), or the amount of dry matter not accounted for by crude protein, crude fiber, lipids and ash (Robbins 1993, Fox et al. 2000).

Nitrogen Free Extract is reported to be up to 90% digestible (Robbins 1993), and has been used to estimate metabolic water for pronghorn in several studies (Whisler 1984, Fox et al. 2000).

Structural carbohydrates, often referred to as fiber, are digestible by ruminants only as the result of fermentation and bacterial breakdown of plant material in the rumen and hind gut (Hudson and White 1985, Fahey and Berger 1988, Robbins 1993). The byproducts of bacterial digestion are volatile fatty acids (VFAs), which enter the pronghorn bloodstream through active and passive transport across the rumen wall (Fahey and Berger 1988). Within individual plant species percentages are lowest when plants are young and increase as they mature (Robbins 1993). This pattern is somewhat different when looking at the carbohydrate content of pronghorn diets. Pronghorn select plants low in structural carbohydrates and higher in other nutrients as seasonal plant communities change (Yoakum and O’Gara 2004). Structural carbohydrates can be used as an inverse indicator of diet quality, and as a very rough measure of metabolic water.

Lipids – Lipids estimated from forage plants are comprised of compounds such as glycerides, phospholipids, sterols, pigments, waxes, volatile oils and resins (Robbins 1993). As with protein, lipid content decreases with age of individual plants (Jones and Wilson 1987). Although lipids yield high levels of

energy, they generally comprise only 3% to 10% of ruminant diets in part due to their ability to inhibit digestibility of cellulose, protein, and possibly magnesium when making up >10% of a plant (Jones and Wilson 1987, Byers and Schelling 1988). In addition, microbial synthesis of lipids is greater when they are present in the diet in smaller amounts, and increased feeding results in decreased overall utilization of these nutrients (Byers and Schelling 1988). This is rarely an issue for pronghorn, since forbs, which make up most of their diet, are lower in lipid content (Ensminger and Olentine 1978). Fox et al. (2000) found between 3.8 and 4.3% lipids in Sonoran pronghorn forage plants; levels which were significantly lower than those of non-forage plants.

Preformed water. – Preformed water in pronghorn diets varies with season, year, and location. Forbs generally contain more moisture than browse or grass, although this depends on the phenotypic stage of the plant (Beale and Smith 1970, Smith and Malechek 1974). Pronghorn diets have been reported to contain from 32% moisture (Fox et al. 2000) to $\geq 75\%$ (Beale and Smith 1970) preformed water. Although some researchers have found preformed water to play a role in pronghorn diet selection (Wesley 1971, Beale and Holmgren 1974, Fox et al. 2000), others found a weak correlation (Smith and Malechek 1974).

Water Requirements

The actual water requirements of pronghorn antelope have been a subject of debate for some time. A number of studies have documented pronghorn utilizing

water sources, confirming this behavior for both Sonoran pronghorn (*Antilocapra americana sonoriensis*) and American pronghorn (Wright and deVos 1986, Hervert et al. 1995, Morgart et al. 2005, Wilson et al. 2009). Morgart et al. (2005) produced photographs of Sonoran pronghorn visiting anthropogenic water sources primarily between May and June, when ambient temperatures were at their highest. I documented American pronghorn seasonal and diurnal drinking patterns on Perry Mesa, Arizona 2009 and found usage increased with rising temperatures (unpublished data). Wilson et al. (2009) observed seasonal drinking patterns of 6 female Sonoran pronghorn from January to December, 2005. Pronghorn were seen drinking regularly starting on 12 April and ending in December. Pronghorn were not observed drinking in early April, when temperatures were lower and more forbs and grass were consumed. The pattern was similar to that observed for pronghorn by Morgart et al. (2005) and by other species in southern Arizona (O'Brian et al. 2006). Although evidence has shown that pronghorn drink water when it is provided, water consumption does not necessarily equate water need (Brown 1998).

Other researchers have measured pronghorn water consumption in order to estimate free water requirements. Sundstrom (1968) measured water consumed by a herd of pronghorn in Wyoming from April through October, 1967. Water consumption followed seasonal patterns, with pronghorn consuming the least in May and June when precipitation was greatest and the most in August when precipitation was lowest and temperatures highest. Beale and Smith (1970)

examined water requirements through observation of feeding and watering behavior, estimation of diets, and measurements of water consumption on the Desert Experimental Range in Utah from 1962 to 1965. They noted that when forage contained $\geq 75\%$ moisture pronghorn ceased to drink, and when conditions were extremely dry and plant moisture averaged 39% pronghorn drank roughly 2.8 L per day. Water consumption varied considerably between years. Beale and Holmgren (1974) conducted similar measurements from stock tanks as part of an experiment in the summer of 1973. They noted that the amount of water consumed increased as plant moisture decreased and ambient temperatures increased. However, measuring water consumption alone tends to underestimate actual water requirements (Robbins 1993).

Researchers have examined pronghorn density and distribution in relation to water sources to evaluate their importance as a habitat component. Deblinger and Alldredge (1991) found that pronghorn distribution and density were influenced by the presence of free water, but distribution did not change when water was removed. They concluded that other factors, such as plant moisture content and availability of forbs, may influence distribution. Sundstrom (1968) found that pronghorn distribution shifted toward water tanks during August. DeVos and Miller (2005) reported that Sonoran pronghorn were found close to water sources significantly more than randomly expected.

Several researchers have attempted to quantify water requirements through modeling biological processes. Whisler (1984) examined pronghorn water

budgets by measuring preformed water, free water consumption, metabolic water production and daily water loss through feces, urine and evaporation for captive pronghorn on the Wyoming's Sybille Experimental Laboratory. Water consumption was measured by taking the percent difference of supplied water corrected for evaporation, preformed water was calculated for air dry feed, and metabolic water was determined according to calculations from Robbins (1993). Water turnover was measured using tritiated water. The pronghorn in Whisler's (1984) experiment required free water during both summer and winter seasons (Table 15), but preformed water of the commercial feed supplied was only 10%.

Fox et al. (2000) modeled free water requirements of wild Sonoran pronghorn in southwestern Arizona by subtracting preformed and metabolic water from water requirement estimates based on several scaling equations. Preformed water for pronghorn forage selection diets based on past microhistological studies showed significantly higher levels of water than that of plants based on availability. Daily calculated intake of dietary water ranged from 1.1 L/day to 6.1 L/day for selection diets. Using a scaling equation based on Richmond et al. (1962) to model total water requirements, pronghorn were able to meet water needs through dietary water alone at 1 of the 2 study sites. The ability of pronghorn to meet their water requirements without drinking was largely dependent on location and consumption of high levels of jumping cholla, which contained up to 86% water.

Water Turnover

Water turnover rate, sometimes referred to as water flux rate, is the most accurate, quantitative way to measure water requirements (Nagy and Peterson 1988). It is a measure of the amount of water passing through an animal within a given time. It assumes a balanced system in which water gains and losses are equal (Whisler 1984). Water turnover is commonly estimated by injecting a hydrogen isotope such as tritiated or deuterated water into an animal and measuring the rate at which it becomes diluted (Nagy and Peterson 1988). Water turnover rate provides an estimate of total water requirements without excluding the contributions of preformed and metabolic water. However, it does not provide an exact requirement due to the tendency to over-estimate total body water (Robbins 1993). Nagy and Peterson (1988) estimated an 8% to 10% error rate in determining water turnover using the tritiated water method.

Water turnover rates are strongly related to body mass (Richmond et al. 1962, Nagy and Peterson 1988, Robbins 1993) and decrease with increases in body fat, which is a function of species, body condition, and age (Whisler 1984, Robbins 1993). Desert adapted animals generally have lower total body water (Whisler 1984, Nagy and Peterson 1988, Squires 1988, Cain et al. 2006). Nagy (2004) found that water turnover in desert-dwelling eutherian mammals to be 55% lower than non-desert counterparts. The lower flux rate may be a function of diet and adaptations to arid habitats. However, larger desert animals and animals with high metabolic rates can have high water flux rates and may mitigate this

with water-conserving behavioral strategies (Nagy and Peterson 1988). Water turnover increases with higher temperature and decreases with lower temperatures and under conditions of dehydration (Whisler 1984, Cain et al. 2006).

Two studies have reported measurements of water turnover in pronghorn. Wesley et al. (1970) conducted a tritiated water experiment on 4 juvenile captive pronghorn and found water turnover to be higher than those reported for other mammals. This may have been a function of age and small sample size. Whistler (1984) measured tritiated water turnover in 5 adult female pronghorn during summer and winter, in both hydrated and dehydrated conditions. She found that water turnover was lower in winter and decreased with water deprivation. Pronghorn had higher total body water than other ungulates. However, water turnover rate was lower than expected for an animal with higher body water. This was attributed to lower fat content. She stated that drinking water requirements may be higher in the wild due to decreased activity of captive animals.

Several researchers have used scaling equations based on water turnover information to estimate pronghorn water requirements with varying results (Table 1). Earlier studies made use of domestic animals or animals under laboratory conditions (Richmond et al. 1962, Altman and Dittmer 1966). Nagy and Peterson (1988) provided regression equations based on a meta-analysis of tritiated water studies, and found that water turnover differed significantly between wild and captive animals as well as desert versus non-desert animals. Fox (1997) utilized a regression based on Richmond et al. (1962) and Altman and Dittmer (1966) to

calculate pronghorn water requirements. Robbins (1993) provided a regression equation based on the most recent meta-analysis of tritiated water studies, broken into relevant categories identified by Nagy and Peterson (1988).

Table 1. Estimates and scaling equations used to predict water turnover for pronghorn. Estimates are for average pronghorn weights of Chihuahuan semi-desert grassland (Brown and Ockenfels 2007). Females = 41.3 kg, males = 48.6 kg unless otherwise noted

Study subject(s)	Equation	Estimate (L/animal/day)	Source
Domestic sheep	$Y(\text{ml})=119 \times W(\text{kg})^{0.82}$	2.5 females, 2.9 males	Aldeman & Dittmer 1969
Free-ranging herbivores	$Y(\text{ml})=0.708 \times W(\text{g})^{0.795}$	3.6 female, 4.0 male	Nagy and Peterson 1988
Free-ranging herbivores	$Y(\text{ml})=0.71 \times W(\text{g})^{0.80}$	3.5 females, 3.9 males	Robbins 1993
From literature	Reported value*	1.8 females, 3.4 males	Fox et al. 2000

*Reported for pronghorn 29 kg and 64 kg.

Water Requirements for Reproduction

Gestation and Parturition. – Additional water may be required for reproductive females during late gestation, parturition, and lactation and for both females and males during the rut, or conception period. There is currently no quantified information on water requirements for pronghorn during gestation or parturition, but sources for other ruminants provide indication that water requirements increase during these times (Schmidt et al. 1988, Squires 1988, Devendra 1987, Olsson 2005). Olsson (2005) stated that water turnover is greater

during pregnancy in ruminants, and Devendra (1988) reported that turnover rates increased during pregnancy for domestic sheep. Squires (1988) stated that the water needs of pregnant livestock are greater than those of non-pregnant livestock, since gestation increases maternal energy expenditures and results in increased heat production and subsequently increased water loss. In dairy cattle water intake increased as heifer weight increased due to additional water needed for both maintenance functions as well as turnover of embryonic fluid (Schmidt et al. 1988). Increased energy expenditure associated with parturition, in addition to actual fluid loss, may increase water requirements at this time.

Lactation. – Lactation presents the greatest additional water and nutrient requirements for mammals (Devendra 1987, Squires 1988). Large amounts of water are needed to synthesize milk (Schmidt-Nielsen 1964, Swenson 1977). Maltz and Shkolnik (1980) reported that the water turnover rate for lactating black Bedouin goats was twice as high as for non-lactating goats, and lactating goats drank 3 times as much. Lactating camels use 44% more water than non-lactating camels (Squires 1988). In addition, maternal nutrition influences milk yield. Lactation is 2 to 3 times more costly than gestation in terms of energy requirements (Robbins 1993, Hackmann 2011). In several studies domestic sheep, red deer (*Cervus elaphus*), and reindeer (*Rangifer tarandus*) failed to increase milk yield on poor range conditions (Ofteidal 1985). If food increase is necessary to obtain the energy and nutrients needed, greater amounts of water may also be necessary.

Peak lactation for Arizona pronghorn often falls at the hottest, driest times of the year. Typically giving birth to twins (Yoakum and O’Gara 2004), the water demands of a lactating pronghorn are under additional pressure (Martin 1995). Beale and Holmgren (1974) observed that adult females and fawns were most affected by water deprivation. The udders of lactating does appeared limp and fawns seemed to grow more slowly. Water deprivation in other mammals is known to decrease milk supply and adds stress to lactating females during a period when they are already under nutritional constraints and preformed water is low (Olsson 2005). However, physiological water conservation mechanisms may help mitigate these effects to a certain degree. Desert adapted species such as the black Bedouin goats have been known to decrease plasma volume in response to dehydration in order to minimize the effects of dehydration on milk supply (Devendra 1987) and camels have been known to maintain milk supply during short dehydration periods (Olsson 2005).

Little is known about pronghorn milk quality and production. Einarsen (1945) reported that pronghorn milk is 75.1% water, 6.9% protein, 13.0% fat and 4.0% lactose. In the first of a 2 part study on pronghorn lactation, Martin (1995) measured milk composition, water turnover, and nursing behavior of a single lactating pronghorn doe with twins on the Wyoming’s Sybille Wildlife Research and Conservation Education Center. Milk composition in mid-lactation (32-53 days) contained 19% dry matter, 5.3% fat, 4.3% energy. At 40 days milk contained an estimated 6% crude protein, 1.3% ash and 4.5% carbohydrates. The

doe lactated for approximately 74 days, with one fawn reaching peak lactation at 7 days and the other at 42 days. Both studies indicate that pronghorn appear to produce smaller amounts of nutritionally dense milk than dairy cattle, which provided milk that is an average of 90% water (Schmidt et al. 1988). Milk higher in solids and lower in water may reflect adaptations to arid environments (Schmidt-Nielsen 1964). This may allow pronghorn to reduce water requirements for lactation while increasing fawn weight more quickly than other wild ungulates (Martin 1995).

Martin (1995) reported the average daily milk intake per fawn as 468 ± 22 ml/day. Maximum milk intake was 506 ml/day for the first fawn and 505 ml/day for the second. Fawns grew slightly slower than bottle-raised pronghorn, although they remained healthy. The study provides the only direct, quantitative estimate of pronghorn milk yield using tritiated water so far, but the sample size of 1 precludes extrapolation.

In the second part of the study, Martin (1995) concurrently hand-raised 10 pronghorn fawns on 1/3 diluted evaporated milk, which was of lower quality than milk obtained from the single doe in the first part of the study. Previous studies involving bottle-fed pronghorn given *ad libitum* amounts of milk resulted in high levels of diarrhea and mortality (Schwartz et al. 1976), so feedings were timed to approximate natural feeding cycles and avoid gastrointestinal dysfunctions. The average maximum milk solution consumed per fawn was 1087 ± 151 ml/day. Growth rates were slightly higher but not significantly different than those of

dam-raised fawns. However, fawns may have consumed less if the milk was nutritionally equivalent to pronghorn milk.

Wild et al. (1994) compared growth rates between dam-raised and bottle raised elk (*Cervus elaphus*), bighorn sheep (*Ovis canadensis*) and pronghorn neonates. Nineteen bottle-fed pronghorn were ultimately included in the study and 1 dam-fed male pronghorn provided the control. Pronghorn were fed evaporated milk *ad libitum* for the duration of the study, with only 2 instances of gastrointestinal problems. Mean milk consumption peaked at approximately 1200 ml/day. Growth rates between the dam-raised and hand-raised pronghorn were not significantly different. These studies involving bottle-fed animals may provide insight into milk yield, although the methodology tends to overestimate need as ruminants fawns given milk *ad libitum* have been known to over consume (Wild et al. 1994, Martin 1995).

Hackmann (2011) developed a system for calculating protein and energy requirements for wild ruminants which included an equation for milk yield at peak lactation based on maternal body weight. Studies have shown that maternal body weight is a reliable predictor of peak milk yields (Taylor and Murray 1987, Robbins 1993), and measurements of milk yield in peak lactation are more accurate than other times during the lactation cycle (Ofstedal 1985, Hackmann 2011).

Robbins (1993) stated that milk demand increases 67% with each additional fawn. Tritiated water results from Martin (1995) suggest a 2-fold increase, but peak consumption from bottle-fed pronghorn was double that of each single fawn. Given the potential error in extrapolating based on a sample size of 1 pronghorn in captivity and the inherent over-estimation involved in bottle-feeding, estimates based on the regression equation from Hackmann (2011) and known increase from Robbins (1993) provide the most reliable estimate of milk yield for does with single fawns and twins.

There are no studies that have specifically attempted to measure the water required for pronghorn milk production. Currently accepted methods for calculating these requirements in dairy science state that for milk which is comprised of 90% water, milk output multiplied by 0.90 equals additional lactation water requirements (Schmidt et al. 1988). More water may be required to synthesize milk, but a conversion coefficient was unavailable.

Conception. – Increased physical activity during the rut may present an additional water requirement, as energetic expenditure translates into heat production and evaporative water loss. Many herbivores expend great amounts of energy during this time (Price and White 1985). One study found that non-lactating cattle (*Bos indicus*), walking an extra 8 km per day, required between 4.4 ml/kg/day and 11 ml/kg/day more water, depending on the intensity of solar radiation (Squires 1988). However, both male and female pronghorn activity patterns during rut are highly variable and depend on mating systems, which

change with resource availability (Kitchen 1974, Maher 1997, Yoakum and O’Gara 2004).

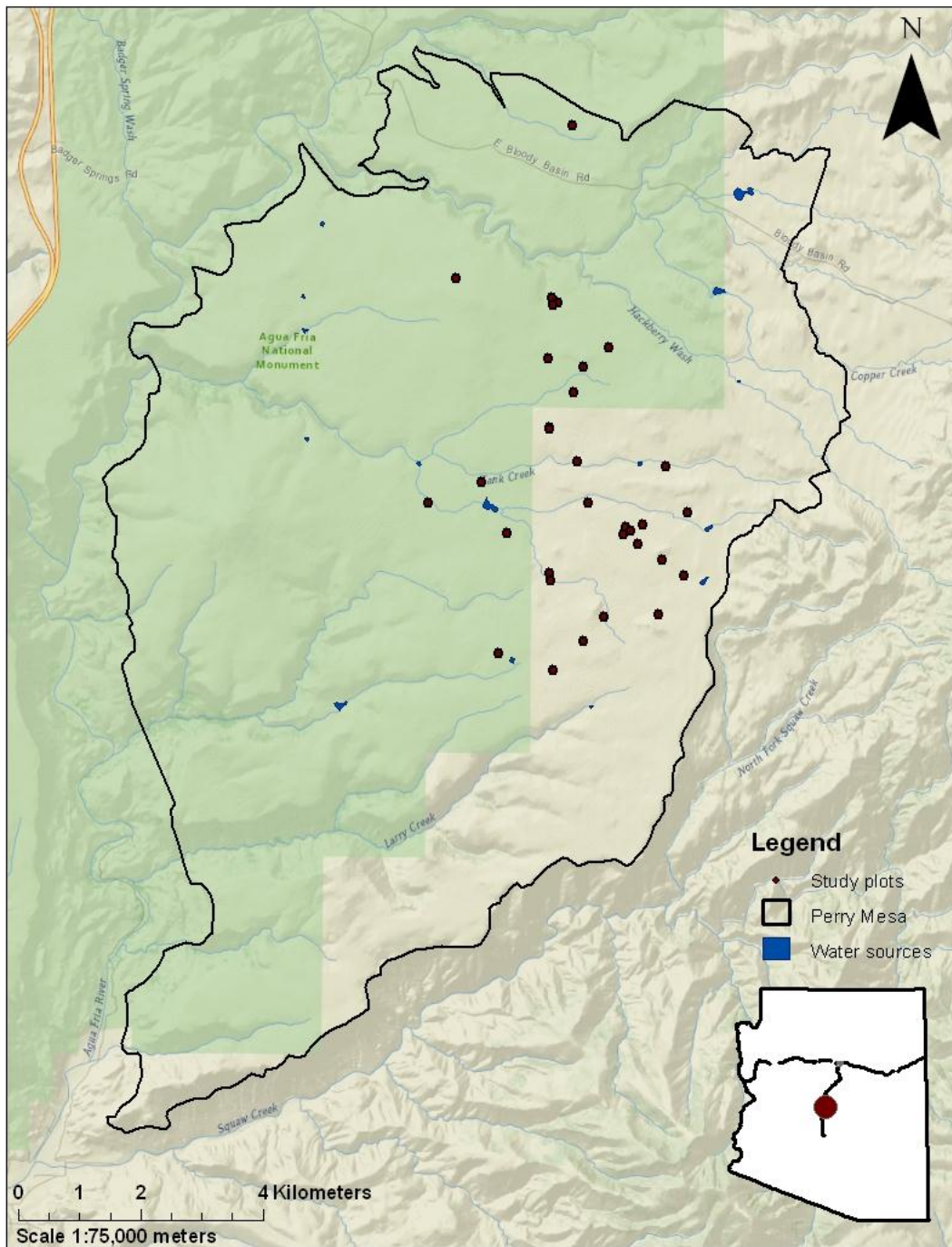
Chapter 3

METHODS

Study Area

This study was conducted on Perry Mesa, which lies approximately 88 km north of central Phoenix, Arizona (34.2144 N° 112.0372 W°), (Fig. 1). Perry Mesa is part of a larger network of mesas within Game Management Unit (GMU) 21, which extends from New River and Barlett Lake northward to Camp Verde. Perry Mesa encompasses approximately 133 km² with an elevation range of 1,120 m to 1,232 m. It is buffered by a perennial section of the Agua Fria River to the west, Silver Creek to the north, and Squaw Creek to the south and east. The bulk of Perry Mesa lies within the Agua Fria National Monument (AFNM), managed by the United States Bureau of Land Management (BLM). The southern end of Perry Mesa, from 34.2125 N°, belongs to the Tonto National Forest. The Horseshoe Ranch was the only private allotment on Perry Mesa during the study. In 2006 cattle were removed from the Horseshoe Ranch grazing allotment and remained absent throughout the duration of the study period. Prescribed fires were used as a management tool on the AFNM since 1983 (Brock 1998).

Figure 1. Geographic location of the Perry Mesa study site in central Arizona.



The GMU 21 pronghorn population has been historically unstable. Survey data collected since 1959 showed an historic low of 39 animals in 1961 followed by an upward trend around 1984, which gave way to a decline between 1993 and 2002 (Warnecke and Brunner 2006). Contributing factors cited for these declines include: habitat fragmentation, fire suppression, shrub encroachment, intensive grazing, drought, lack of water accessibility (Warnecke and Brunner 2006) and sampling error (D. E. Brown, personal communications). Two transplants between 1997 and 1999 and a transplant of 40 animals in 2009 provided temporary increases (Warnecke and Bruner 2006, AZGFD 2009). The population in 2008 was estimated at 75 animals but increased steadily, reaching 249 in the spring of 2012 (D. D. Warnecke, AZGFD, personal communications). Although part of this increase may be attributed to transplants, the 2010 fawn:doe ratio of 55:100 (AZGFD 2011) was well above the estimated ratio of 35:100 that is considered to be a long term norm for Arizona (Brown and Ockenfels 2007).

Perry Mesa encompasses approximately 21% of GMU 21 and consistently supports a moderate percentage of the GMU 21 population. Winter herd counts were between 25 and 31 individuals in both 2007 and 2008 (personal observation). Pronghorn in GMU 21 moved throughout the network of mesas using 3 distinct corridors that connect Perry Mesa and Black Mesa with the northern area containing East Pasture and Marlow Mesa (Ockenfels 1994*b*). Perry Mesa is considered to be high quality habitat in relation to surrounding areas (Ockenfels et al. 1996). New Mill Pasture on the north end of Perry Mesa was

identified as the premier fawning grounds for GMU 21 (Warnecke and Brunner 2006).

Vegetation on the mesa top consisted of semi-desert grassland community (Brown 1994) with tobosa (*Pleuraphis mutica*) as the dominant grass and barley (*Hordeum* spp.) common in the spring. Nomenclature followed that of the United States Department of Agriculture Plants Database (USDA 2012). A variety of grasses were present in lesser abundance, including curly mesquite (*Hilaria belangeri*), sacaton (*Sporobolus* spp.), and grama grasses (*Bouteloua* spp.). Common forbs during the sampling periods included redstem stork's bill (*Erodium cicutarium*), fiddleneck (*Amsinckia* spp.), mustards, ragweed (*Ambrosia* spp.), longleaf false goldeneye (*Heliomeris longifolia* var. *annua*) woolly plantain (*Plantago patagonica*), spreading fleabane (*Erigeron divergens*), and Lindley's silverpuffs (*Microseris lindleyi*). Sub-shrubs included Wright's buckwheat (*Eriogonum Wrightii*), globe mallow (*Sphaeralcea* spp.), and broom snake weed (*Gutierrezia sarothrae*). Cacti such as prickly pear and cholla (*Opuntia* spp. And *Cylindropuntia* spp.) were common. Dominant trees and shrubs included catclaw acacia (*Acacia greggii*), velvet mesquite (*Prosopis velutina*), wait-a-minute bush (*Mimosa biuncifera*), shrub-live oak (*Quercus turbinella*) and juniper (*Juniperus* spp.).

The AFNM and GMU 21 were home to other large herbivores such as mule deer (*Odocoileus hemionis*), white-tailed deer (*Odocoileus virginianus*), a few elk (*Cervus elaphus*) and javelina (*Pecari tajacu*). Predator species inhabiting

the monument included mountain lion (*Puma concolor*), coyote (*Canis latrans*), bobcat (*Lynx rufus*) and golden eagle (*Aguila chrysaetos*).

The historic average annual maximum temperature between 1925 and 2011 was 24.2° C and the average minimum was 8.3°C, with average total annual precipitation of 36.8 cm (Western Regional Climate Center [WRCC] 2012) (Fig. 2). Precipitation peaked between December and March, and again for the monsoon between July and September (Warnecke and Bruner 2006) (Fig. 3). The study period spanned 2 years of distinct precipitation, one above average and the other below. Total precipitation for 2008 of 42.1 cm was above average, while 2009 received only 27.8 cm (WRCC 2011). In 2009 monsoon rains were considerably below normal (Fig. 3). For example, no rain fell on Perry Mesa during the sampling period from 14 to 17 August (Table 2). Palmer Hydrologic Severity Indices (PHSI) showed Yavapai County in moderate to mid-level drought in 2008 and 2009. This was preceded by moderate to extreme drought conditions in 2006 and 2007 (Historic Palmer Drought Indices [HPDI] 2012).

Figure 2. Average monthly air temperature (C) and % relative humidity for Sunset Point weather station, Arizona in 2008 and 2009 (WRCC 2011).

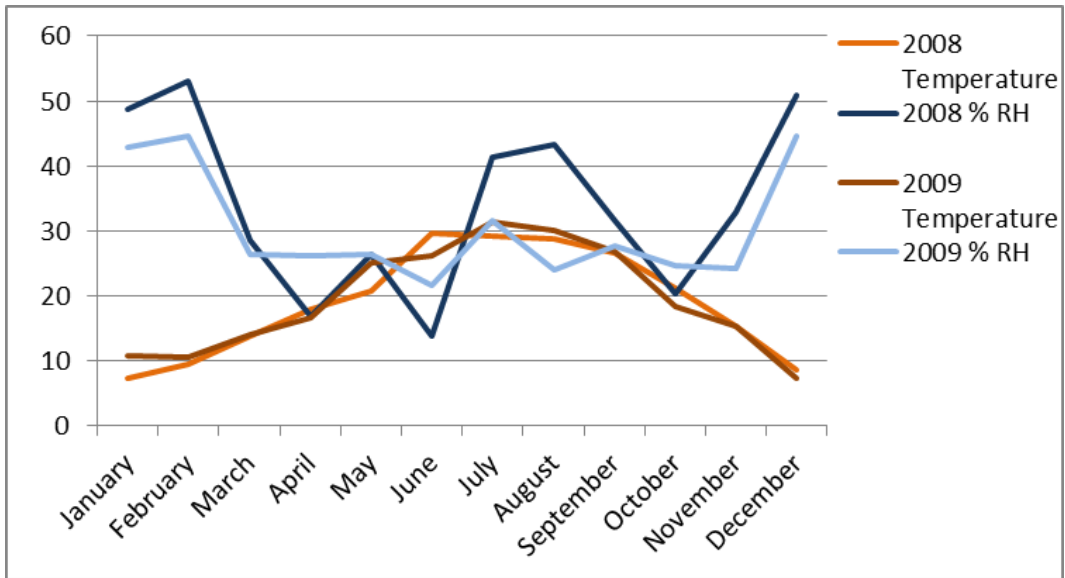
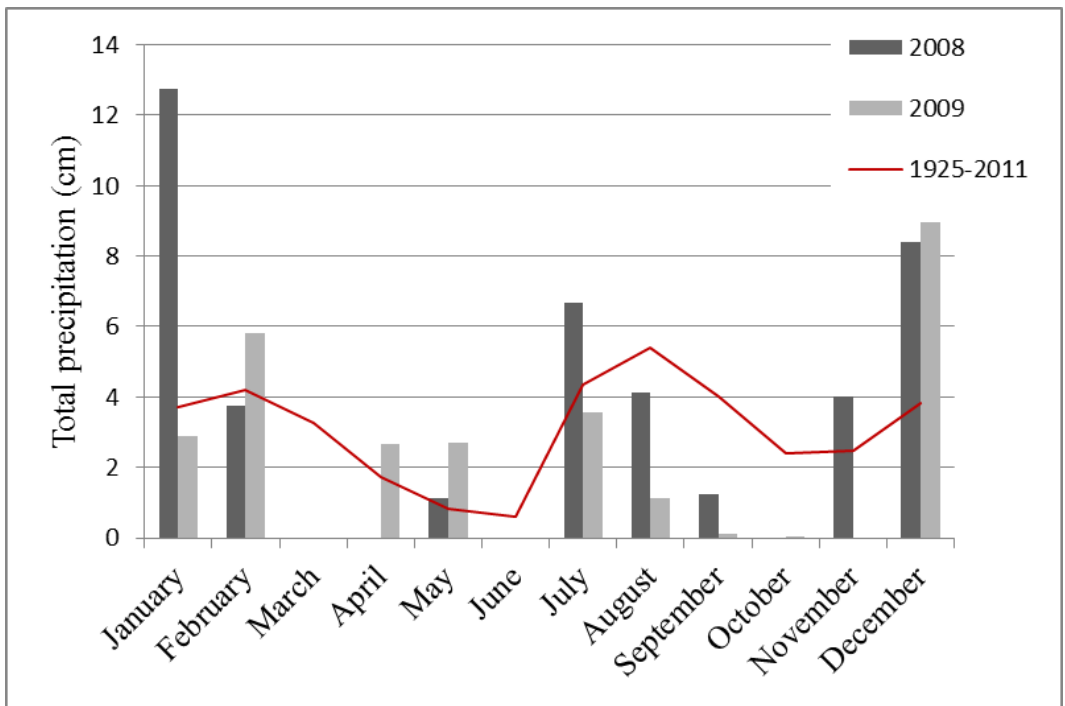


Figure 3. Total monthly precipitation (cm) for Sunset Point weather station, Arizona in 2008 and 2009 (WRCC 2011). Average annual precipitation from 1925 to 2011 is for Cordes weather station, Arizona (WRCC 2012).



Thirteen separate water sources were present on Perry Mesa. There were 9 rain filled earthen tanks originally constructed for livestock, 2 windmill fed troughs, and 2 AZGFD catchments. Several of the livestock were commonly used by wildlife including pronghorn, mule deer, white-tail deer, javelina and numerous bird and small mammal species (personal observation). Coyote, mountain lion and bobcat also frequented the water sources. One elk was captured on camera at a livestock tank during the study period. Several of the tanks did not have fences, and for those that did the gates were usually left open. Tanks and catchments filled naturally with the rainwater. Many of the earthen tanks went dry in summer and winter, depending on the rainfall patterns (personal observation). The AZGFD catchments were observed to retain water even in the hottest parts of the summer. The windmill troughs on Perry Mesa were operating and continuously full during the study period. In addition there were a number of ephemeral streams that flowed periodically during the rainy seasons.

Field Data Collection

I collected samples of fecal and plant material for pronghorn diet composition and forage quality during 4 reproductively critical periods (bio-periods) in 2008 and 2009 (Table 2). These sampling periods tracked the most nutritionally stressful points of the female pronghorn biological cycle. These bio-periods also corresponded to the changing temperature and precipitation gradient. I determined timing of parturition using Ticer et al. (2000) estimates of pronghorn fawning dates by elevation. For conception and gestation I back calculated from

parturition using known gestation period of 250 days (Yoakum and O’Gara 2004).

I determined peak lactation using predictive models based on equations from Robbins (1993).

Table 2. Dates of plant and fecal sample collection for American pronghorn antelope on Perry Mesa, Arizona in 2008 and 2009.

Biological period	2008	2009
Late gestation	10-14 March	14-17 March
Parturition	1-3, 12 May	3-6 May
Peak lactation	14-17 June	15-17, 21 June
Conception	13-16 August	14-17 August

In order to determine the area of greatest use for each sampling day I located and observed pronghorn in the morning from ≥ 1 km away until approximately 1300 h. I determined the sampling location (use area) as the place where the majority of the observed animals had spent the greatest amount of time (≥ 10 minutes) within the last hour of observation. I visually established the location of the use area using landmarks and a compass. Upon arrival, I identified the center of the use area by the presence of numerous fresh pellet groups, hoof prints, and scratch marks in the soil. I took a GPS point at the location with the highest density of pellet groups. This served as the center of the use area.

Before the plant collection began I collected fresh pellet groups in separate paper bags labeled with date, location, and a unique identifier. Fresh pellet groups can be distinguished from old using characteristics such as the presence of moisture, urine markings nearby, and absence of sun bleaching. I collected a

minimum of 4 pellet groups within each bio-period, and every attempt was made to collect all pellets within a group.

I sampled plants for a total of 2 hours during the hottest, driest time of day (between 1300 and 1700 hours) and resampled at the same location for 2 hours during the coolest, most humid point in the day (between 0300 and 0630 hours). I collected plant species starting at the center of the use area, radiating outward in a concentric circle. I collected at least 100 g of each plant species encountered in a paper bag and weighed to the gram using a tube scale. I usually made collections from within 50 m of the central point, although in dry periods with low species diversity I collected from farther away to increase the number of species. For herbaceous material I collected the entire plant above ground, whereas for trees and shrubs, I cut leaves and twig tips. I created herbarium specimens for species that could not be readily identified in the field. I collected additional plants throughout the day when possible for use as microhistological vouchers. I repeated collections 4 times within each bio-period for a total of 4 replications to ensure statistical validity.

Herbarium specimens will be donated to Arizona State University Vascular Plant Herbarium and the Desert Botanical Gardens Herbarium, and microhistological voucher slides will be donated to the Wildlife Ecology lab at Arizona State University Polytechnic campus.

Laboratory Analysis

Sample preparation. - Upon returning to the lab, I dried plants and scat samples in a forced air oven at 50° C for 48 hours or until all moisture was gone. I re-weighed plants using the same field scales and recorded weights in order to determine the percent moisture content. I hand-ground a small amount of plant material of each species with a mortar and pestle to make voucher slides for the microhistological analysis. I prepared plant voucher slides according to the methods outlined in Davitt and Nelson (1980). I ground the remaining plant material in a Wiley mill with a 1 mm filter and stored in airtight bottles for nutrient analysis. I pooled day and night samples from individual species within each year and sampling period for nutrient analysis since diurnal differences in nutrient content were not the intent of this study.

I combined fecal samples to form 4 composite diets within each bio-period and year, for a total of 32 diets. For each diet, I mixed a random sample of approximately 2 ounces of pellet material with water and agitated it in a blender before processing for microhistological analysis according to Davitt and Nelson (1980).

Diet composition. – I used microhistological analysis to determine the percent plant species composition of each pronghorn diet following the techniques outlined in Holt et al. (1992). The microhistological technique utilizes the epidermis of the plant cell to identify plants to forage class, family, genus or

species. Plant epidermal cells often differ in appearance by a combination of characteristics including cell length and shape, stoma shape, texture, trichome shape, trichome base shape, and other consistently outstanding characteristics. The microhistological analysis is currently accepted as the most accurate method of herbivore diet determination (Kessler et al. 1981, Mohammad et al. 1995, Shrestha 2006).

I built a reference library of 140 plant species to develop a key based on cell characteristics. Of these, I removed 8 species from analysis due to lack of distinguishing features. The remaining 132 species included in the key were comprised of 94 forbs, 18 shrubs and 20 grasses. Within species plant cells can differ depending on the age of the plant and location on the leaf or stem (Johnson et al. 1983, Mauseth 1988). For shrubs, I made separate voucher slides for woody and non-woody material in order to ensure that cells for woody stem material were included. For herbaceous material I made 1 slide per species, but characterized each different plant cell encountered consistently within each species and entered them into the key separately.

I preserved a random sample of fecal material from pronghorn diets on 6 microscope slides per diet according to methods outlined by Davitt and Nelson (1980). I viewed plant material on the slides through a 10 x 10 grid mounted on the microscope ocular in order to determine the percent cover of each plant species. I identified plant fragments at 100x magnification. I determined the relative cover of each identifiable species for 50 random fields on each slide, for a

total of 300 fields per diet. I calculated percent species composition by taking the total cover values for each species and dividing them by the summed cover values for all species. I normalized cover values for microscope slide density by dividing the total cover of the replicate with largest total cover by the total cover of replicate being adjusted. I performed all microhistological analyses to the 90% confidence level.

Applying a digestibility coefficient improves the accuracy of ruminant diets by correcting for the underrepresentation of digestible species in fecal matter (Hansen et al. 2000, Yoakum and O’Gara 2000, Drake 2009). I subjected forage plants to an *in vitro* digestion according to Tilly and Terry (1963) as modified by Goering and VanSoest (1971). I applied a correction coefficient for digestibility of each available forage species using calculations from Drake (2009), and applied an average for each forage class to species that were found in the diets but lacked forage samples.

Nutrients. –I determined percent nitrogen for the most prevalent individual forage plant species in each bio-period with 2 replicates each. I used the Perkin-Elmer 2400 Series II CHNS/O nitrogen analyzer in the Barry Goldwater lab on the Tempe campus of Arizona State University to determine percent nitrogen, hydrogen and carbon. I combined replicates using weighted averages and converted nitrogen values to crude protein by multiplying by 6.25.

I used structural carbohydrates as a rough measure of available carbohydrates due to equipment failure in obtaining measurements of ash that are required to determine NFE. I determined structural carbohydrates using tests for Neutral Detergent Fiber (NDF), Acid Detergent Fiber (ADF), and the acid digestion portion of Acid Detergent Lignin (ADL) in order to calculate cellulose and hemicellulose content of diets according to the methods outlined in Goering and Van Soest (1971). I calculated percent hemicellulose as the remainder of NDF minus ADF. I calculated percent cellulose as ADF minus the post-acid weight from the acid digestion portion of the ADL test. I then determined the percent structural carbohydrate as the sum of cellulose and hemicellulose.

I performed analyses for carbohydrate on composite samples which were based on the percent plant composition found in each of the 32 pronghorn diets. I weighed the amount of plant material needed to comprise a sample to the 0.0001 of a gram and hand mixed the material. Because more plants were found in the microhistological analysis than were collected for nutrient analysis, composite samples constructed using available plants differed in composition to some degree. The percent of plant species available for reconstructing each diet ranged between 37.0% and 92.3%, with averages of 54.3% for gestation, 60.0% for parturition, 61.5% for lactation and 74.9% for conception.

I developed averages for percent fat (lipid) content of each diet using values derived from the percent ether extract of plant species found in Ensminger and Olentine (1978). For forbs and grasses I used data from plant species

occurring within the Desert Botanical Gardens' flora of the AFNM. Data for shrubs were less available so I broadened my search by using shrubs known to be consumed by pronghorn (Sexton et al. 1981, Smith and Malechek 1974, Koerth et al. 1994, Stephenson et al. 1995, Smith et al. 1998, Miller and Drake 2005, Brown et al. 2008) which also occur within 50 km of the AFNM (Southwest Environmental Information Network (SEINET) 2012). I multiplied these values by percent forb, shrub and grass in each diet in order to estimate percent fat for each forage class.

Preformed water. – I determined preformed water based on wet and dry plant weights using this equation:

$$PW = WW_i - DW_i \div WW_i$$

Where:

PW_i is the preformed water content of plant species i ,

WW_i is the wet weight of plant species i and

DW_i is the dry weight of plant species i .

Water Model Development

I used equations reported in Fox et al. (2000) to construct a model to estimate the amount of free water pronghorn would theoretically need to drink during each bio-period (Appendix B). I modified the equations to calculate free water requirements on a per diet basis. I used average American pronghorn weights of

41.3 kg for females and 48.6 kg for males reported for a semi-desert grassland biotic community (Brown and Ockenfels 2007).

Robbins (1993) provided the most recent equation available for estimating baseline water requirements (Equation 1c). I used an equation from Hackmann (2011) (Equation 2a) to estimate milk production and an equation from Schmidt et al. (1988) modified for water content of pronghorn milk (Einarsen 1948) to calculate lactation water requirement per ml of milk for a single fawn (Equation 2b). I multiplied the additional water requirement by 1.49 for twins (Robbins 1993).

I calculated daily dry matter intake rates as 2.5% of animal body weight (Robbins 1993) (Appendix B, equation 3d). I modeled pronghorn crude protein requirements and availability for peak lactation to determine if additional crude protein, and thus dry matter, was needed using equations proposed in Robbins (1993) and Hackmann (2011). If a deficit were found, I would adjust Dry Matter Intake accordingly to account for increased nutritional need (Appendix B, equation 3e).

I calculated metabolic water using equations from Robbins (1993) as reported in Fox et al. (2000) using structural carbohydrates as an estimate of available carbohydrates (Appendix B, equation 4). I reduced gross metabolic water by half to account for losses due to increased excretion of nitrogen during the oxidation process (Robbins 1993, Fox et al. 2000).

Statistical Analysis

I performed statistical tests using the R (R version 2.14.1, www.r-project.org, accessed 12 January 2012), MICROSOFT EXCEL 2010, PC-ORD 6 (MjM Software, Glenden Beach, OR) and ESTIMATES (ESTIMATES version 8.2.0, <http://purl.oclc.org/estimates>, accessed 6 June 2012). Prior to testing I inspected data sets for homogeneity of variance using Levene's test and normality by plotting the residual values in R. When parametric assumptions were violated I selected the appropriate alternative. I conducted all statistical tests at $\alpha = 0.05$ unless otherwise noted.

Diet composition. –I tested species richness data using a 2 factor ANOVA with year and bio-period as factors. I used the Tukey's Honestly Significant Difference (HSD) multiple range test to investigate differences between means during years and bio-periods. I examined forage class data using a ranked-mean non-parametric 3 factor factorial ANOVA with forage class, year, and bio-period as factors and performed a non-parametric multiple range test to investigate factors with significant differences (Zar 2010).

I examined relative differences between pronghorn diets by year and bio-period using nonmetric multidimensional scaling (NMS) with PC-ORD. Data sets which contain a high degree of zeros and do not fit the normal distribution are problematic when applying statistical methods such as ANOVA (Delucchi et al. 2004, Martin et al. 2005). The pronghorn diet datasets in this study contained an average of 72% zeros due to the presence of uncommon species detected as a

result of increased sampling. Nonmetric multidimensional scaling is especially well suited for comparing ecological communities with non-normal distribution and a high degree of zeros (McCune and Grace 2002), and has been used successfully in several animal diet studies (Di Stefano and Newell 2008, Sampson et al. 2009, Forsyth and Davis 2011). Nonmetric multidimensional scaling ranks components of each sample and makes comparisons based on a dissimilarity matrix drawn from the ranks. It then calculates the best fit model based on dissimilarity, or stress, and visually displays relationships (McCune and Grace 2002, Forsyth and Davis 2011). It is currently the most defensible method of analysis for community-type datasets with the limitations mentioned above and is quickly becoming more common in ecological studies (McCune and Grace 2002, Ramette 2007).

I transformed data using arcsine square-root and used the recommended Sorensen distance measure with a random starting location using the slow and thorough autopilot method (McCune and Grace 2002). PC-ORD automatically assessed the stress, or fit of the model using Monte Carlo tests. I performed a Bray-Curtis similarity index in ESTIMATES to quantify percent differences between diet means by season and year (McCune and Grace 2002).

Nutrients. – I prepared data for crude protein and structural carbohydrates by calculating total grams of nutrient in each diet for female pronghorn (Appendix B, equations 5a and 5b). I used 2 factor factorial ANOVA tests to examine crude protein and structural carbohydrates for differences between bio-periods and

years, and Tukey HSD means separation tests to examine differences between factor levels.

Preformed water. – I prepared data for dietary preformed water using equation 3a from Appendix B. I tested the diurnal, bio-period and yearly differences in preformed water using a ranked mean 3 factor factorial non-parametric split plot ANOVA in R and completed in Microsoft Excel 2010. I performed the ranked sum Tukey-style means separation test in Microsoft Excel 2010 according to Zar (2011).

Water model. – I tested the results of the water balance model for differences between water requirement and dietary water using a paired student's t test in R. I used dietary water data calculated for female pronghorn and included lactation requirements for twins in the water requirement, because population management is most often concerned with reproductive females.

Chapter 4

COMPOSITION OF PRONGHORN DIETS ON A SEMI-DESERT GRASSLAND

INTRODUCTION

Historic population instability of pronghorn antelope in Arizona has been a source of concern among wildlife managers. Perry Mesa, included within GMU 21, provides a case in point. Since the first survey in 1959, the population estimates have fluctuated between 39 and 249 animals with low numbers resulting from habitat fragmentation, fire suppression, grazing pressures, drought, and sampling error (Warnecke and Brunner 2006, D. D. Warnecke, personal communications). Perry Mesa contains one of the premier fawning grounds for the network of mesas within the unit (Warnecke and Brunner 2006) and makes up 21% of the GMU. Given the importance of Perry Mesa to the dynamics of the GMU 21 population, understanding of the diet composition will provide baseline information that will benefit management planning for the entire unit.

According to Yoakum and O’Gara (2004) pronghorn diet information aids in decision making regarding translocations, vegetation manipulation, provisioning of water, and assessing habitat quality. Pronghorn diets are often evaluated at times of population stress (Bayless 1969, AZGFD 1981, Drake 2009). However, diet studies conducted during population increases can be equally important by providing data on diet composition when conditions are more favorable. During my study period of 2008 and 2009, the GMU 21

pronghorn population was increasing and the Horseshoe Ranch allotment on Perry Mesa had been rested since 2006. The drought that had been in effect since 1999 was temporarily eased in 2008 when precipitation was above the historical average (WRCC 2011). In 2009 precipitation was slightly lower than the average, but still above the previous drought conditions (WRCC 2011). This study provided a look at 2 years of different precipitation during a respite period from grazing.

My objectives for this chapter are to: 1) determine yearly and seasonal differences in species richness within pronghorn diets on Perry Mesa 2) determine differences in forage class composition and 3) determine relative differences in species composition. The results will help describe the composition and patterns of pronghorn diets during 2 years of different precipitation, and will provide information for plant monitoring efforts and management on Perry Mesa.

RESULTS

Species Richness

Species richness, as estimated by number of plant species in pronghorn diets, was 5% greater during 2008 than 2009 ($F_1 = 7.19$, $P = 0.005$) with significant differences between bio-periods ($F_3 = 7.55$, $P < 0.001$) and between years and bio-periods ($F_3 = 3.10$, $P = 0.045$) (Table 3, Appendix C Table 1). Richness was highest during lactation 2008 and lowest during conception 2009. In 2008 richness increased from gestation to lactation and then decline in conception to

below gestation levels. In 2009 richness declined linearly as the year progressed. In lactation it declined significantly from parturition by 7.8 species (Tukey HSD, $P = 0.002$). The decline from lactation and conception was not statistically different.

Table 3. Mean number of plant species for American pronghorn antelope diets on Perry Mesa, Arizona in 2008 and 2009.

Year	Gestation	Parturition	Lactation	Conception	Total
2008	32	33	34.3	27.5	94
2009	33.5	32.3	24.5	20.5	89

Forage Classes

Forage classes did not differ between 2008 and 2009. Ranked means were different between bio-periods ($H_3 = 5.24$, $P=0.02$), forage class ($H_2 = 69.70$, $P < 0.001$), and the interaction between bio-periods and forage classes ($H_6 = 14.88$, $P < 0.001$). In parturition, lactation, and conception all forage classes were significantly different (Appendix C, Table 2). During gestation forbs and shrubs were different ($P < 0.001$) as well as forbs and grass ($P < 0.001$), but shrubs and grass were not significantly different.

Forbs were the dominant forage class in all bio-periods and were significantly greater than grasses ($P < 0.001$) and shrubs ($P < 0.001$). Forbs were different than other forage classes in all bio-periods combinations except lactation and conception ($P \leq 0.05$). They were highest during parturition and lactation when they comprised over 97% of the diet, and lowest in gestation with 78% in

2008 and 67% in 2009. They were lower in 2009 gestation and conception periods than the 2008 counterparts (Table 4).

Shrubs were present in the diets in significantly greater amounts than grasses ($P < 0.001$). This pattern was consistent between all combinations of bio-periods. Shrub use was highest in gestation and lowest in parturition, then increased again in conception. The 2009 diets contained more shrubs than 2008. The 2 most abundant shrubs were Wright’s buckwheat and fairyduster, which together comprised 8.2%, 0.3%, 1.2% and 2.4% for gestation, parturition, lactation and conception, respectively (Table 4).

Grass was detected the least of all the forage classes. Amounts in the diet differed between gestation and lactation ($P < 0.001$), gestation and parturition ($P < 0.001$), gestation and conception ($P < 0.001$), and conception and lactation ($P = 0.006$). Grass was highest in gestation and declined to <2% of the diet in all other bio-periods.

Table 4. Mean % forage class composition of American pronghorn antelope diets on Perry Mesa, Arizona in 2008 and 2009. G = gestation, P = parturition, L = lactation, and C = conception.

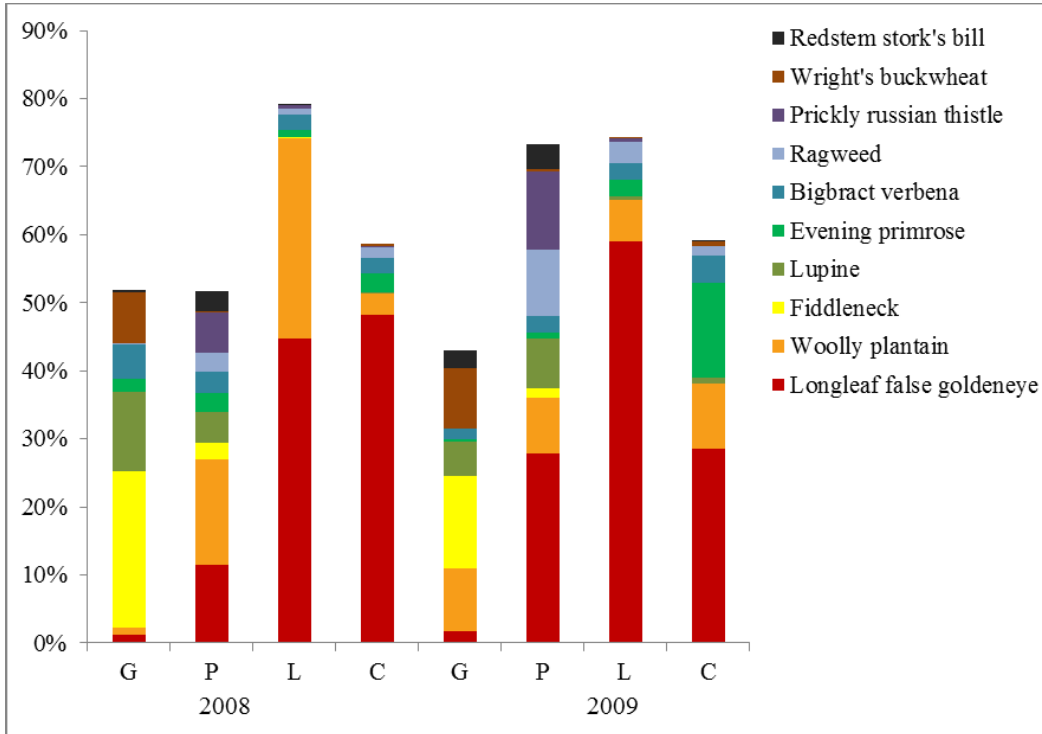
Forage class	2008				2009			
	G	P	L	C	G	P	L	C
Forbs	78.3	98.9	97.2	94.2	67.3	99.2	97.2	88.0
Shrubs	12.9	0.8	2.7	4.4	15.7	0.6	2.5	11.7
Grass	8.8	0.3	0.1	1.4	17.0	0.2	0.3	0.3

Species composition

A complete table of mean percent composition for each plant species found during the bio-periods in 2008 and 2009 is available in Appendix A. Out of the 132 species used to build the microhistological key, 68 forbs, 19 shrubs and 15 grasses were identified to species or genus. Ten species were present in the diets in amounts >1%, and these comprised between 42% and 79% of seasonal diets. Of these, 9 were forbs and 1 was a shrub (Fig. 4).

The most dominant forb was longleaf false goldeneye (*Heliomeris longifolia* var. *annua*), comprising an average of 1.4% in combined gestation diets and 51.9% in combined lactation diets. Woolly plantain (*Plantago patagonica*) was the second most dominant with 5.3% in gestation and 17.7% in lactation. Fiddleneck (*Amsinckia* sp.) was the most dominant in gestation (18.3%), but was <2.0% in all other bio-periods. Lupine (*Lupinus* sp.) comprised 8.3% of gestation diets but fell to <1.0% in lactation and conception diets, while evening primrose (*Oenothera* sp.) comprised 1.2 % of the diets in gestation and rose to 8.4% in conception. Bigbract verbena (*Verbena bracteata*) was present in all bio-periods and ranged from 1.5% to 5.0% of the diets. Wright's buckwheat (*Eriogonum Wrightii*) was the most abundant shrub species, making up an average of 8.1% of the diet in gestation and 0.03% in lactation. Other plants that were dominant in gestation and parturition were ragweed (*Ambrosia* sp.), prickly Russian thistle (*Salsola tragus*), and redstem stork's bill (Fig. 4).

Figure 4. Mean % of plants comprising $\geq 1\%$ of American pronghorn antelope diets on Perry Mesa, Arizona in 2008 and 2009. G= gestation, P = parturition, L = lactation, and C = conception.



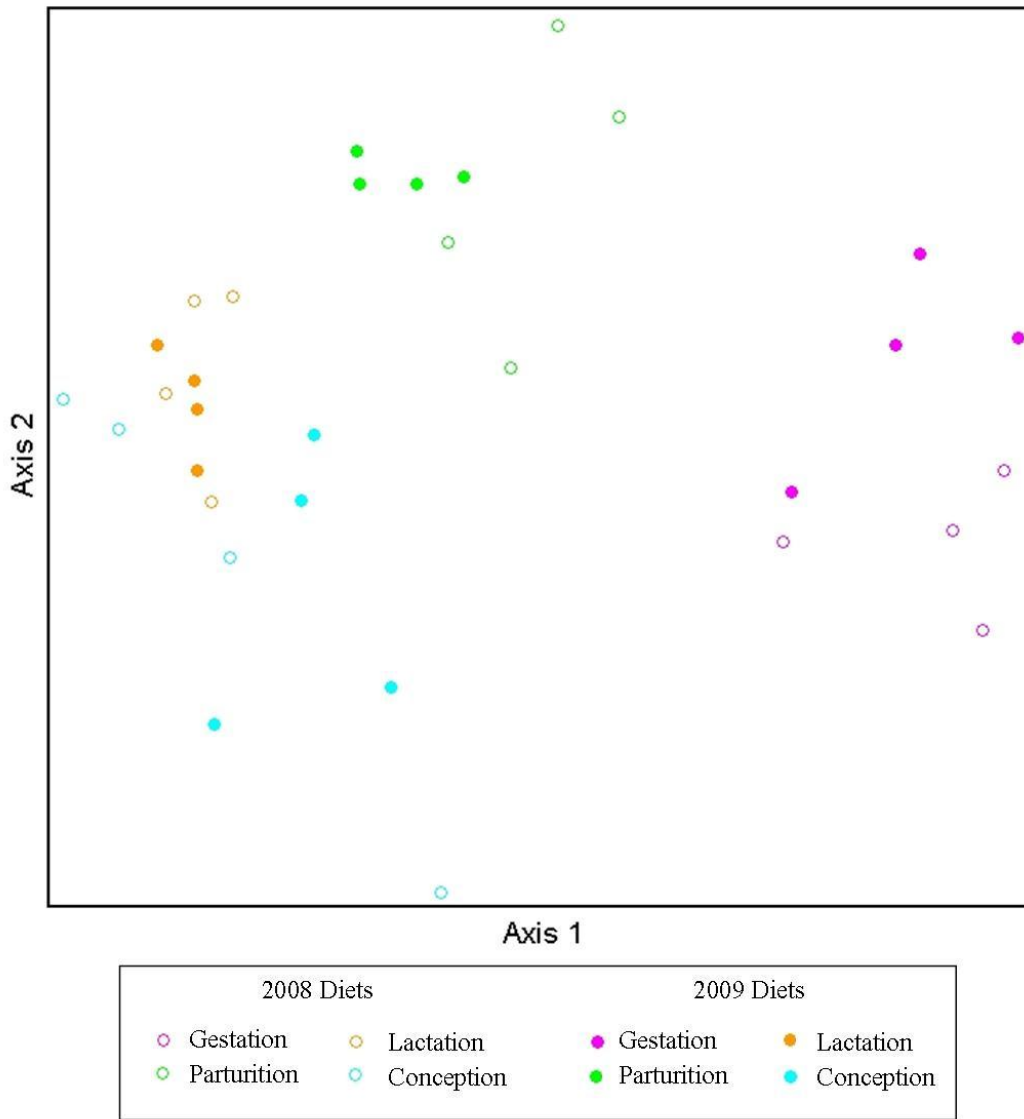
Several plants could not be identified to species in the microhistological analysis due to homogeneity of cell structures within the genus. Ragweed (*Ambrosia* sp.) refers to either cuman ragweed (*Ambrosia psilostachya*) or weakleaf bur ragweed (*Ambrosia confertiflora*). Evening primrose (*Oenothera* sp.) refers to either yellow evening primrose (*Oenothera flava*) or desert evening primrose (*Oenothera primiveris*). Two species of *Descurainia* could only be identified in the diets as trichomes due to the high digestibility of the cell material.

The best fit nonmetric multidimensional scaling solution had a stress score of 12.4 and $P = 0.0040$ with 250 randomized Monte Carlo runs. A score of <20 is

considered an adequate model (McCune and Grace 2002) and a goodness of fit measure of $P < 0.02$ is considered sufficient to describe results in 2 dimensions (Sampson et al. 2009).

The variability in species composition of diets was reflected in the nonmetric multidimensional scaling analysis, which displayed distinct groupings by bio-period and year (Fig. 5). Diet groupings were more similar between years than between bio-periods. Gestation diets had the highest degree of dissimilarity from other bio-periods. Lactation and conception showed the most similarity to each other. Gestation diets and lactation diets were the least similar, although several 2008 conception samples diverged from gestation to a greater degree. Lactation was the only bio-period with a high degree of overlap between years, and individual diets were most similar within years. Conception diets overlapped due to an outlier. Conception diets were less grouped than other bio-periods.

Figure 5. Nonmetric multidimensional scaling scatterplot of American pronghorn antelope diet replicates on Perry Mesa, Arizona in 2008 and 2009.



The Bray-Curtis index showed the most similarity between conception 2008 and lactation 2009, closely followed by lactation 2008 and lactation 2009 (Table 5). The least similar diets were gestation 2008 and lactation 2008 followed by gestation 2008 and lactation 2009. Diet combinations between the same bio-

period of different years were all $\geq 54\%$ similar. Diet combinations between different bio-periods within the same year were variable, with the highest degree of similarity between lactation and conception. Gestation diets were the most divergent from the other bio-periods. Similarity decreased with temporal distance between bio-periods within years.

Table 5. Bray-Curtis index indicating % similarity between means of American pronghorn antelope diets on Perry Mesa, Arizona inc 2008 and 2009. Numbers are between 1 and 0, 1 representing complete similarity. G = gestation, P = parturition, L = lactation, and C = conception.

	2008				2009			
	G	P	L	C	G	P	L	C
2008 G	1							
2008 P	0.43	1						
2008 L	0.20	0.46	1					
2008 C	0.32	0.49	0.66	1				
2009 G	0.62	0.46	0.28	0.29	1			
2009 P	0.28	0.54	0.53	0.50	0.35	1		
2009 L	0.23	0.41	0.72	0.75	0.26	0.54	1	
2009 C	0.37	0.57	0.55	0.68	0.38	0.52	0.56	1

The results of the nonparametric ranked-means ANOVA (Zar 2010) support the patterns that can be seen in nonmetric multidimensional scaling and Bray-Curtis similarity index. Ranked means for species composition between 2008 and 2009 diets were significantly different ($H_1 = 4.33$, $P = 0.03$), as were the differences between bio-periods ($H_3 = 24.00$, $P \leq 0.001$) and individual species ($H_{105} = 1262.59$, $P \leq 0.001$). All interactions were significant including that of year, bio-period and species ($H_{315} = 232.81$, $P \leq 0.001$), (Appendix C Table 3).

DISCUSSION

Species Richness

Species richness followed different patterns between the 2 years. In 2008 it increased from gestation and peaked in lactation, then decreased in conception. In 2009 it was highest in gestation and decreased continually to a low in conception. The most notably significant drop in richness was a 16% decrease that occurred between the lactation and conception periods of 2009, presumably due to the dry summer and resulting lack of species availability.

Patterns of species richness in the pronghorn diets roughly followed decreases in precipitation. 2008 had above average precipitation (42.1 cm), a wetter monsoon (4.1 cm, -1.26 PHDI), and higher richness overall (Table 3). 2009 was drier (27.8 cm) with very little August precipitation (1.1 cm) and drought conditions worsening as the summer progressed (-2.31 PHDI) (WRCC 2011, HDPI 2012). This drop in richness following declining precipitation and worsening drought conditions suggests that richness in pronghorn diets may track richness in available forage plants and thus provide a relative measure of range quality.

Drake (2009) used the same microhistological protocol and found species richness on Anderson Mesa in 2002 that was comparable with 2008 richness data of this study. Anderson Mesa was considered to be more heavily impacted by grazing than the paired study site of Garland Prairie, which had significantly

higher richness. Brown et al. (2008) found between 18 and 25 species in August diets in GMU 21, although direct comparisons between the studies cannot be made due to methodological differences. However, 18 species were found in 2004, the driest year (0.5 cm, -4.85 PHDI) and 25 found in 2005, the wettest year (3.7 cm, 3.74 PHDI) (HPDI 2012).

Pronghorn recruitment rates for GMU 21 were 25:100 and 54:100 fawns:does during the severe drought years of 2003 and 2004 respectively, and 38:100 fawns:does in the wet year of 2005 (AZGFD 2008, HPDI 2012). During the moderate drought conditions and greater precipitation of 2008 the ratio was 34:100, and 37:100 in the drier year of 2009. The high recruitment in 2004 corresponded with low relative richness (Brown et al. 2008), and the subsequent drop to 38:100 fawns:does in 2005 occurred with an increase in richness. Based on these data, recruitment rates did not appear to follow yearly fluctuations in the species richness of pronghorn diets. More information would be necessary to accurately compare recruitment rates with dietary richness.

Forage class

Forbs were the most consumed forage class in both years and in all bio-periods, a pattern that is typical of grassland pronghorn diets (Stevenson et al. 1985, Yoakum and O’Gara 2004, Brown et al. 2008, Drake 2009). This is especially true of diets that incorporate the differential digestion coefficient, which corrects for the underrepresentation of highly digestible plants (Hansen et al. 2000,

Yoakum and O’Gara 2000, Drake 2009). Higher amounts of forbs are indicative of climactic and range conditions that are favorable to pronghorn (Beale and Smith 1970, Stephenson 1985, Drake 2009). Drake (2009) found an average of 95% forbs in the optimal Garland Prairie diets for all bio-periods, and 73% on the more heavily grazed Anderson Mesa. Stephenson et al. (1985) reported that forb use increased during years of high precipitation and decreased during low precipitation. Beale and Smith (1970) found similar results, where forbs comprised over 90% of pronghorn diets in years of above average precipitation and fell to about 20% in dryer years.

Shrubs increase in pronghorn diets when forbs become less available, whether due to drought, season change, or competition from other large herbivores (Yoakum and O’Gara 2004). On Perry Mesa shrub usage was highest during gestation and conception periods. Shrubs were used more when forbs were less available, as in gestation, or as precipitation decreased. This followed patterns well established in the literature (Beale and Smith 1970, Stephenson et al. 1985, Yoakum and O’Gara 2004, Autenrith et al. 2006, Brown et al. 2008).

Grass was used the least in all bio-periods (Table 4). It was at the highest in the gestation period of 2009 when it comprised 17% of the diets. Grasses are used most by pronghorn when immature (Autenrith et al. 2006), and on Perry Mesa they may have been more desirable due to lower forb availability during gestation. Barley (*Hordeum* sp.) was the most abundant grass. Immature epidermal cells of this genus could be distinguished from mature cells and made

up 2.5% of the diets in gestation 2008 and 12% in gestation 2009. Barley was only present in trace amounts during the other bio-periods. This grass was one of the first grasses to emerge in the early spring and was abundant on Perry Mesa in both years (personal observation).

Species Composition

Species composition analysis of the pronghorn diets on Perry Mesa revealed several plants that were seasonally abundant and present in multiple bio-periods. The most dominant plant, longleaf false goldeneye, has not been documented in previous Arizona diets (AZGFD 1981, Miller and Drake 2005, Brown et al. 2008). This biannual forb persisted throughout the lactation and conception periods, reaching up to 59.0% of the diet in lactation when many other forbs had expired.

Longleaf false goldeneye is aromatic and the leaves and stems are covered with long, dense trichomes. These traits are usually associated with herbivore deterrents (Robbins 1993, Walters 2010). However, herbivores are more likely to select less palatable plants if they are available in abundance (Yoakum and O’Gara 2004). During both 2008 and 2009 parturition and lactation periods longleaf false goldeneye was one of the most dominant forbs in pronghorn use areas on Perry Mesa (personal observation). This forb was most prevalent in the diets during lactation, and highest in lactation of 2009 when species richness was

considerably lower than previous bio-periods. It may have been present in such high levels in the diet due to opportunistic utilization.

Woolly plantain, a small annual forb, was present in high levels during parturition and persisted into lactation and conception. This forb was found in several other studies (Koerth 1984, Brown et al. 2008) along with the closely related desert Indianwheat (*Plantago ovata*) (AZGFD 1981). Its increased presence in lactation 2008 may be the result of greater availability due to higher precipitation from the relatively wet winter and milder drought conditions (HPDI 2012). Woolly plantain generally flowers in the spring and produces seeds in summer, losing moisture at this time. Despite the summer senescence it was still utilized by pronghorn. Researchers in southern Arizona noted that pronghorn consumed plantain even after it had become dry (AZGFD 1981). Perhaps it retains nutrients even in this stage, or is eaten for its protein rich seeds.

Fiddleneck emerged as an important plant during gestation of both years despite the numerous stiff hairs that are normally considered a deterrent to herbivory (Walters 2010). This forb contained 81% water in the spring of 2009 (Tluczek, unpublished data). Pronghorn consumed it most often in March in the early stages of growth when the hairs were underdeveloped and would not be as much of an irritant. It may also be that the tough, cornified upper palate of a pronghorn's mouth allows them to consume more hirsute vegetation if it contains desirable nutrients (Yoakum and O'Gara 2004).

Bigbract verbena was consistently present in all bio-periods of both years in low levels. This forb is common around stock tanks and may remain green for longer periods of time due to the presence of water (personal observation). Stock tanks may provide greater nutrition at drier times of the year by harboring green vegetation in much the same way that craters made from aircraft missile testing on the Berry Goldwater Range provide microhabitat for Sonoran pronghorn (Krausman et al. 2005).

Rusby's globemallow (*Sphaeralcea rusbyi*) and redstem stork's bill are 2 plants that bear mention as they may be consumed at higher levels than the microhistological analysis indicated. Rusby's globemallow was infrequent on Perry Mesa but consistently present in pronghorn use areas. Often it was grazed nearly bare of leaves, sometimes with the stems eaten halfway down. Due to the indistinct cell structure, this shrub could not be readily identified by fragments without the presence of both cells and trichomes, and may have escaped identification in many cases. Redstem stork's bill may have been underrepresented for the same reasons. It is one of the first forbs to emerge during the spring green-up and was often seen recently browsed at pronghorn use sites (personal observation).

Wright's buckwheat was the most abundant shrub in the diets and highest during gestation. This shrub was documented in other diets both in Arizona (Brown et al. 2008) and in New Mexico (Stephenson et al. 1985). Brown et al. (2008) found Wright's buckwheat between 7% and 28% in all bio-periods in

GMU 21 between 2003 and 2005. Wright's buckwheat in this study varied between 0.04% and 9%. Brown et al. (2008) reported that percentages increased from parturition to lactation, while levels in 2008 and 2009 were at their highest in gestation and decreased to <1% in lactation, increasing again slightly in conception. Methodological differences between the studies, such as the use of differential digestion and 3-fold increase in microscope fields in this study, may account for varying percentages. However, these methodological differences are unlikely to affect seasonal patterns, and patterns of Wright's buckwheat were opposite between the 2 studies.

A reasonable ecological explanation for the seasonal difference in patterns of use for Wright's buckwheat is that grazing pressure and drought during the 2003 to 2005 study may have resulted in lower forb availability and increase in shrub consumption. Intense grazing is known to decrease forb availability (Ockenfels et al. 1994b), and several studies have found higher use of forbs and lower use of shrubs on lightly grazed as opposed to more heavily grazed ranges (Salwasser 1980, Drake 2009). Brown et al. (2008) found that Wright's buckwheat was taken in higher quantities during severe drought conditions in 2004 and lower in moist conditions in 2005, further supporting lower use of this shrub in better conditions. In addition, the 2008 to 2009 study saw more forbs such as longleaf false goldeneye and wooly plantain that persisted into the summer diets and possibly displaced the need for shrubs such as Wright's buckwheat. Wright's buckwheat is the most commonly consumed shrub species

in both studies and appears to be an important survival plant when range conditions suffer as a result of drought or competition.

Fairyduster was the second most dominant shrub during this study and the most dominant in conception diets for both 2008 and 2009. Utilization by pronghorn corresponds with its period of active growth (personal observation). Consumption of fairyduster doubled during the dry monsoon of 2009, when plant moisture (Tluczek, unpublished data) and species richness of the diets were lowest. This indicates that fairyduster is an important browse plant during conception and especially when precipitation and species richness are low. It should be noted that the absence of fairyduster in Brown et al. (2008) does not necessarily indicate that it was not eaten; it may be the result of a difference in sampling methodology or non-inclusion in the voucher library.

Cacti were not included in the voucher library and therefore not found in the diets. This is unlikely to affect the analysis to a great degree. Brown et al. (2008) found that prickly pear comprised an average of only 3% of the diet in March, May, June and August. Pronghorn consumed prickly pear most in the dry summer of 2004 and not at all in June of 2005. Precipitation in 2008 and 2009 was higher than any of the years in Brown et al. (2008). In addition, preliminary DNA analysis of the 2009 fecal pellets revealed no cacti in any of the diets (S. Fehlberg et al., Desert Botanical Gardens, unpublished data). Stephenson et al. (1985) found only trace amounts of cacti in pronghorn diets on a New Mexico

grassland, and Smith and Malechek (1974) found none in Utah summer diets, even though it was available.

The variability in Perry Mesa pronghorn diets was consistent with that found in other grassland pronghorn diets (Yoakum and O’Gara 2004). The NMS analysis showed gestation and parturition diets as more distinct from others, but lactation and conception diets overlapped. The strongest overlap occurred between 2008 and 2009 lactation diets, possibly due to the lack of available species at this time. There was a clear separation between the gestation and parturition diets in the earlier part of the year and lactation and conception diets in the summer, corresponding with the drop in precipitation. Diet switching is more pronounced at this point, whether it is due to the changing plant species availability or selection to increase nutrient intake.

The comparatively moderate levels of species richness relative to that found on Anderson mesa by Drake (2009) indicate adequate conditions for pronghorn during the study period on Perry Mesa. However, the high level of forbs is more comparable to Garland Prairie diets, indicating favorable conditions. Pronghorn population estimates, which had dropped from 145 to 92 during the extreme drought conditions of 2007, rose to 100 by the end of 2009, although the addition of 40 translocated animals from Utah influenced this increase (AZGDF 2009). The population has continued to increase despite drought conditions through 2012 and the fawn:doe ratio has remained > 30 (AZGFD 2011) indicating that Perry Mesa and GMU 21 are capable of supporting a large population

through climactic variation, provided that the range remains in good condition and water supplies adequate.

Chapter 5

MODELING PRONGHORN FREE WATER REQUIREMENTS

INTRODUCTION

In the arid southwest water is often thought of as a limiting factor to the survival and perpetuation of desert animal populations (Leopold 1933, Sundstrom 1968, Yoakum 1994, Marshall et al. 2006). Physiological and behavioral adaptations allow many species to survive with variable access to water resources (Wesley et al. 1970, Whisler 1984, Yoakum 1994, Yoakum and O’Gara 2004, Cain et al. 2006, Brown and Ockenfels 2007). The pronghorn antelope is a small ruminant that has numerous adaptations to desert conditions. Pronghorn readily drink water when it is available (Yoakum 1994, Morgart et al. 2006, Wilson et al. 2009), but actual requirements are unknown (Brown 1998). Researchers have examined this question from different angles and often obtained conflicting results (Einarsen 1948, Yoakum 1994, Krausman et al. 2006).

A number of researchers have suggested that pronghorn do not always need to drink free water, and may obtain enough moisture from preformed water in plants and metabolic water (AZGFD 1981, Cancino 1994, Brown and Ockenfels 2007). They proposed that like several African ruminants, pronghorn may increase their moisture intake by feeding at night and in the early morning when plant moisture is at its highest (Sundstrom 1968, AZGFD 1981, Yoakum 1994, Brown and Ockenfels 2007). Sonoran and Peninsular pronghorn have been observed feeding at night (Cancino 1994, Wilson et al. 2009), but attempts to

document this behavior with American pronghorn in a quantitative fashion have not been successful.

In light of the ongoing controversy over whether pronghorn need to drink freestanding water (Yoakum 1994, Krausman et al. 2006) several researchers have attempted to quantify pronghorn water budgets (Whisler 1984, Fox et al. 2000). Fox et al. (2000) examined Sonoran pronghorn free water requirements using a model based on calculating preformed water from measurements of plant moisture and known dietary composition, metabolic water produced by the oxidation of 3 important nutrients, and scaling equations to estimate water requirements. This approach is so far the most simple, efficient, and replicable method of estimating pronghorn water needs. I used this model as the basis for examining free water requirements American pronghorn on a semi-desert grassland, and modified it to include calculations for additional lactation water needs.

My objectives were to: 1) determine major nutrients of pronghorn diets as indicators of forage quality and to model metabolic water, 2) examine preformed water content of pronghorn diets, 3) model pronghorn free water requirements to determine if night feeding would provide a water allocation advantage, and 4) examine whether pronghorn can meet water requirements through preformed and metabolic water during biologically stressful seasons and years of different precipitation.

RESULTS

Nutrients

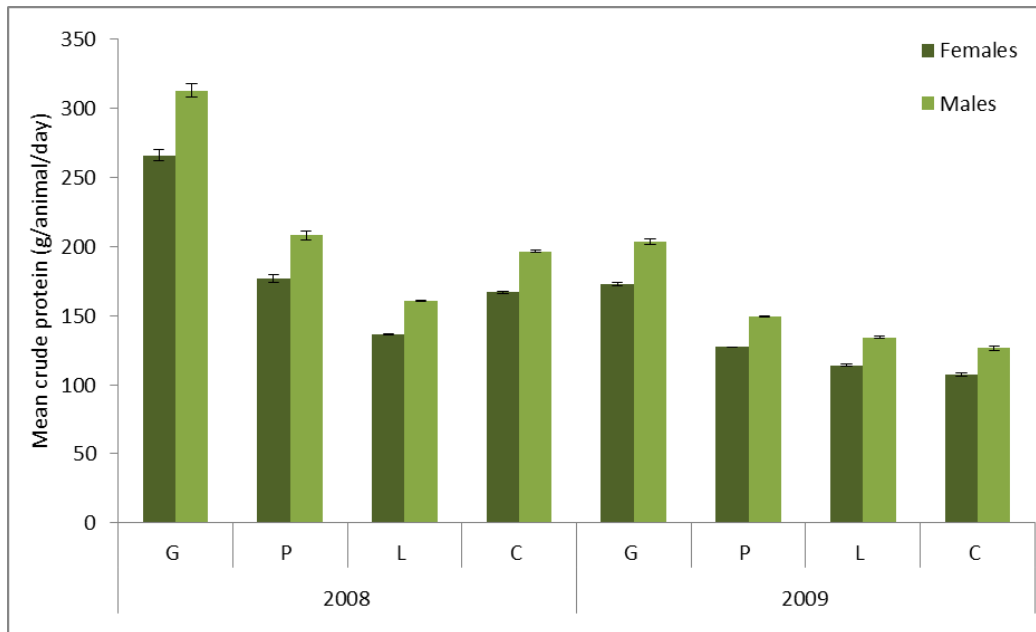
Crude protein. – Dietary crude protein was 30% greater in 2008 than 2009 ($F_1 = 1663.30, P < 0.001$) (Table 6, Fig. 6, Appendix C Table 4). Bio-period means were significantly different ($F_3 = 930.90, P < 0.001$), with the greatest amount of crude protein in gestation followed by parturition, conception and lactation (Tukey HSD, $P < 0.001$). Crude protein levels for all 2008 bio-periods were significantly higher than their counterparts in 2009 (Tukey HSD, $P < 0.001$). In 2008 the most drastic difference occurred between gestation and conception periods (Tukey HSD, $P < 0.001$), with 37% more crude protein in gestation diets (Table 6, Fig. 6). In 2009 the difference between gestation and conception was greatest (Tukey HSD, $P < 0.001$), with 38% more crude protein in gestation diets. In 2008 the dietary crude protein increased between lactation and conception, and in 2009 it declined, although only the 2008 difference was significant (Tukey HSD, $P < 0.001$) (Appendix C Table 4). Average metabolic water produced by protein oxidation was between 21 ml/animal/day and 53 ml/animal/day. This accounted for approximately 1% to 2% of the overall water requirement.

Table 6. Mean % crude protein in diets of American pronghorn antelope on Perry Mesa, Arizona in 2008 and 2009.*

Year	Gestation	Parturition	Lactation	Conception
2008	25.7 (0.33)	17.1 (0.25)	13.2 (0.04)	16.2 (0.07)
2009	16.7 (0.13)	12.3 (0.02)	11.0 (0.06)	10.4 (0.12)

* Values in () are the standard error of each mean.

Figure 6. Mean crude protein (g/animal/day) and SE in diets of female (41.3 kg, 1033 g/day DMI) and male (48.6 kg, 1215 g/day DMI) American pronghorn antelope on Perry Mesa, Arizona in 2008 and 2009. G = gestation, P = parturition, L = lactation, C = conception.



Dietary crude protein at peak lactation in both 2008 and 2009 was above estimated requirements from both Robbins (1993) and Hackmann (2011). According to equations from Robbins (1993), a doe would require 69.4 g/animal/day crude protein to nurse a single fawn and 110.0 g/animal/day for twins. The Hackmann (2011) equation yielded a requirement of 59.8 g/animal/day for a doe with a single fawn and 89.1 g/animal/day for twins. At peak lactation in 2008, Perry Mesa pronghorn diets contained an average of 136.5 (SE 0.44) g/animal/day crude protein when calculated for a 41.3 kg female (DMI = 1033 g). In 2009 crude protein was lower but still above estimated requirements at 114.0 (SE 0.73) g/animal/day. Results of the equations from Robbins (1993) for a doe in all 4 bio-periods are presented in table 7.

Table 7. Required and dietary crude protein (g/animal/day) of an American pronghorn antelope doe (41.3 kg) on Perry Mesa, Arizona in 2008 and 2009.*

Year	Gestation		Parturition		Lactation		Conception	
	Req.	Dietary	Req.	Dietary	Req.	Dietary	Req.	Dietary
2008	47.6	26.0	82.9	176.8	110.0	136.5	24.4	207.6
2009	47.6	172.8	82.9	127.2	110.0	114.0	24.4	135.5

* Requirements are based on a 41.3 kg pronghorn doe consuming 2.5 g/kg body weight/day. Lactation requirements are for a doe with twins.

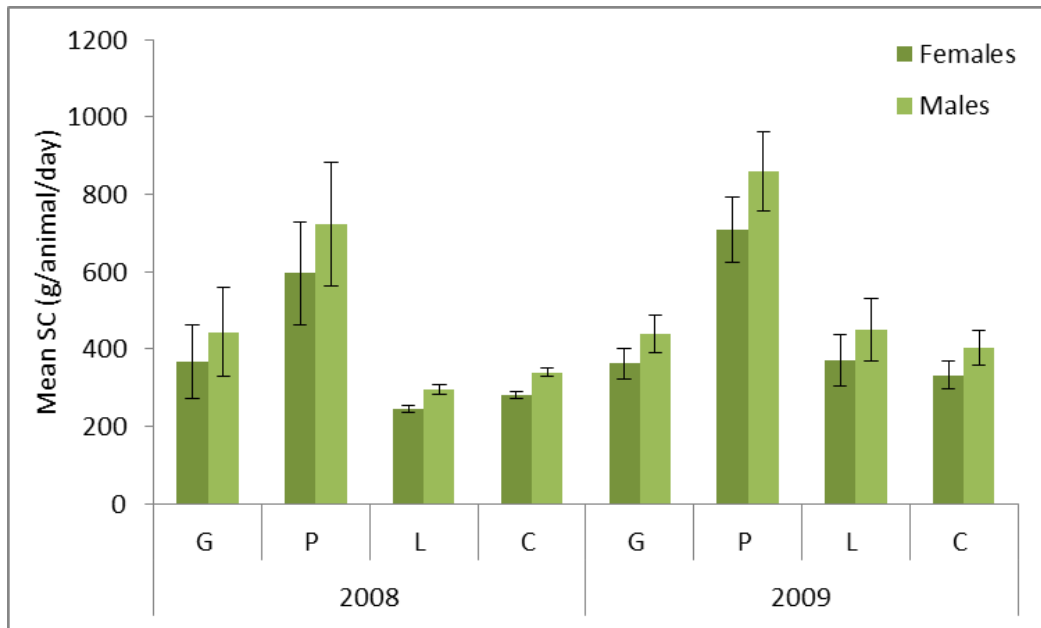
Structural carbohydrates. – Two outliers (2008 parturition diet 4 and 2009 parturition diet 2) were removed due to technical problems in the laboratory analysis. Structural carbohydrates were not significantly different between 2008 and 2009 or by the interaction of year and bio-period, although pronghorn diets contained roughly 8% more in 2009 (Table 8, Appendix C Table 5). However, when I dropped the alpha level to $\alpha = 0.1$, the difference between years was significant ($F_1 = 3.20$, $P = 0.086$). Carbohydrate levels differed between bio-periods ($F_3 = 8.84$, $P < 0.001$). The Tukey’s HSD test detected differences between parturition and all other bio-periods ($P \leq 0.05$), parturition having the highest values (Table 8). No other bio-periods were significantly different. Average metabolic water produced by structural carbohydrates was between 76 ml to 184 ml. This contributed approximately 2% to 5% to the total water requirements.

Table 8. Mean % structural carbohydrates in diets of American pronghorn antelope on Perry Mesa, Arizona in 2008 and 2009.*

Year	Gestation	Parturition	Lactation	Conception
2008	36.4 (0.09)	50.0 (0.13)	24.4 (0.01)	27.9 (0.01)
2009	36.1 (0.04)	63.8 (0.04)	37.0 (0.07)	33.1 (0.04)

* Values in () are the standard error of each mean.

Figure 7. Mean structural carbohydrates (g/animal/day) and SE in diets of female (41.3 kg, 1033 g/day DMI) and male (48.6 kg, 1215 g/day DMI) American pronghorn antelope on Perry Mesa, Arizona in 2008 and 2009. G = gestation, P = parturition, L = lactation, and C = conception.



Lipids. – Average lipid values for forbs were 3.42 (n=9), grasses were 2.42 (n=16) and shrubs were 4.3 (n=9). Total lipids per bio-period fell within 0.01 standard deviation of the lipid content reported by Fox et al. (2000) in gestation, parturition and conception (Table 9). Lipid content of lactation diets was lower than those of Fox et al. (2000), with a standard error of 0.38. Average metabolic water produced by lipid oxidation based on these values was between 18 ml and 19 ml, and contributed $\leq 1\%$ to the total water requirements.

Table 9. Mean % lipid values per bio-period developed from Ensminger and Olentine (1978), and averages from selection diets reported in Fox et al. 2000.

Bio-period averages	Perry Mesa	Fox et al. 2000	SD	SE
Gestation	3.419	3.450	0.02	0.01
Parturition	3.427	3.445	0.01	0.01
Lactation	3.444	4.515	0.54	0.38
Conception	3.485	3.245	0.12	0.08

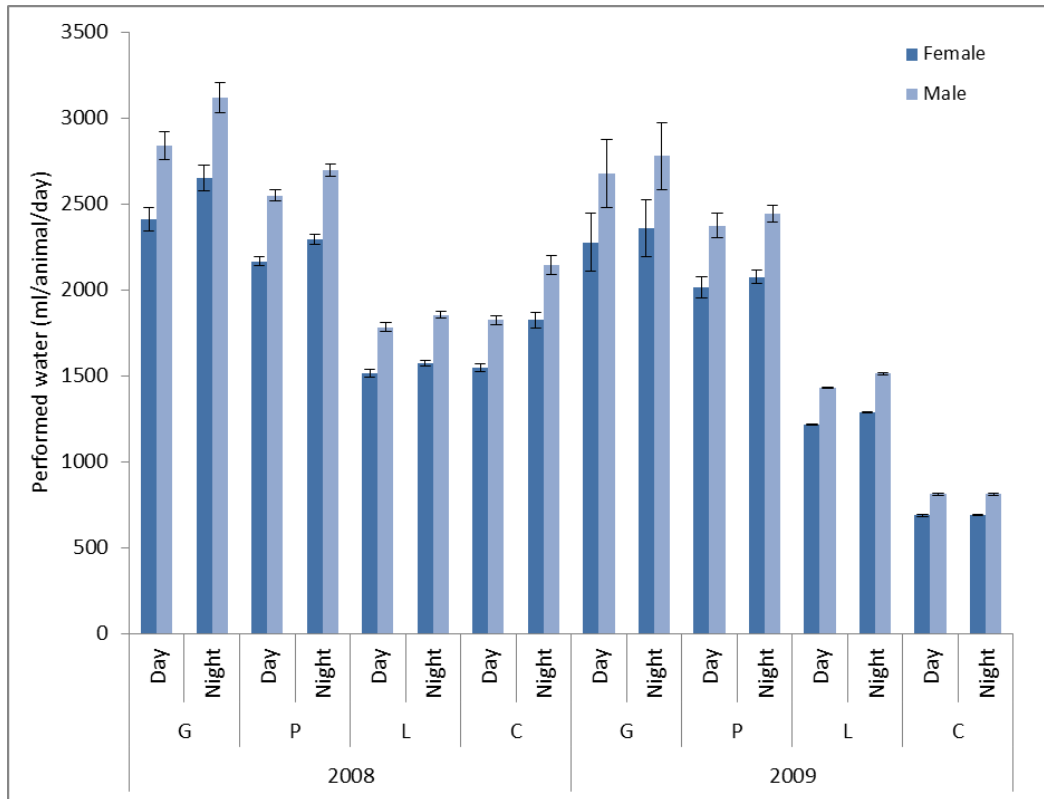
Preformed water. – Ranked means for day and night were not significantly different. In 2008 moisture content was 9% higher during the night sampling and in 2009 it was only 3% higher. However, preformed water was 21% higher in 2008 than in 2009 ($H_1 = 7.56, P = 0.005$). Preformed water also differed between bio-periods ($H_3 = 53.75, P < 0.001$) (Table 10, Appendix C Table 6). All bio-period comparisons were significantly different ($P \leq 0.03$) except for that of lactation and conception, which were relatively similar due to the dry monsoon of 2009. The highest amount of preformed water was in gestation, followed by parturition, conception, and lactation. None of the interactions involving time were significantly different.

Table 10. Mean % preformed water in diets of American pronghorn antelope on Perry Mesa, Arizona in 2008 and 2009.

Bio-period	2008		2009	
	Day	Night	Day	Night
Gestation	70.0 (0.01)	71.9 (0.01)	68.5 (0.02)	69.3 (0.01)
Parturition	67.7 (0.00)	68.9 (0.00)	66.1 (0.01)	66.8 (0.00)
Lactation	59.5 (0.00)	60.4 (0.00)	54.1 (0.00)	55.4 (0.00)
Conception	60.0 (0.00)	63.8 (0.01)	40.1 (0.00)	40.0(0.00)

*Values in () are the standard error of each mean.

Figure 8. Mean performed water (ml/animal/day) and SE in diets of female (41.3 kg, 1033 g/day DMI) and male (48.6 kg, 1215 g/day DMI) American pronghorn antelope on Perry Mesa, Arizona in 2008 and 2009. G = gestation, P = parturition, L = lactation, and C = conception.



Water model

Minimum water requirements for a non-lactating female were 3.4 L/animal/day, a lactating doe with 1 fawn required 4.2 L/animal/day and a doe with twins required 4.5 L/animal/day. Water requirement for males during all bio-periods was 3.9 L/animal/day. Combined preformed and metabolic water yielded a minimum mean of 0.83 (SE 0.01) L/animal/day for females during conception 2009 during the day, and a maximum of 3.33 (SE 0.07) L/animal/day for males during gestation 2008 at night (Table 11). On average, net metabolic water provided about 5% of the total water requirement in both years. The paired t test for pooled

data (Appendix C, Table 7) showed that water requirements for a lactating doe with twins were significantly higher than available dietary water in lactation ($t_{63}=16.1311$, $P < 0.001$).

Table 11. Dietary water (L/animal/day) (preformed + metabolic water) for female (41.3 kg, 1033 g DMI) and male (48.6 kg, 1215 DMI) American pronghorn antelope on Perry Mesa, Arizona in 2008 and 2009. Female water requirements were 3.4 L/animal/day during gestation, parturition and conception. Lactation requirements were 4.2 L/animal/day for 1 fawn and 4.5 L/animal/day for twins. Requirements for males were 3.9 L/animal/day year round.

Sex	Bio-period	2008		2009	
		Day	Night	Day	Night
Female	Gestation	2.59 (0.05)	2.83 (0.06)	2.43 (0.18)	2.52 (0.17)
	Parturition	2.37 (0.03)	2.49 (0.03)	2.25 (0.05)	2.30 (0.03)
	Lactation	1.64 (0.02)	1.70 (0.02)	1.36 (0.02)	1.43 (0.02)
	Conception	1.68 (0.02)	1.96 (0.05)	0.83 (0.01)	0.83 (0.01)
Male	March	3.05 (0.06)	3.33 (0.07)	2.86 (0.21)	2.96 (0.20)
	May	2.78 (0.03)	2.93 (0.03)	2.64 (0.06)	2.71 (0.03)
	June	1.93 (0.02)	2.00 (0.02)	1.61 (0.03)	1.69 (0.02)
	August	1.98 (0.03)	2.03 (0.05)	0.97 (0.01)	0.97 (0.01)

Pronghorn did not meet the calculated requirements through dietary water during any bio-periods of 2008 or 2009 (Table 11). Free water requirements of pronghorn were lowest during gestation of 2008 and highest during conception of 2009 (Table 12). Both male and female pronghorn required ≥ 0.66 (SE 0.07) L/animal/day free water at all times of the year. Night time requirements were lower by 18 ml in gestation, 10 ml in parturition, 7 ml in lactation and 15 ml in conception. In conception 2008 free water requirements were lower by 30 ml and in conception 2009 night and day free water requirements were the same.

Table 12. Mean free water requirements (L/animal/day) for female (41.3 kg, 1033 DMI) and male (48.6 kg, 1215 DMI) American pronghorn antelope on Perry Mesa, Arizona in 2008 and 2009. FWR = Total water requirements – (preformed + metabolic water).

Sex	Bio-period	2008		2009	
		Day	Night	Day	Night
Female	Gestation	0.91 (0.05)	0.67 (0.06)	1.07 (0.18)	0.98 (0.17)
	Parturition	1.13 (0.03)	1.01 (0.03)	1.25 (0.05)	1.20 (0.03)
	Lactation ^a	2.52 (0.02)	2.46 (0.02)	2.79 (0.02)	2.72 (0.02)
	Lactation ^b	2.84 (0.02)	2.79 (0.02)	3.12 (0.02)	3.05 (0.02)
	Conception	1.82 (0.02)	1.54 (0.05)	2.67 (0.01)	2.67 (0.01)
Male	March	0.94 (0.06)	0.66 (0.07)	1.12 (0.21)	1.02 (0.02)
	May	1.20 (0.05)	1.06 (0.05)	1.34 (0.06)	1.27 (0.03)
	June	2.06 (0.02)	1.99 (0.02)	2.38 (0.03)	2.30 (0.02)
	August	2.01 (0.03)	1.68 (0.05)	3.01 (0.01)	3.01 (0.01)

^a Single fawn

^b Twins

DISCUSSION

Nutrients

Crude protein. –Crude protein in pronghorn diets exceeded requirements by all measures on Perry Mesa in 2008 and 2009. The higher levels in 2008 attest to the higher quality of available forage as a result of increased precipitation. Crude protein levels between 10% and 26% found in this study corresponded with those reported by other researchers. Koerth et al. (1984) found between 9.8% and 11.4% crude protein in pronghorn diets in Texas. Smith and Malechek (1974) evaluated Utah pronghorn diets that contained between 10% and 24% crude protein. Schwartz et al. (1977) considered the crude protein the found in pronghorn forage plants between 7% and 21% to be adequate for maintenance. If

requirements are met during these sensitive bio-periods, it is reasonable to assume they will be met at other times of the year.

Structural carbohydrates. – Structural carbohydrates were higher in the drier year of 2009. They were highest in parturition 2009 and lowest in lactation 2008. Schwartz et al. (1977), studying pronghorn diets on lightly and heavily grazed ranges in Colorado, examined cell wall constituents (CWC), which provides a comparable measure of carbohydrates. CWC varied between 34% and 63% on the lightly grazed range. Diets on Perry Mesa contained between 24% and 64% structural carbohydrates. When compared to similar seasons in Schwartz et al. (1977), structural carbohydrates for Perry Mesa diets were lower than the lightly grazed range in all seasons but parturition.

Within individual plant species there is normally an inverse relationship between structural carbohydrates and protein, since structural carbohydrates increase as plants age and protein decreases (Schwartz et al. 1977, Fahey and Berger 1988). However, in pronghorn diets this pattern can be confounded by the high degree of diet selection. The higher levels of structural carbohydrates in parturition and subsequent lower levels in lactation and conception in both 2008 and 2009 may have been the result of diet switching to plants lower in structural carbohydrates. In addition, plants increase in lignin content as they mature, which may replace some of the available cellulose (Fahey and Berger 1988). Lignin was subtracted from estimates of structural carbohydrates in this study, and may be

partly responsible for the decreased structural carbohydrate percentages in lactation and conception diets (Table 8, Fig. 7).

In the absence of reliable data for NFE, I used structural carbohydrates to approximate contributions of carbohydrates to metabolic water. This may have underestimated metabolic water in several ways. The conversion from Robbins (1993) of 1 g carbohydrates to 0.56 ml metabolic water is for all anhydrous carbohydrates, and structural carbohydrates only measure cellulose and hemicellulose. These components are incompletely available to ruminants through bacterial digestion (Fahey and Berger 1988, Robbins 1993), and the resulting Volatile Fatty Acids (VFAs) are structurally more similar to lipids. Thus, metabolic water yields presented in this paper should be considered a rough estimate.

However, the total net metabolic water estimates of 101 ml/animal/day to 308 ml/animal/day were comparable to the average estimates from Whisler (1984) of 75 ± 11 ml/animal/day to 311 ± 11 ml/animal/day, and Fox (1997) between 200 ml/animal/day and 500 ml/animal/day. Regardless of differences in measurement, metabolic water generally contributes only 5% to 10% to water intake in ruminants (Swenson 1977, Whisler 1984) and rarely up to 20% (Fox et al. 2000). In this study it only contributed between 3% and 7% to total water requirements. Adjustments to the estimates are unlikely to produce different results in the model.

Preformed water. – Preformed water accounted for between 68% and 78% of total water requirements in gestation 2008, but only 20% in conception 2009. It was highest during gestation and higher in 2008 than 2009 (Table 10, Fig. 8). High levels of preformed water and crude protein during gestation and parturition indicate that pronghorn diets are the most nutritious at these times of year.

Several studies involving desert ruminants reported free water consumption inversely related to precipitation and plant moisture (Bannikov et al. 1967, Beale and Smith 1970, Nagy and Knight 1994). Estimates of percent preformed water required for pronghorn to meet water requirements on Perry Mesa were comparable to those studies, despite differences in methodology. Female pronghorn on Perry Mesa required 75% to 77% preformed water during gestation, parturition and conception and 80% to 81% preformed water during lactation. Males required between 78% and 79% year round. Beale and Smith (1970) observed that pronghorn stopped drinking when preformed water content was $\geq 75\%$. During dry seasons, African springbok antelope shifted their seasonal diets which allowed them to meet water requirements when plant moisture was $\geq 67\%$ (Nagy and Knight 1994).

Night feeding

Although night feeding could theoretically provide between 9% and 3% more water, the difference was neither statistically significant nor instrumental in allowing pronghorn to meet their requirements. Dietary water obtained from feeding at night provided only a marginal advantage which was highest when

plant moisture was high and decreased as plant moisture dropped (Tables 11 and 12). This pattern suggests that pronghorn would gain a small amount of dietary water by feeding at night in years of higher precipitation, but the advantage would decrease as drought conditions became more critical.

Fox et al. (2000) reported no significant difference between night and day preformed water in the Sonoran Desert. Despite this, Sonoran pronghorn have been reportedly observed feeding at night (Wilson 2009), as were Peninsular pronghorn (Cancino 1994). In addition this behavior has been documented in oryx (*Oryx leucoryx*), eland (*Taurotragus oryx*), African buffalo (*Syncerus caffer*), desert bighorn sheep, desert mule deer (Cain et al. 2006) and springbock antelope (Nagy and Knight 1994). The prevalence of this behavior in desert ungulate species suggests an advantage, however marginal, that may be part of a complex suite of shifting physiological and behavioral adaptations that help balance water shortages with other environmental factors such as predation risk.

Requirements by Year and Season

Preformed water for 2008 was 21% higher than 2009. In 2008 precipitation was above average and the advantage of night feeding, although small, was 3 times greater than that of 2009. However, this increase did not translate into independence from free water sources for pronghorn. If pronghorn were unable to meet water requirements through dietary water in a year with above average precipitation and moderate drought conditions, they are unlikely to meet them during years of average precipitation.

Perry Mesa pronghorn were unable to meet water requirements through dietary water alone in any season. The lowest free water requirement calculated was a nighttime estimate of 0.66 ± 0.07 L/animal/day for male pronghorn during the gestation bio-period (Table 12) when preformed water was 71.9% (Table 10). A difference this large cannot be alleviated by increasing metabolic water through ingesting greater quantities of nutrients.

Using the scaling equation from Aldeman and Dittmer (1969) (Table 1), would decrease baseline requirements to 2.5 L/animal/day for females and 2.9 L/animal/day for males, allowing pronghorn to meet water requirements through dietary water during gestation of 2008. Values from Fox et al. (2000) (Table 1) of 1.8 L/animal/day and 3.4 L/animal/day would allow female pronghorn to meet requirements during gestation and parturition, but these were calculated using different animal weights. The earlier scaling equations are likely to be less accurate since they were based on smaller pools of data that did not include wild ruminants. Nagy and Peterson (1988) found significant differences between water turnover rates in wild and domestic animals. Additionally, there is strong evidence that pronghorn, although desert adapted, have higher water turnover rates than other wild ruminants (Wesley et al. 1970, Wesley 1971, Wesley et al. 1973, Lust et al. 2007). The equation by Robbins (1993) provides the most recent, standardized estimate of water turnover available for free-ranging desert eutherian herbivores and in absence of more species specific information, can be considered the most reliable.

Season was the most important factor influencing the amount of water that pronghorn required. It is well established that animal water requirements increase with rising temperatures (Whisler 1984, Squires 1988, Yoakum 1994, Olsson 2005). The model results show greater deficits in the summer when ambient temperatures are high and humidity and plant moisture are low, and females require greater amounts of water for lactation (Tables 11 and 12). The deficits of between 0.66 ± 0.07 L/animal/day and 3.12 ± 0.02 L/animal/day are comparable to values reported by many of the previous researchers (Table 13), despite the different methodological tools used to measure water requirement. According to the literature sources, pronghorn are reported to drink roughly 1 L/animal/day of free water in cool, wet seasons (Sundstrom 1968, Whisler 1984, Yoakum 1994, Fox 1997). When ambient temperatures were greater, pronghorn were estimated to require around 3 L/animal/day (Sundstrom 1968, Whisler 1984, Beale and Holmgren 1974, Yoakum 1994, Fox 1997).

This pattern corresponds with pronghorn use of free water. During 2009 I found that pronghorn used tanks significantly more ($P \leq 0.05$) in July than May or August (unpublished data). Similar seasonal use patterns were reported for numerous other desert animals as well (Rosenstock et al. 2004, Cain et al. 2006, O'Brian et al. 2006).

Table 13. Estimates of water consumption and water requirements from literature sources.

Source	Measurement	Estimate (L/animal/day)	Notes
Sundstrom 1968	Water consumption	0.34	May-June
		4.5	August
Beale and Smith 1970	Water consumption	2.8	Average over 4 year.
Wesley et al. 1970	Total water requirement	3.4	Average under laboratory conditions.
Beale & Holmgren 1974	Water consumption	1.9-7.6	Summer
Whisler 1984	Water consumption	1.0	Hydrated animals in winter
		3.2	Hydrated animals in summer
Yoakum 1994	Recommendations based on literature review	0.9	Wet season
		3.81	Dry season
Cain et al. 2006	Total water requirement	1.9-2.4	General, depending on weight
Fox 1997	Free water requirement at Charlie Bell site *	0.2-2.3	Feb. – May
		0.7-2.1	June – September

* Water balance models from the Agua Dulce study site showed Sonoran pronghorn (24 kg and 63 kg) met water requirements in all seasons (Fox 1997). This was later revised in Fox et al. (2000).

Seasonal precipitation and resulting plant moisture content may play a role in fawn survival and ultimately herd health. Beale and Smith (1970) observed that fawns reared in years with high precipitation with succulent forage appeared healthier, but a regression analysis showed little relationship between the previous year's precipitation and fawn survival. Brown et al. (2002) found that winter precipitation correlated with higher fawn recruitment in some locations of

Arizona and New Mexico, but not others. Brown et al. (2006) found a strong correlation between midsummer drought and fawn mortality. Oftedal (1985) stated that “Fertility of the herd as a whole is closely correlated to body condition of the female, which in turn is a function of the food supply.” Perhaps there is a more direct link between summer precipitation, plant moisture, and the ability of pronghorn does to meet the milk demands of a growing fawn at peak lactation. In the case of water deprivation during this time physiological and behavioral adaptations may allow pronghorn does to go short periods of time without water if necessary (Whisler 1984, Olsson 2005, Lust et al. 2007). However, longer-term lack of water is likely to negatively affect milk supply at critical times (Beale and Holmgren 1974, Squires 1988, Olsson 2005) and decrease fawn recruitment.

Pronghorn must balance free water requirements against the risk of predation. In semi-desert grasslands of central Arizona, mountain lion predation on adult pronghorn is substantial where ranges overlap (Ockenfels 1994a). Livestock tanks and other water sources can provide vegetative cover that may conceal predators, effectively creating or extending an area of range overlap. In July and August of 2009 I found 2 dead pronghorn bucks <100 m from livestock tanks; both animals had the front of their skulls crushed (personal observation). Mountain lions had been photographed utilizing both these tanks that August (Tluczek, unpublished data). These water sources on Perry Mesa were heavily vegetated and adjacent to either an ephemeral stream or more rugged terrain, and provided both the draw of water in a dry monsoon and the hiding cover needed to

stalk prey. Increased free water demands during lactation mean pronghorn does must expose themselves and fawns to predation risk more frequently. Conversely, an increase in dietary water may not alleviate the water requirement, but could reduce the time spent at water tanks, thus decreasing exposure to predation.

The Influence of Location and Diet

Pronghorn ability to meet water requirements through dietary sources is influenced by local climate and plant communities. Whisler (1984) stated that “Drinking water requirements for pronghorn vary from one location to another depending on forage succulence, climate, age, activity patterns, and physiological and behavioral characteristics.” Cancino (1994) noted that peninsular pronghorn persist in the complete absence of free water. Night foraging may be of greater advantage in the more humid conditions of coastal Mexico where preformed water and condensation on plants may be significantly higher (Yoakum 1994, D. E. Brown, personal communications).

Fox et al. (2000) reported that on 1 of 2 study sites, both male and female Sonoran pronghorn were able to meet water requirements through dietary sources in the springtime, where dissimilarities in micro climate and available forage produced drastically different results. Cholla fruit, which can contain up to 86% water, was key to pronghorn’s ability to meet water requirements through dietary sources (Fox 1997). Given current diet information for Perry Mesa, pronghorn would need to consume 55% prickly pear in order to increase dietary water by 1 L/animal/day. This is unlikely, as pronghorn diets in grasslands rarely contain

>28% prickly (Sexton et al. 1981, Stephenson et al. 1985, Smith et al. 1998, Brown et al. 2008). Brown et al. (2008) found an average of 3% prickly pear in bio-periods corresponding to this study, with 10% in June of 2003 and none in June of 2005. Furthermore, prickly pear and cholla are low in nutritional value and generally taken when forbs are not available (AZGFD 1981). Since water is supplied year round on Perry Mesa, there is little reason for it to feature prominently in the diets. It is possible that access to free water may allow pronghorn to forego use of lower quality, water rich plants for a higher quality diet. Whether it was utilized more before the establishment of livestock tanks and water catchments is unknown.

Robbins (1993) stated that adding water can only increase a population if 1) water is a limiting factor and 2) other needs are in excess. The results for pronghorn on Perry Mesa show that in years of favorable climactic and range conditions, dietary water does not meet estimated requirements and is therefore limiting. One of the major nutrients, protein, was available in excess. Based on this model it is reasonable to say freestanding water was necessary for pronghorn on Perry Mesa during years of above and below average precipitation, and is necessary for herd health. However, pronghorn free water requirements are a function of vegetation, season, and precipitation. Water may not be a limiting factor in areas where greater precipitation is available, or where succulents are an established part of the diet.

Evaluation of Water Model

In constructing this model, I made every attempt to include the most pertinent and up to date information available for estimating pronghorn water requirements. However, there is a paucity of information in several areas. Additional water requirements during gestation, parturition, and conception may come from a number of sources, including: 1) water needed for pregnant does to fuel metabolic processes for growth of reproductive tissue in gestation; 2) water lost in blood and amniotic fluids during parturition and 3) increased water needed for both males and females for rise in energy demand associated with breeding. However, whether these potential water losses are mitigated by other physiological and behavioral strategies is unknown.

Evidence suggests that water requirements for female pronghorn may be greater than those of males year round. Wesley et al. (1970) found the 2 female pronghorn in their study to have higher water turnover rates than the 2 males. Knox et al. (1969) found a similar pattern with mule deer. Higher body temperatures may be indicative of higher metabolic rate and thus water turnover. Lust et al. (2007) found that female pronghorn abdominal temperatures varied an average of 1.8 °C in a day, which was greater than the male measured in the study. Although samples sizes were small for Wesley et al. (1970) and Lust et al. (2007), the pattern warrants further investigation.

Leopold (1933) suggested that in order to know the true water requirement, one must quantify the requirement for minimal maintenance. However, Nagy (2004) stated “When animals are not eating or drinking enough to maintain weight, their rates of water intake are relatively low and not representative of minimum maintenance needs.” Water requirements for maintaining recruitment rates must exceed the basic, minimum requirements for survival. Evaluating pronghorn water needs based on scaling equations developed from healthy animals provides estimates for adequate body condition, which is conducive to managing for higher recruitment. This model provides a conservative estimate of pronghorn water requirements based on ecological data and known equations with high predictive value (Robbins 1993, Hackmann 2011). It is currently the most simple and broadly applicable method for modeling pronghorn water requirements, and can easily be adjusted to estimate free water requirements of other wild ruminants.

Chapter 6

MANAGEMENT IMPLICATIONS

Plant Monitoring

Forbs make up the vast majority of pronghorn diets in optimal conditions and are highly variable as a group. The composition of available forbs on Perry Mesa shifts between years, with different species dominating in response to environmental variables (D. D. Warnecke, personal communications). In this study longleaf false goldeneye dominated parturition and lactation diets, but this may change in subsequent years. Given the variable nature of this forage class and the well-established preference for it as a whole, monitoring forbs as a forage class is recommended. This would provide an indicator of range condition as well as potential nutrition for pronghorn. Monitoring for biannual forbs that persist into the lactation period would provide managers with an indicator of diet quality at this critical time.

Several perennial plants in the Perry Mesa pronghorn diets emerged as important for monitoring. These are Wright's buckwheat and fairyduster. Wright's buckwheat was the most dominant shrub during the gestation bio-period. There is strong indication that it is a survival plant in less than optimal conditions. Fairyduster is the most dominant shrub during the conception bio-period, which corresponds to its growing season and thus higher protein content. Several other shrubs were present in amounts over 1% throughout the year, but were not

consistent between years or bio-periods. Monitoring efforts should focus on these 2 shrubs, which also provide nutrition for deer.

Managing Water Sources

The diet model showed that pronghorn on Perry Mesa were unable to meet their water requirements at any of the critical bio-periods in either 2008 or 2009. While feeding during the night provided a marginal advantage, it was not enough for either male or female pronghorn to subsist without free water given the available diet information. Female pronghorn were especially vulnerable during peak lactation in June, when relative humidity and precipitation were lowest and temperatures and water demand were highest.

Managing water sources for pronghorn currently involves 3 possible actions: 1) building additional waters 2) maintaining current water sources, or 3) taking no action. On Perry Mesa 10 of the 14 water sources are earthen tanks, 2 are windmill fed troughs, and 2 are AZGFD water catchments. All sources are self-sustaining as long as they are maintained. Given the pronghorn need for free water and the status of Perry Mesa as a premier fawning ground for GMU 21, I recommend ensuring that water is available in key locations during critical biological periods, especially during lactation. This would involve a step-wise approach of 1) monitoring, 2) maintenance and 3) provisioning if necessary.

Monitoring. – Water sources should be monitored in the summer to ensure that pronghorn have access to free water during peak lactation and conception.

Pronghorn lactation period can last anywhere from early May through July. Many of the earthen tanks go dry in June and earlier during dry years, and remaining water may reach salinity levels that make it unpalatable. If water is found to be lacking or does not meet quality standards, measures should be taken to provide it.

Maintenance. – Maintain windmill-fed troughs and catchments with occasional repair as needed. Earthen tanks should be repaired if erosion becomes a problem.

Provisioning. – In dry years it may be prudent to provide water during critical bio-periods to relieve reproductive stress. Most sources recommend that pronghorn have access to a water source every 1.6-8.0 km (Krausman et al. 2006). On Perry Mesa water sources are present nearly every 1.5 miles, but not all contain water in critical bio-periods (personal observation). Key water sources should be selected for ease of accessibility, visibility, and ability to retain enough water to avoid salinity problems. If provisions are necessary, efforts should focus on selected tanks that provide high visibility and retain water. Perry Mesa tank and South Campbell tank may be worth consideration. Adding new tanks or catchments on Perry Mesa would be unlikely to provide any real advantage. Since many tanks retain water in all but the dry period, water provisioning may only be necessary during the lactation period from May through July, depending on precipitation levels.

Additional Work

Additional data collection. – Failure of pronghorn to meet water requirements through dietary water during these biological periods raises questions about their ability to meet requirements at other times of the year, such as the dry season between September and December. An evaluation of dietary composition, quality, and preformed water for each month of the year would provide a more complete baseline data set.

Extrapolation of results. – This study was conducted on a single range and therefore is not representative of all grasslands. However, the model results, which were based on generalized calculations using average body weights, do indicate that pronghorn can meet water requirements if their diets contain $\geq 76\%$ water. This estimate is comparable to results from of Beale and Smith (1970), and Nagy and Knight (1994). In locations where water provisioning is being considered, it may be prudent to evaluate the moisture content of known pronghorn forage plants prior to supplying water. In addition, the contribution of snow to the pronghorn water budget should be evaluated for northern populations (Yoakum 1994).

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APPENDIX A

PRONGHORN ANTELOPE DIET COMPOSITION ON PERRY MESA,
ARIZONA IN 2008 AND 2009

Fig. 1 Mean relative % diet composition by species for American pronghorn antelope on Perry Mesa, Arizona in 2008 and 2009.

Common Name	Scientific Name	2008				2009			
		G	P	L	C	G	P	L	C
Forbs									
Trailing Windmills	<i>Allionia incarnate</i>	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00
Ragweed	<i>Ambrosia</i> sp.	0.24	2.85	0.87	1.63	0.11	9.73	3.16	1.35
Fiddleneck	<i>Amsinckia</i> sp.	22.97	2.52	0.20	0.00	13.54	1.48	0.00	0.00
Field Anoda	<i>Anoda pentaschista</i>	0.00	0.00	0.00	0.00	0.15	0.00	0.00	0.00
White Sagebrush	<i>Artemisia ludoviciana</i>	0.00	1.30	0.03	0.17	0.00	0.00	0.00	0.00
Spider Milkweed	<i>Asclepias asperula</i>	0.00	0.00	0.00	0.00	0.19	0.00	0.00	0.00
Smallflowered Milkvetch	<i>Astragalus nuttallianus</i>	0.00	0.19	0.12	0.89	0.67	0.01	0.10	0.41
Ashen Milkvetch	<i>Astragalus tephrodes</i>	0.00	0.45	0.04	0.00	0.00	0.00	0.04	0.00
Wheelescale Saltbush	<i>Atriplex cf. elegans</i>	0.00	0.00	0.16	0.00	0.00	0.00	0.00	0.00
Desert Marigold	<i>Baileya multiradiata</i>	0.67	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Scarlet Spiderling	<i>Boerhavia coccinea</i>	0.00	0.00	0.00	0.00	1.23	0.28	0.00	0.00
Forget-me-not Family	Boraginaceae	0.18	0.00	0.00	0.00	0.93	0.00	0.00	0.00
Mustard family	Brassicaceae	0.19	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Northwestern Indian Paintbrush	<i>Castilleja angustifolia</i>	0.00	0.00	0.02	0.16	0.07	0.00	0.19	0.00
Shepherd's Purse	<i>Capsella bursa-pastoris</i>	0.01	0.01	0.00	0.00	0.00	0.01	0.00	0.00
Head Sandmat	<i>Chamaesyce capitellata</i>	0.13	0.00	0.79	1.62	0.00	0.61	0.58	0.00
Goesfoot	<i>Chenopodium</i> sp.	1.11	2.14	1.56	0.01	0.33	0.58	0.65	0.16
Rose Heath	<i>Chaetopappa ericoides</i>	0.00	0.60	0.76	0.00	0.22	0.00	0.00	0.00
Texas Bindweed	<i>Convolvulus equitans</i>	0.00	0.00	0.12	0.00	0.39	0.00	1.09	0.00
American Wild Carrot	<i>Daucus pusillus</i>	0.00	0.00	0.00	0.00	0.10	0.00	0.00	0.00
Western Tansymustard	<i>Descurainia pinnata</i>	0.91	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Table (continued)

Common Name	Scientific Name	2008				2009			
		G	P	L	C	G	P	L	C
Tansymustard	<i>Descurainia</i> sp.	0.21	0.11	0.00	0.00	0.43	0.01	0.00	0.00
Tall Mountain Larkspur	<i>Delphinium scaposum</i>	0.19	0.38	0.00	0.00	0.86	0.62	0.00	0.00
Herb Sophia	<i>Descurainia sophia</i>	0.40	0.00	0.00	0.00	0.34	0.00	0.00	0.00
Bluedicks	<i>Dichelostemma capitatum</i>	0.06	0.00	0.00	0.23	0.03	0.54	0.00	0.00
California Draba	<i>Draba cuneifolia</i>	0.92	0.15	0.00	0.00	0.00	0.00	0.00	0.00
Redstem Stork's Bill	<i>Erodium cicutarium</i>	0.33	2.99	0.08	0.00	2.70	3.65	0.00	0.20
Flatcrown Buckwheat	<i>Eriogonum deflexum</i>	0.01	0.00	0.28	0.00	0.00	0.00	0.00	0.00
Spreading Fleabane	<i>Erigeron divergens</i>	0.00	0.43	0.52	2.06	0.79	1.71	1.13	0.25
Miniature Woollystar	<i>Eriastrum diffusum</i>	1.29	0.47	0.03	0.00	0.66	3.79	0.01	0.00
Spreading Wallflower	<i>Erysimum repandum</i>	0.15	0.49	0.00	0.00	0.00	4.76	0.15	0.00
Fringed Twinevine	<i>Funastrum cynanchoides</i>	0.00	0.19	0.00	0.00	0.00	0.00	0.00	0.00
Mexican Bedstraw	<i>Galium mexicanum</i>	1.01	0.35	1.53	0.27	0.93	0.03	2.59	0.00
Longleaf False Goldeneye	<i>Heliomeris longifolia</i> var. <i>annua</i>	1.20	11.52	44.77	48.17	1.66	27.84	58.95	28.58
Babyslippers	<i>Hybanthus verticillatus</i>	0.00	0.19	0.00	0.00	0.01	0.00	0.00	0.99
Arizona Poppy	<i>Kallstroemia grandiflora</i>	0.00	0.00	0.00	0.00	0.37	0.00	0.00	0.00
Whitedaisy Tidytips	<i>Layia glandulosa</i>	0.00	0.01	0.43	0.00	0.22	0.00	0.00	0.00
Golden Linathus	<i>Leptosiphon aureus</i>	0.00	3.34	0.00	0.00	0.00	0.00	0.00	0.00
Pepperweed	<i>Lepidium</i> sp.	0.58	1.22	0.20	0.00	3.63	0.46	0.00	0.00
Lewis Flax	<i>Linum lewisii</i>	0.00	0.00	0.00	0.00	1.04	0.00	0.00	0.00
Foothill Deervetch	<i>Lotus humistratus</i>	0.00	0.00	0.06	0.00	0.00	0.00	0.01	0.00
Nevada Biscuitroot	<i>Lomatium nevadense</i>	0.00	0.00	0.00	0.00	0.00	1.37	0.00	0.00
Lupine	<i>Lupinus</i> sp.	11.58	4.60	0.13	0.08	5.04	7.21	0.55	0.75

Table (continued)

Common Name	Scientific Name	2008				2009			
		G	P	L	C	G	P	L	C
Tansyaster	<i>Machaeranthera</i> sp.	0.00	0.00	0.67	0.00	0.00	0.00	0.25	0.02
Adonis Blazingstar	<i>Mentzelia multiflora</i>	0.01	0.62	0.00	0.00	0.00	0.00	0.00	0.00
Slender Phlox	<i>Microsteris gracilis</i>	0.11	0.00	0.00	0.00	0.10	0.00	0.73	0.00
Seep Monkeyflower	<i>Mimulus guttatus</i>	0.93	0.19	0.00	0.00	0.00	0.00	0.00	0.00
Narrowleaf Four O'clock	<i>Mirabilis linearis</i>	0.00	0.00	0.00	0.00	0.00	0.25	0.00	0.00
Lindley's Silverpuffs	<i>Microseris lindleyi</i>	0.00	0.00	0.01	1.05	0.00	0.72	0.00	0.00
Texas False Garlic	<i>Nothoscordum texanum</i>	0.00	0.00	0.00	0.00	0.00	0.54	0.00	0.00
Hooker's Evening Primrose	<i>Oenothera elata</i> ssp. <i>hirsutissima</i>	0.00	0.00	0.00	0.00	0.49	0.00	0.00	0.00
Evening Primrose	<i>Oenothera</i> sp.	2.03	2.80	1.01	2.77	0.39	0.96	2.41	14.05
Beardlip Penstemon	<i>Penstemon barbatus</i>	0.25	1.91	0.28	0.00	0.08	0.00	0.00	0.00
Desert Penstemon	<i>Penstemon pseudospectabilis</i>	0.00	0.24	0.00	0.00	0.25	0.00	0.00	0.00
Moth Combseed	<i>Pectocarya setosa</i>	0.19	0.29	0.31	0.00	0.10	0.33	0.00	0.00
Distant Phacelia	<i>Phacelia distans</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03
Arizona Popcornflower	<i>Plagiobothrys arizonicus</i>	0.05	0.00	0.03	0.08	0.00	0.00	0.00	0.00
Woolly Plantain	<i>Plantago patagonica</i>	1.12	15.39	29.33	3.28	9.38	8.20	6.15	9.61
Prostrate Knotweed	<i>Polygonum aviculare</i>	0.67	0.00	0.00	0.00	0.30	0.00	0.00	0.00
Shrubby Purslane	<i>Portulaca suffrutescens</i>	0.00	0.00	0.02	2.55	0.00	0.00	0.00	0.22
Prickly Russian Thistle	<i>Salsola tragus</i>	0.00	5.85	0.52	0.01	0.00	11.45	0.61	0.00
Twinleaf Senna	<i>Senna bauhinioides</i>	0.00	0.00	0.00	0.00	0.15	0.00	0.00	0.10
London Rocket	<i>Sisymbrium irio</i>	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.00
Silverleaf Nightshade	<i>Solanum elaeagnifolium</i>	0.03	0.15	0.03	0.38	0.00	0.04	0.10	0.00
Buffalobur Nightshade	<i>Solanum rostratum</i>	1.57	2.38	0.30	0.00	0.37	0.10	0.34	0.00

Table (continued)

Common Name	Scientific Name	2008				2009			
		G	P	L	C	G	P	L	C
Rancheria Clover	<i>Trifolium albopurpureum</i>	0.13	0.16	0.21	0.76	0.33	0.08	3.75	0.09
Pinpoint Clover	<i>Trifolium gracilentum</i>	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.61
Bigbract Verbena	<i>Verbena bracteata</i>	5.00	3.04	2.21	2.32	1.47	2.46	2.40	3.94
Neckweed	<i>Veronica peregrine</i>	0.00	0.00	0.00	0.11	0.00	0.00	0.00	0.00
Sleepydaisy	<i>Xanthisma pinnatifida</i>	0.00	0.15	0.04	0.00	0.00	0.00	0.00	0.00
Unknown forbs		0.22	21.88	29.23	9.24	25.58	17.26	9.30	11.29
Shrubs									
Dwarf Indian Mallow	<i>Abutilon parvulum</i>	0.13	0.03	0.00	0.12	0.00	0.02	0.00	0.01
Catclaw Acacia	<i>Acacia greggii</i>	0.00	0.01	0.06	0.31	0.21	0.01	0.04	0.91
Thurber's Desert Honeysuckle	<i>Anisacanthus thurberi</i>	0.15	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Common Sandweed	<i>Athysanus pusillus</i>	0.00	0.00	0.00	1.22	0.00	0.00	0.00	0.00
Desertbroom	<i>Baccharis sarothroides</i>	0.36	0.03	0.00	0.00	0.57	0.00	0.00	0.00
Fairyduster	<i>Calliandra eriophylla</i>	0.14	0.01	1.18	1.39	0.04	0.00	1.09	2.13
Netleaf Hackberry	<i>Celtis laevigata var. reticulata</i>	0.44	0.01	0.01	0.00	1.67	0.00	0.00	0.00
Eastern Mojave Buckwheat	<i>Eriogonum fasciculatum</i>	0.36	0.01	0.01	0.00	0.21	0.00	0.00	0.45
Wright's Buckwheat	<i>Eriogonum wrightii</i>	7.45	0.20	0.04	0.41	8.80	0.34	0.02	0.78
Beeblossom	<i>Gaura</i> sp.	0.09	0.22	0.00	0.01	0.04	0.02	0.01	0.00
Broom Snakeweed	<i>Gutierrezia sarothrae</i>	0.03	0.00	0.19	0.04	0.14	0.01	0.38	0.01
Juniper	<i>Juniperus</i> sp.	0.00	0.00	0.06	0.00	0.34	0.00	0.00	1.70
Snapdragon Penstemon	<i>Keckiella antirrhinoides</i>	0.00	0.00	0.01	0.00	0.03	0.00	0.00	0.00
Littleleaf Ratany	<i>Krameria erecta</i>	0.00	0.02	0.01	0.00	0.02	0.00	0.00	0.00
Rough Menodora	<i>Menodora scabra</i>	0.00	0.02	0.11	0.05	0.18	0.00	0.14	1.12

Table (continued)

Common Name	Scientific Name	2008				2009			
		G	P	L	C	G	P	L	C
Velvet Mesquite	<i>Prosopis velutina</i>	0.00	0.00	0.02	0.01	0.00	0.00	0.01	0.04
Wingleaf Soapberry	<i>Sapindus saponaria</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.08
Globemallow	<i>Sphaeralcea</i> sp.	0.02	0.04	0.01	0.16	0.03	0.02	0.07	0.02
Rusby's Globemallow	<i>Sphaeralcea rusbyi</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Unknown shrubs		0.04	3.71	0.23	1.01	0.68	3.40	0.18	0.73
Grass									
Sixweeks Threawn	<i>Aristida adscensionis</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Spidergrass	<i>Aristida ternipes</i>	0.08	0.00	0.00	0.40	0.09	0.00	0.00	0.00
Wild Oat	<i>Avena fatua</i>	0.00	0.00	0.00	0.00	0.06	0.00	0.00	0.01
Needle Grama	<i>Bouteloua aristidoides</i>	0.06	0.00	0.00	0.02	0.00	0.00	0.00	0.00
Cane Bluestem	<i>Bothriochloa barbinodis</i>	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Sideoats Grama	<i>Bouteloua curtipendula</i>	0.00	0.00	0.00	0.00	0.06	0.00	0.00	0.00
Hairy grama	<i>Bouteloua hirsute</i>	0.04	0.00	0.00	0.00	0.01	0.00	0.00	0.00
Field Brome	<i>Bromus japonicas</i>	0.09	0.00	0.00	0.15	0.00	0.01	0.01	0.02
Lehmann Lovegrass	<i>Eragrostis lehmanniana</i>	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00
Curly-Mesquite	<i>Hilaria belangeri</i>	0.11	0.00	0.00	0.00	0.00	0.00	0.01	0.00
Barley	<i>Hordeum</i> sp.	0.09	0.00	0.00	0.00	0.90	0.01	0.01	0.00
Barley (immature)	<i>Hordeum</i> sp. (immature)	2.50	0.04	0.00	0.00	12.05	0.03	0.02	0.00
Seaside Barley	<i>Hordeum murinum</i> (mature)	0.00	0.00	0.00	0.01	0.12	0.03	0.00	0.00
Little Barley	<i>Hordium</i> cf. <i>pusillum</i> (mature)	0.06	0.16	0.00	0.07	1.18	0.07	0.07	0.03
Tobosagrass	<i>Pleuraphis mutica</i>	0.13	0.00	0.00	0.02	0.05	0.00	0.00	0.00
Mucronate Sprangletop	<i>Leptochloa panacea</i>	0.60	0.02	0.02	0.11	0.09	0.01	0.01	0.04

Table (continued)

Common Name	Scientific Name	2008				2009			
		G	P	L	C	G	P	L	C
Vine Mesquite	<i>Panicum obtusum</i>	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00
Unknown grass		5.03	0.05	0.04	0.63	2.41	0.07	0.15	0.24

APPENDIX B

PRONGHORN ANTELOPE WATER BALANCE MODEL

1. Water requirements (Fox et al. 2000)

a. Free water requirement

$$FWR(ml) = TWR(ml) - (PW(g) + NMW(g))$$

Where:

TWR = total water requirement

PW = Preformed water

NMW = Net metabolic water

b. Total Water Requirements

$$TWR (ml) = BWR(ml) + LWR(ml)$$

Where:

BWR(ml) = Baseline water requirements

LWR(ml) = Lactation water requirements

c. Baseline Water Requirements (Robbins 1993)

$$BWR(ml) = 0.71 \times W(g)^{0.80}$$

Where:

W = Animal weight (g)

2. Water required for lactation

a. Milk yield (Hackmann 2011)

$$MY = 3.2 \times 10^{-2} M^{0.89}$$

Where:

M = maternal body weight (kg)

- b. Lactation Water Requirements, 1 fawn

$$LWR \text{ single fawn } (ml) = MY(ml) \times 0.75$$

- c. Lactation Water Requirements, twins

$$LWR \text{ twins } (ml) = (MY(ml) \times 1.49) \times 0.75$$

3. Preformed Water (ml)

- a. Preformed water

$$PW (ml) = AFI - DMI$$

Where:

AFI = As Fed Intake

DMI = Dry Matter Intake

- b. As Fed Intake

$$AFI(g) = DMI(g) \div (1 - \% DPW)$$

Where:

DPW = Dietary Preformed Water

- c. Dietary Preformed Water

$$\% DPW(ml) = \sum (\% PM \text{ species}_{a\dots z}) \times (\% DC \text{ species}_{a\dots z})$$

Where:

PM = Plant moisture

DC = Dietary composition, percent of plant species

- d. Dry Matter Intake (g)

$$DMI(g) = W(g) \times 0.025$$

- e. Dry Matter Intake adjusted for additional protein requirements

$$\text{Adjusted DMI} = (\%CP \div 100) \div PR (g)$$

Where:

CP = Crude Protein

PR = Protein requirements (g) beyond availability

4. Net Metabolic Water (ml)

$$NMW(ml) = (CP(g) \times 0.4) + (SC(g) \times 0.56) + (L(g) \times 1.07) \times 0.5$$

Where:

CP = Crude Protein

SC = Structural Carbohydrates

L = Lipids

5. Nutrients per diet (g)

- a. Crude Protein

$$CP (g) = \sum (\%CP \text{ species}_{a\dots z}) \times (\%DC \text{ species}_{a\dots z}) \times DMI$$

- b. Structural Carbohydrates (SC)

$$SC (g) = (\% \text{ cellulose} + \% \text{ hemicellulose}) \times DMI$$

- c. Lipids

$$L(g) = \% L \times DMI$$

115APPENDIX C

STATISTICAL ANALYSIS RESULTS OF DIET COMPOSITION AND
NUTRIENT QUALITY OF PRONGHORN ANTELOPE ON PERRY MESA
DURING 2008 AND 2009

Table 1. Completely random two factor factorial ANOVA for species richness of American pronghorn antelope diets on Perry Mesa, Arizona 2008 and 2009.

Source	df	SS	MS	F	P	Sig
Total	31	1124.875				
Cells	7	697.375				
Year	1	128	128	7.185965	0.005576	**
Period	3	403.625	134.5417	7.553216	0.000743	***
Year:Period	3	165.75	55.25	3.101754	0.045137	*
Within error	24	427.5	17.8125			

Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Table 2. Non parametric ANOVA for forage class differences in American pronghorn antelope diets on Perry Mesa, Arizona 2008 and 2009.

Factor	DF	SS	MS	H	P value	Sig
Year	1	70	70	0.0902062	0.764	
Period	3	4068	1356	5.242268	0.022	*
Forage	2	54087	27044	69.699742	0.000	***
Y:P	3	38	13	0.0489691	0.825	
Y:F	2	230	115	0.2963918	0.586	
P:F	6	11548	1925	14.881443	0.000	***
Y:P:F	6	424	71	0.5463918	0.460	
Residuals	72	3255	45			
Total MS	776					
Total observations	96					

Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Table 3. Non parametric ranked means three factor factorial NOVA for species composition of American pronghorn antelope diets on Perry Mesa, Arizona 2008 and 2009.

	DF	SS	MS	H	P value	Sig
Year	1	2.42E+06	2416820	4.33E+00	0.037	*
Period	3	1.34E+07	4477340	23.99823	0.000	***
Species	105	7.05E+08	6717556	1262.593	0.000	***
Y:P	3	3.29E+06	1095693	5.892102	0.015	*
Y:S	105	4.39E+07	417866	7.86E+01	0.000	***
P:S	315	3.10E+08	985156	555.1829	0.000	***
Y:P:S	315	1.30E+08	412756	232.8186	0.000	***
Residuals	2544	6.86E+08	269666			
Total MS	5.58E+05					
Total observations	3392					

Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Table 4. Completely random two factor factorial ANOVA for dietary protein for American pronghorn antelope on Perry Mesa, Arizona in 2008 and 2009.

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Year	1	25281	25281	1663.3	< 2e-16 ***
Period	3	42450	14150	930.9	< 2e-16 ***
year:period	3	5113	1704	112.1	2.97e-14 ***
Residuals	24	365	15		

Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Table 5. Completely random two factor factorial ANOVA for dietary fiber for American pronghorn antelope on Perry Mesa, Arizona in 2008 and 2009.

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	Sig.
Year	1	46657	46657	3.1975	0.0863847	.
Period	3	386806	128935	8.8361	0.0003998	***
year:period	3	24975	8325	0.5705	0.6398383	
Residuals	24	350205	14592			

Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Table 6. Non-parametric ranked mean three factor factorial split-plot ANOVA for preformed water in American pronghorn antelope diets on Perry Mesa, Arizona in 2008 and 2009.

Error: Whole	Df	Sum Sq	Mean Sq	H	P	Sig
Year	1	2425.6	2425.6	7.558051	0.005974	**
Period	3	17248.8	5749.6	53.74641	2.28E-13	***
Y:P	3	545.2	181.7	1.698816	0.192443	
Residuals	24	1198.5	49.9			

Error: Within	Df	Sum Sq	Mean Sq	H	P	Sig
Time	1	276.391	276.391	0.861221	0.353397	
T:Y	1	58.141	58.141	0.181165	0.670374	
T:P	3	4.297	1.432	0.013389	0.907881	
T:Y:P	3	45.047	15.016	0.140364	0.707919	
Residuals	24	37.125	1.547			
Total MS	320.9293					
Total	64					
Observations						

Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Table 7. Paired student's t test for water requirements* and dietary water of doe American pronghorn antelope on Perry Mesa, Arizona in 2008 and 2009.

Student's t	Df	P	CI 95%	CI 95%
16.1311	63	< 2.2e-16	1.571811	2.016314

* Water requirements in lactation calculated for doe with twins.

