

# Evaluation of Factors Potentially Influencing a Desert Bighorn Sheep Population

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## ABSTRACT

We studied a desert bighorn sheep (*Ovis canadensis*) population in the Mazatzal Mountains (primary study area) in central Arizona and population indices on reference areas between 1989 and 2003. We evaluated disease exposure and nutritional status of desert bighorn sheep, vegetation parameters, predator diets, and mountain lion (*Puma concolor*) harvest and abundance (1999–2003) and mountain lion predation (1995–2003) as factors potentially affecting desert bighorn sheep and population parameters. We measured rainfall monthly, monitored demography and relative abundance of desert bighorn sheep using aerial surveys, captured and placed radio collars on desert bighorn sheep, and collected samples of blood, parasites, and other pathogenic agents from captured animals. We measured mineral content, relative use, and structural composition of vegetation and determined diets of desert bighorn sheep adults and lambs, dietary intakes of nitrogen (FN), 2,6-diaminopimelic acid (FDAPA), neutral detergent fiber, and minerals using fecal analyses. We incorporated mountain lion reductions as an experimental element, monitored harvest, and used track surveys as an index of relative abundance of the predator and monitored radio-collared desert bighorn sheep to determine mortalities and causes of death. We determined diets of bobcats (*Lynx rufus*), coyotes (*Canis latrans*), and mountain lions using fecal analyses. Drought conditions occurred during summer (July–September) and winter (November–April) during 4 and 3 years, respectively, between 1999 and 2003. Annual surveys indicated that the Mazatzal Mountains population declined during drought between 1994 and 1997, experienced low growth and lamb production coincident with above-normal rainfall in 1998 and drought in 1999, and exhibited higher growth, production, and productivity during 2000–2003 despite persistent drought conditions during this period. We observed no clinical symptoms of disease in radio-collared desert bighorn sheep, and hematological and other evidence of exposure to disease agents was unremarkable. Population indices on the primary study and reference areas were positively correlated with winter (November–April) rainfall. We found no evidence of forage overutilization on the primary study area. Rainfall on Mazatzal Mountains was associated with differences in primary production, particularly of forbs, forage mineral concentrations, and diets, nutritional status, and demographic attributes of desert bighorn sheep between 1999 and 2003. Higher winter rainfall was associated with higher forb growth, and higher rainfall was associated with higher concentrations of P and Se but lower levels of Fe in browse; higher concentrations of Ca, P, and Zn in forbs; and higher levels of P, Se, and Zn in grasses. Narrower mean Ca:P ratios of browse and forbs were associated with higher rainfall. Diets of desert bighorn sheep adults and lambs generally were similar, particularly near summer, and forbs tended to predominate in diets during wetter and drier years. Higher winter rainfall was associated in adult feces with more prolonged winter-to-spring increases in FN and FDAPA concentrations, higher fecal phosphorus, lower fecal Ca levels, and narrower fecal Ca:P and Na:K ratios, but levels of fecal Na increased during the driest year. Higher winter rainfall corresponded in lamb feces with higher levels of FN, FDAPA, and fecal P; lower concentrations of fecal Ca; and narrower fecal Ca:P ratios. Thus, we hypothesized that diets and nutritional status of desert bighorn sheep adults and lambs tended to correspond with rainfall patterns and associated differences in relative abundance and mineral content of forages. We found no evidence that bobcats or coyotes preyed on or scavenged desert bighorn sheep. Decline of desert bighorn sheep abundance during 1994–1997 was greater than declines on reference areas lacking mountain lions despite continually higher, and a lesser decline in, winter rainfall on the primary study area. In comparison, population indices on a reference area and on Mazatzal Mountains increased between 1999 and 2003 in association with predator reductions and lower abundance of mountain lions and predation of radio-collared animals despite continued occurrences of drought during this period. We thus identified 2 proximate factors that likely acted to influence demographic trends of the Mazatzal Mountains desert bighorn sheep population: nutritional status (higher rainfall [ultimate factor] was associated with higher availability and differences in mineral content of forages and improved indices of desert bighorn sheep nutritional status) and predation by mountain lions. We hypothesize that nutritional status and mountain lion predation during a period of drought influenced desert bighorn sheep population parameters in Mazatzal Mountains and that short-term removal of mountain lions by lethal harvest contributed to higher growth and productivity of the small, isolated population, even during periods of drought.

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## KEY WORDS

Arizona, desert bighorn sheep, disease, mountain lions, nutrition, *Ovis canadensis*, populations, predation, *Puma concolor*, rainfall, Sonoran Desert.

# Evaluación de Los Factores Que Podrían Afectar a Una Población de Borregos Cimarrones del Desierto

## RESUMEN

Estudiamos una población de borregos cimarrones (*Ovis Canadensis*) del desierto en las montañas de Mazatzal (área primaria del estudio), zona central de Arizona, así como índices poblacionales en las áreas de referencia entre 1989 y 2003. Evaluamos la susceptibilidad a

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enfermedades y el estado alimenticio de los borregos cimarrones del desierto, los parámetros de la vegetación, las dietas de los depredadores y el aprovechamiento y abundancia del puma (*Puma concolor*) (1999–2003) y la depredación del puma (1995–2003) como factores que potencialmente afectaban a los borregos cimarrones del desierto y a los parámetros de población. Medimos las precipitaciones mensuales de lluvia, monitoreamos la demografía y la abundancia relativa de los borregos cimarrones del desierto empleando estudios aéreos, capturamos y colocamos radiocollares en los borregos cimarrones del desierto y recolectamos muestras de sangre, parásitos y otros agentes patógenos de los animales capturados. Medimos las substancias minerales, el uso relativo y la composición estructural de la vegetación y, por medio de análisis fecales, determinamos las dietas de los borregos cimarrones del desierto, tanto en adultos como en corderos, las ingestiones dietéticas de nitrógeno (FN), 2, el ácido 6-diaminopimélico (FDAPA), fibra de detergente neutral y minerales. Incorporamos, como elemento experimental, una reducción en los pumas, monitoreamos el aprovechamiento y utilizamos estudios de trayectoria como índice de la abundancia relativa del depredador y monitoreamos los radiocollares de los borregos cimarrones para determinar las mortalidades y las causas de muerte. Determinamos las dietas de gatos monteses, coyotes y pumas por medio de análisis de materia fecal. Se produjeron situaciones de sequía durante el verano (julio a septiembre) y el invierno (noviembre a abril), durante 4 y 3 años, respectivamente, entre 1999 y 2003. Los estudios anuales indicaron que la población de las montañas de Mazatzal declinó durante la época de sequía entre 1994 y 1997, el bajo crecimiento experimentado y la producción de corderos coinciden con la precipitación normal antedicha en 1998 y la sequía en 1999 y presentaron un crecimiento, una producción y una productividad más altos durante 2000–2003 a pesar de las condiciones persistentes de sequía durante este período. No observamos ningún síntoma clínico de enfermedad en los borregos cimarrones del desierto con radiocollar y la evidencia hematológica y la procedente de otras exposiciones a agentes de enfermedad no fue fuera de lo común. Los índices de población en las áreas primarias del estudio y de la referencia fueron correlacionados positivamente con las precipitaciones de invierno (noviembre a abril). No encontramos ninguna evidencia de utilización excesiva de forraje en el área primaria del estudio. La precipitación en las montañas de Mazatzal fue asociada a diferencias en la producción primaria particularmente de hierbas, de concentraciones minerales del forraje y de dietas, del estado alimenticio y de cualidades demográficas de los borregos cimarrones del desierto entre 1999 y 2003. Una precipitación más elevada durante el invierno se asoció a un crecimiento más alto de hierbas y una precipitación más alta se asoció a concentraciones más altas de P y Se pero a niveles más bajos de Fe en el ramón, concentraciones más altas de Ca, P, y Zn en hierbas y niveles más altos de P, Se y Zn en pastos. Un promedio más restringido de cantidades de Ca:P en ramones y otras hierbas fue relacionado con precipitaciones más elevadas. Las dietas de adultos y corderos de los borregos cimarrones del desierto eran generalmente similares, particularmente cerca del verano y las hierbas tenían tendencia a predominar en las dietas tanto durante los años de más precipitaciones como durante los más secos. Las precipitaciones más elevadas del invierno fueron asociadas a heces en los adultos con un mayor aumento en las concentraciones de FN y de FDAPA prolongados en invierno y primavera, fósforo fecal más alto, niveles de CA más bajos en la materia fecal y cocientes fecales más limitados de Ca:P y de Na:K, pero los niveles de Na fecal aumentaron durante el año más seco. Las precipitaciones más elevadas del invierno correspondieron con que las heces del cordero contenían niveles más altos de FN, de FDAPA, y de P fecal, concentraciones más bajas de CA fecal y cocientes fecales más limitados de Ca:P. En consecuencia, presumimos que las dietas y el estado alimenticio de adultos y corderos de los borregos cimarrones del desierto tienden a corresponder con los patrones de precipitación y diferencias asociadas en abundancia relativa y al contenido mineral de forrajes. No encontramos ninguna evidencia de que los gatos monteses (*Lynx rufus*) o los coyotes (*Canis latrans*) cazaran borregos cimarrones del desierto o se alimentaran de ellos. La disminución de la abundancia de los borregos cimarrones del desierto durante 1994–1997 fue mayor que las disminuciones en las áreas de referencia que carecían de pumas, a pesar de una cantidad mayor continuada, y de una disminución reducida, en las precipitaciones de invierno en el área primaria del estudio. En comparación, los índices de la población en el área de referencia y en las montañas de Mazatzal aumentaron entre 1999 y 2003 en conexión con las reducciones de depredadores y una menor abundancia de pumas y la depredación de animales con radiocollares, a pesar de que durante este período continuaron las sequías. Identificamos así 2 factores relacionados que probablemente han influenciado las tendencias demográficas de la población de los borregos cimarrones de las montañas de Mazatzal: el estado alimenticio (precipitaciones más elevadas [último factor] fueron asociadas a una disponibilidad y a diferencias más altas en el contenido de minerales en el forraje y mejoraron los índices del estado alimenticio de los borregos cimarrones del desierto) y la depredación de los pumas. Presumimos que el estado nutricional y la depredación del puma durante el período de sequía influyó sobre los parámetros de la población de los borregos cimarrones del desierto en las montañas de Mazatzal, y el retiro a corto plazo de los pumas, cuyo aprovechamiento es letal, contribuyó a un crecimiento y a una productividad más altos de la pequeña y aislada comunidad, incluso durante períodos de sequía.

# Évaluation des Facteurs Influant Éventuellement Sur Une Population de Mouflons D'Amérique du Désert

## RÉSUMÉ

Nous avons étudié une population de mouflons d'Amérique du désert (*Ovis canadensis*) dans les montagnes Mazatzal (principale zone d'étude), au centre de l'Arizona, et les indices des populations dans les zones de référence de 1989 à 2003. Nous avons évalué l'exposition à la maladie et l'état nutritionnel des mouflons d'Amérique du désert, les paramètres de la végétation, le régime alimentaire des prédateurs, la prise et l'abondance du couguar (*Puma concolor*) (de 1999 à 2003) et la prédation par les couguars (de 1995 à 2003) comme facteurs susceptibles de toucher le mouflon d'Amérique du désert et les paramètres de la population. Nous avons mesuré les précipitations de façon mensuelle, surveillé la démographie et l'abondance relative du mouflon d'Amérique du désert à l'aide de relevés aériens en plus de capturer des individus et de leur placer des colliers émetteurs. De plus, nous avons recueilli des échantillons de sang, des parasites et d'autres agents pathogènes sur les individus capturés. Nous avons mesuré la teneur en minéraux, l'utilisation relative et la composition structurale de la végétation, puis déterminé le régime alimentaire du mouflon d'Amérique du désert adulte et juvénile, les apports alimentaires en azote (FN), en 2, en acide diaminopimélique 6 (FDAPA), en cellulose au détergent neutre et en minéraux à l'aide d'analyses fécales. Nous avons incorporé la diminution du nombre de couguars à titre d'élément expérimental, surveillé les prises et utilisé des relevés des pistes en tant qu'indice de l'abondance relative du prédateur, puis surveillé les mouflons d'Amérique du désert munis d'un collier émetteur pour déterminer les mortalités et les causes du décès. Nous avons déterminé le régime alimentaire des lynx roux, des coyotes et des couguars à l'aide des analyses fécales. Des conditions de sécheresse ont prévalu au cours de l'été (de juillet à septembre) et de l'hiver (de novembre à avril) pendant 4 et 3 ans, respectivement, de 1999 à 2003. Les relevés annuels ont indiqué que la population des montagnes Mazatzal a subi un déclin lors de la sécheresse entre 1994 et 1997, connu une faible croissance et une faible production de petits qui ont coïncidé avec des précipitations au-

dessus de la moyenne en 1998 et la sécheresse en 1999, puis montré une croissance, une production et une productivité accrues de 2000 à 2003 malgré la sécheresse persistante au cours de cette période. Nous n'avons observé aucun symptôme clinique de maladie chez les mouflons d'Amérique du désert munis d'un collier émetteur, et aucune preuve hématologique ou autre d'exposition à des maladies n'a été remarquée. Les indices de population dans la principale zone d'étude et la zone de référence ont été mis en corrélation de façon positive avec les précipitations connues en hiver (de novembre à avril). Nous n'avons trouvé aucune preuve de surpâturage dans la principale zone d'étude. Les précipitations dans les montagnes Mazatzal ont été associées aux différences de production primaire, particulièrement de latifoliés, aux concentrations de minéraux du pâturage ainsi qu'aux régimes alimentaires, aux états nutritionnels et aux attributs démographiques du mouflon d'Amérique du désert de 1999 à 2003. Les précipitations plus importantes de l'hiver ont été associées avec une croissance accrue de latifoliés et ces précipitations plus importantes ont été associées avec de plus grandes concentrations de P et de Se, mais avec un niveau moindre de Fe dans le pâturage, des concentrations plus élevées de Ca, de P, et de Zn dans les latifoliés ainsi que des niveaux accrus de P, de Se et de Zn dans les graminées. Le rapport moyen plus étroit entre le Ca et le P du pâturage et des latifoliés a été associé aux précipitations plus importantes. Le régime alimentaire du mouflon d'Amérique du désert, tant adulte que juvénile, est généralement très semblable, particulièrement à l'approche de l'été, et les latifoliés ont eu tendance à être prédominants dans les régimes au cours des années plus humides et plus sèches. Les précipitations plus importantes de l'hiver ont été associées, dans les matières fécales des adultes, à une augmentation plus prolongée en hiver et au printemps des concentrations de FN et de FDAPA, à davantage de phosphore fécal, à des niveaux moindres de Ca fécal ainsi qu'à des rapports entre le Ca et le P et le Na et le K fécaux plus étroits. Cependant, les niveaux de Na fécal ont augmenté lors de l'année la plus sèche. Les précipitations élevées connues en hiver se sont traduites, dans les matières fécales des petits, par des niveaux accrus de FN, de FDAPA et de P fécal, des concentrations moindres de Ca fécal et un rapport entre le Ca et le P fécal plus étroit. Par conséquent, nous avons émis l'hypothèse que les régimes alimentaires et les états nutritionnels du mouflon d'Amérique du désert, tant adulte que juvénile, avaient tendance à correspondre au modèle des précipitations et aux différences connexes de l'abondance relative et de la teneur en minéraux des pâturages. Nous n'avons trouvé aucune preuve selon laquelle les couguars (*Lynx rufus*) ou les coyotes (*Canis latrans*) avaient pris le mouflon d'Amérique du désert comme proie ou s'étaient nourris de leurs carcasses. Le déclin de l'abondance de mouflons d'Amérique du désert connu de 1994 à 1997 a été plus importante que les déclins connus dans les zones de référence où on ne trouvait pas de couguars, malgré les précipitations hivernales toujours croissantes et une baisse moins importante de celles-ci dans la principale zone d'étude. Par comparaison, les indices de population dans une zone de référence et dans les montagnes Mazatzal ont connu une augmentation de 1999 à 2003 de concert avec la réduction des prédateurs, de l'abondance de couguars et de la prédation des animaux munis d'un collier émetteur, malgré l'occurrence continue de la sécheresse au cours de cette période. Nous avons donc déterminé deux facteurs immédiats susceptibles d'avoir influé sur les tendances démographiques de la population de mouflons d'Amérique du désert des montagnes Mazatzal: l'état nutritionnel (les précipitations accrues [principal facteur] ont été associées à une plus grande disponibilité et aux différences de teneur en minéraux des pâturages ainsi qu'aux indices améliorés de l'état nutritionnel du mouflon d'Amérique du désert) et la prédation par les couguars. Nous avons formulé l'hypothèse que les états nutritionnels et la prédation par les couguars au cours d'une période de sécheresse ont influé sur les paramètres de population du mouflon d'Amérique du désert dans les montagnes Mazatzal, et que la suppression à court terme des couguars par la prise a contribué à une croissance plus importante et à la productivité de la population, qui est petite et isolée, même au cours de périodes de sécheresse.

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## INTRODUCTION

Desert bighorn sheep inhabit arid, naturally fragmented environments with unpredictable rainfall in the southwestern United States, and populations often consist of <100 animals (Krausman and Leopold 1986; Bleich et al. 1990, 1996). Abundance varies spatially and temporally (Rubin et al. 1998, McKinney et al. 2003), and population declines or extirpations present concerns regarding conservation and management (Schwartz et al. 1986; Bleich et al. 1990, 1996; Kamler et al. 2002; Rominger et al. 2004). Disease, interspecific competition, nutritional status, population densities, predation, weather, and available escape terrain are among variables postulated to influence abundance or persistence of desert bighorn sheep populations (Jessup 1985; Berger 1990; Rubin et al. 1998; McKinney et al. 2001, 2003), but mechanisms affecting demographic trends of populations remain poorly understood.

Nutritional status of wild herbivore populations as a limiting factor also is poorly understood, and evaluations of food resources and nutritional ecology are of central importance in developing predictions underlying decision-making processes in range and wildlife management (Wallmo et al. 1977, Hobbs and Swift 1985, Robbins 1992, Irwin et al. 1993, Sams et al. 1998). Variability in annual and seasonal rainfall influences primary production in xeric environments (Herbel et al. 1972, Beatley 1974, Goldberg and Turner 1986, Ernest et al. 2000, Marshal et al. 2005), subsequently affecting ungulate population dynamics (Coe et al. 1976, White 1978, Smith and LeCount 1979, Leopold and Krausman 1991).

Among large herbivores, higher quantity and quality of forages, survival of preweaning young, and female fecundity often correspond with higher precipitation during winter to spring, and studies indicate importance of abundance of young in affecting growth rates of populations (Gaillard et al. 2000). Extended periods of lower rainfall might reduce desert bighorn sheep lamb production, and seasonal inadequacies in rainfall correspond with lower abundance in desert bighorn sheep populations (Leslie and Douglas 1982, Douglas and Leslie 1986, Wehausen et al. 1987, Holt et al. 1992, Douglas 2001), presumably acting via lower forage quality or quantity. Drought is a normal part of climatic fluctuation (Thurow and Taylor 1999) and has been associated with population declines of bighorn sheep and other ungulates in desert environments (Anthony 1976, Brown 1984, Smith 1984, Mouton et al. 1991, McKinney et al. 2001). Inadequate seasonal rainfall patterns often correspond with lower production, productivity, and recruitment in populations of desert bighorn sheep (Berger 1982, McKinney et al. 2001), variables that influence population trends of large herbivores (Gaillard et al. 2000).

Normal variations in plant chemistry (nutrient content) caused by seasonal changes in plant phenology and physiology likely have important implications to diets and nutrition of wild ruminants (Short et al. 1966, Krausman et al. 1997). Seasonal variability characterizes composition and quality of diets (Seegmiller and Ohmart 1982, Meyer et al. 1984, Jones and Weeks 1985, Scrivner et al. 1988, Miller and Gaud 1989) and nutritional quality of forages (Krausman et al. 1989, 1990; Seegmiller et al. 1990; Bleich et al. 1997; Alldredge et al. 2002). Diets of ruminants also might change under drought conditions compared

to periods of adequate rainfall (Anthony 1976, Stephenson et al. 1985), and composition of diets might influence dietary quality (Mubanga et al. 1985, Massey et al. 1994, Bleich et al. 1997). Concentrations of FN and FDAPA have been used widely to index quality of diets and relationships between composition and quality of diets of wild ruminants (Massey et al. 1994, Hodgman et al. 1996, Bleich et al. 1997, Osborn and Ginnett 2001, Oehler et al. 2003).

Concentrations of mineral nutrients in forages may be influenced by precipitation, thus affecting dietary quality of ruminants. Patterns of rainfall can affect soil moisture (Salve and Allen-Diaz 2001), moisture available to plants (Halvorson and Patten 1974, Kemp 1983), and concentrations of minerals in vegetation (Greene et al. 1987, Grings et al. 1996, Sprinkle et al. 2000). Possible dietary deficiencies of Cu, Fe, Na, P, S, Se, and Zn may occur for free-ranging wild ruminants (Urness et al. 1971, Scrivner et al. 1988, Flueck 1994, Fox et al. 2000, O'Hara et al. 2001). Nonetheless, dietary requirements of minerals for wild ruminants are poorly understood (Robbins et al. 1985, Grasman and Hellgren 1993, Krausman et al. 1999).

Forage selection to maintain quality of diets is common in wild ruminants, including bighorn sheep (Hobbs and Spowart 1984, Provenza 1995, Hanley 1997, Alldredge et al. 2002, Oehler et al. 2003). Nonetheless, inadequate nutrition of ruminants might delay or prevent estrus and ovulation and influence survival of young animals and relative abundance of populations (Murphy and Coates 1966, Meyer et al. 1984, DePerno et al. 2000, Cook et al. 2001, Blanchard et al. 2003). Behavioral and physiological mechanisms might tend to counteract dietary deficiencies of Na, P, and other minerals in wild ruminants (Robbins et al. 1987, Robbins 1992, Grasman and Hellgren 1993, Provenza 1995, Hanley 1997).

Desert bighorn sheep commonly are exposed to a number of diseases associated with domestic livestock and wild ungulates (Prestwood et al. 1974, Stauber et al. 1977, Jessup 1985, deVos 1989, Elliott et al. 1994), and disease outbreaks may contribute to bighorn sheep population declines (Sandoval 1980, DeForge and Scott 1982, Cassirer et al. 1998, Monello et al. 2001). Contact with domestic livestock or wild ungulates, population density, inadequate nutrition, weather, and other environmental variables have been suggested to influence disease outbreaks (Clark et al. 1985, Sandoval et al. 1987, Foreyt 1989, Callan et al. 1991, Monello et al. 2001).

Exposure to various disease agents in desert bighorn sheep in Arizona has been widely documented, generally with no known relationship to clinical disease or population die-offs, but several diseases have been reported to influence relative abundance in bighorn sheep populations (deVos 1989). Notable diseases in bighorn sheep include scabies, chronic sinusitis, leptospirosis, contagious ecthyma, epizootic hemorrhagic disease, bluetongue, and pneumonia (deVos 1989). Lesions consistent with hemorrhagic disease recently were documented in a desert bighorn sheep and a Rocky Mountain bighorn sheep in Arizona (Noon et al. 2002). Declines of desert bighorn sheep populations likely associated with disease epizootics affecting population abundance or survival of bighorn sheep lambs have been documented in California (DeForge et al. 1997), Utah (Douglas 2001), and New

Mexico (Clark and Jessup 1992). Nutritional status of the host ostensibly is a key factor affecting the outcome of most diseases, and better nutrition associated with higher precipitation likely confers a higher probability of lambs surviving disease (Wehausen et al. 1987).

Predation by mountain lions can be a substantial source of mortality in some bighorn sheep populations (Logan and Sweanor 2001), and mountain lions appear to be the only predators that can cause significant mortality in bighorn sheep populations that occupy suitable habitat (Sawyer and Lindzey 2002). Young bighorn sheep are more likely than adults to be killed by coyotes (Bleich 1999). In comparison, predation by coyotes, mountain lions, or wolves (*Canis lupus*) can be a significant mortality factor affecting deer populations (Ballard et al. 2001). Variables influencing mountain lion predation on bighorn sheep are uncertain but might include relative availability of primary and alternative prey and escape terrain, vulnerability of individual prey, weather, and behavior of individual predators (Leopold and Krausman 1986, Ross et al. 1997, Krausman et al. 1999, Logan and Sweanor 2001, Kamler et al. 2002).

Mule deer (*Odocoileus hemionus*) are important prey of mountain lions throughout western North America (Bleich and Taylor 1998), but relative abundance of mountain lions and mule deer may be weakly linked (Lindzey et al. 1994). Nonetheless, effects of mountain lion predation on bighorn sheep likely are limited to areas where mule deer occur sympatrically at densities adequate to provide a primary prey (Schaefer et al. 2000). High occurrence of desert bighorn sheep in mountain lion diets might correspond with higher abundance of desert bighorn sheep relative to abundance of mule deer (Rosas-Rosas et al. 2003). Predation of desert bighorn sheep by mountain lions in New Mexico involved primarily desert bighorn sheep near escape terrain (Creeden and Graham 1997), consistent with the notion (Sawyer and Lindzey 2002, Mooring et al. 2004) that escape terrain might provide limited benefit to avoidance of mountain lion predation. Mountain lions may select steep, rugged topography (Logan and Irwin 1985, Riley and Malecki 2001) but while hunting or traveling also may use terrain less rugged than general surroundings (Dickson et al. 2005).

Adult female bighorn sheep, whether or not they have lambs, tend to select steeper terrain than randomly available (Etchberger and Krausman 1999) and to select steeper, more open habitats than do mature males (Bleich et al. 1997, Mooring et al. 2004). Predation of bighorn sheep by mountain lions may be independent of sex of prey and densities of predator and prey (Ross et al. 1997, Hayes et al. 2000, Logan and Sweanor 2001, Mooring et al. 2004). Mountain lions may kill primarily adult bighorn sheep, or predation may not show sex-related differences among adults (Ross et al. 1997, Mooring et al. 2004). Mountain lion predation of Rocky Mountain bighorn sheep was selective for lambs, and prey-class vulnerability was a function of behavior of individual predators (Ross et al. 1997), whereas predation of desert bighorn sheep by mountain lions was highest in the 1–4-year and  $\geq 9$ -year age classes (Hayes et al. 2000).

Comparatively few studies have addressed population-level impacts of predators on bighorn sheep (Sawyer and Lindzey 2002). Mountain lion predation may be variable among years but

potentially affect bighorn sheep demographic characteristics (Wehausen 1996, Creeden and Graham 1997, Ross et al. 1997, Rubin et al. 1998, Hayes et al. 2000). Recent studies indicate that mountain lion predation in some cases might have population-level effects on bighorn sheep (Wehausen 1996, Creeden and Graham 1997, Ross et al. 1997, Hayes et al. 2000, Ernest et al. 2002), including translocated populations (Kamler et al. 2002, Rominger et al. 2004). Other studies also recently documented or modeled predation by mountain lions (Kunkel et al. 1999, Schaefer et al. 2000, Logan and Sweanor 2001, Turner and Morrison 2001, Anderson and Lindzey 2003). Predation by mountain lions, disease, and drought were thought to be limiting factors affecting a remnant desert bighorn sheep population (Logan and Sweanor 2001). It likely is inappropriate to argue that food alone or predation alone limits a prey population when strong interaction occurs between these variables (McNamara and Houston 1987).

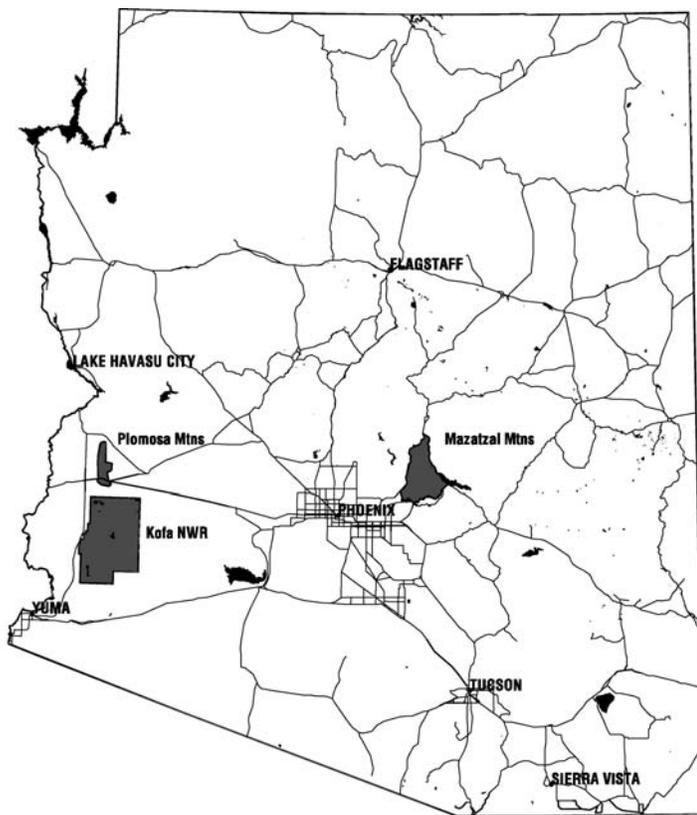
A desert bighorn sheep population in central Arizona declined during recent drought, and winter rainfall was positively associated with demographic patterns (McKinney et al. 2001). Management concerns regarding this population have centered on apparent low abundance and poor lamb production (McKinney et al. 2000). Ecological events commonly have multiple causes (McNamara and Houston 1987, Bleich et al. 1997), and we used multiple working hypotheses (Romesburg 1981, Bleich et al. 1997) to evaluate potential effects of various factors on growth, production, and productivity of this population. Our objective was to evaluate variables potentially affecting dynamics of the desert bighorn sheep population and responses of the population to short-term reductions of mountain lions. We examined rainfall, disease, availability and mineral content of vegetation, dietary nutritional quality, and predators to evaluate factors potentially influencing desert bighorn sheep population parameters.

## STUDY AREAS

### Mazatzal Mountains

We conducted intensive studies on a 53,600-ha primary study area located in the Mazatzal Mountains (Figs. 1, 2) 65 km northeast of Phoenix, Arizona, USA. The desert bighorn sheep population in this study area is comparatively small and isolated, and the area contains limited escape terrain (McKinney et al. 2001, 2003). Elevation ranged from 457 to 2,317 m, and vegetation below 1,100 m was Upper Sonoran Desert scrub. Interior chaparral was extensive above 1,100 m and changed to a limited mixed ponderosa pine (*Pinus ponderosa*) community at high elevations (Brown 1994). Annual rainfall of about 35 cm occurred primarily during winters, and drought (Thurrow and Taylor 1999) prevailed on the study area between 1994 and 1999 (McKinney et al. 2001). Average monthly temperatures ranged from about 10 to 32°C in winter and summer, respectively. Surface water was available in springs, natural pools, intermittently flowing washes, and reservoirs (McKinney et al. 2001).

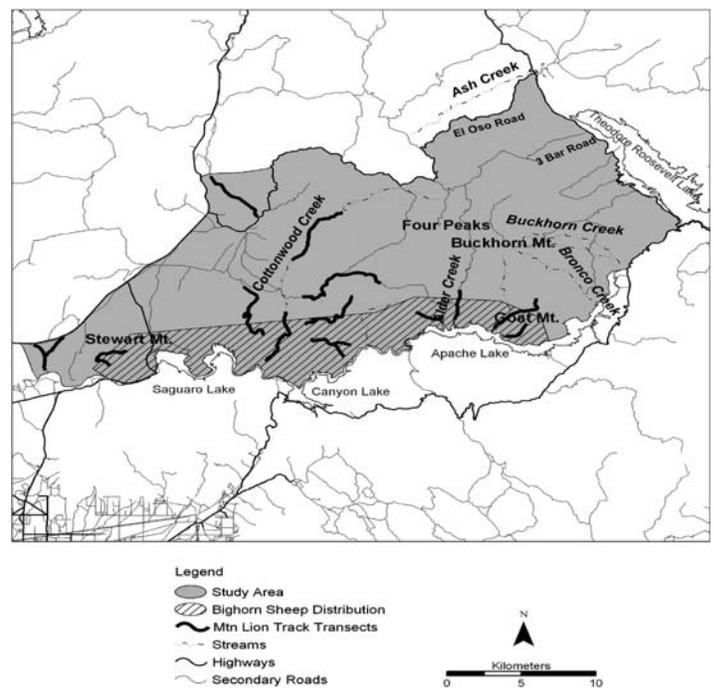
Desert bighorn sheep were reintroduced into vacant historical habitat in Mazatzal Mountains during 1980 and 1981; by 1989, a small, isolated population was distributed within about 8,700 ha (Fig. 2), which included about 800 ha of escape terrain (McKinney et al. 2001, 2003). Mule deer, white-tailed deer (*O. virginianus*),



**Figure 1.** Locations of the primary study area (Mazatzal Mountains [Mazatzal Mtns.]) and reference areas (Kofa National Wildlife Refuge [Kofa NWR], Plomosa Mountains [Plomosa Mtns]), Arizona, USA.

collared peccary (*Pecari tajacu*), a few feral burros, cattle, mountain lion, bobcat, coyote, black bear (*Ursus americanus*), and common gray fox (*Urocyon cinereoargenteus*) also inhabited the area. About 4,000 domestic sheep were driven each year during spring and autumn through April 2001 over a livestock driveway located at the western boundary of the study area; passage each season required  $\leq 2$  days but was discontinued after April 2001 until 2003. Prior to 2000, 400 free-ranging cattle (cow-calf operation) grazed yearlong, and additional localized, variable stocking occurred seasonally, on the western 30,000 ha, or about 56%, of the area.

All cattle were removed from allotments between mid-2000 and February 2001, except that cattle on a year-round allotment narrowly overlapping a northern portion of the study area were reduced from 200 to 35 by mid-2000 (U.S. Forest Service, unpublished data). No human-made obstructions prevented potential comingling of desert bighorn sheep with cattle or domestic sheep. Herders restricted movements of domestic sheep to the livestock driveway, and 4-strand barbed-wire pasture fencing within the study area limited distribution of cattle, but neither of these variables prevented potential movements by desert bighorn sheep. We observed cattle in areas of low topographic relief occasionally used by desert bighorn sheep but observed no cattle within areas of escape terrain.



**Figure 2.** Mazatzal Mountains, Arizona, USA, study area boundary, area of desert bighorn sheep distribution, and locations of mountain lion track transects. Distribution of desert bighorn sheep is constrained by presence of escape terrain and elevations  $< 1,100$  m, above which dense chaparral is extensive (McKinney et al. 2003).

## Reference Areas

We obtained rainfall and survey data for 2 extant desert bighorn sheep populations (McKinney et al. 2003) that inhabited Sonoran Desert mountain ranges with predominantly desert scrub vegetation (Miller and Gaud 1989, Hervert et al. 1998) and used as reference areas the 269,300-ha Kofa National Wildlife Refuge (Kofa) located 215 km west of Phoenix and the Plomosa Mountains (40,000 ha) located 20 km north of Kofa (Fig. 1). Desert bighorn sheep inhabiting reference areas may have comprised a metapopulation (Witham and Smith 1979, Bleich et al. 1996). Estimated mean long-term (1989–2001) population sizes were similar in the primary study area and Plomosa Mountains and larger than in both of these mountain ranges in Kofa (McKinney et al. 2003). Elevations ranged from about 207 to 1,487 m, annual rainfall was about 17 cm, and temperatures ranged from about 0 to 45°C during winter and summer, respectively (Hervert et al. 1998). Mule deer but no domestic livestock except possibly a few feral burros occurred in Kofa (VandenBerge et al. 1984). Mule deer also inhabited Plomosa Mountains (Arizona Game and Fish Department 2003), and cattle grazed there seasonally under a variable stocking regimen. Cattle stocking rate was increased in winter–spring during years of higher winter rainfall and reduced during drier years. Surface water was available in natural pools, ephemeral springs, and developed sources. Mountain lions occurred rarely, if at all, on reference areas (Germaine et al. 2000; Arizona Game and Fish Department 2003, 2005), but bobcats and coyotes inhabited those regions.

## METHODS

### Design

We employed a study design emphasizing observational research incorporating primarily descriptive and correlative studies. We developed a priori research hypotheses, recognizing that inferences derived using our study design are weaker than those obtainable using controlled, replicated experimentation (Eberhardt and Thomas 1991). Nonetheless, considerable inference derives from different investigators obtaining similar results in different areas at different times (Johnson 1999). We implemented short-term removal of mountain lions in Mazatzal Mountains to evaluate the suggestion that active management may be needed in some circumstances to mitigate population-level impacts of predation in a relatively small and isolated bighorn sheep herd (Kamler et al. 2002, Rominger et al. 2004).

We examined desert bighorn sheep population parameters in Mazatzal Mountains and reference areas to compare population trends on areas with similar habitats based on occurrence in Sonoran Desert scrub communities. We were unable to identify as potential reference areas other mountain ranges occupied by desert bighorn sheep where mountain lion predation had been documented (Kamler et al. 2002) but where the predator was not harvested (Arizona Game and Fish Department 2003, 2004). We assumed that mountain lions were absent on reference areas based on surveys (Germaine et al. 2000) and records of hunter harvest locations (Arizona Game and Fish Department 2003, 2004, 2005), thus precluding predation of desert bighorn sheep by mountain lions on those areas.

Reference areas thus allowed comparison of desert bighorn sheep population parameters where we assumed mountain lion predation was absent with population parameters of the ungulate in Mazatzal Mountains, where mountain lions were comparatively abundant (Arizona Game and Fish Department 2004) and predation was documented (Kamler et al. 2002). We assumed that predation of desert bighorn sheep by mountain lions would differ between the primary study area, where presence of the predator was known (Kamler et al. 2002; Arizona Game and Fish Department 2003, 2004), and reference areas, where the predator likely was absent (Germaine et al. 2000; Arizona Game and Fish Department 2003, 2004) and where we assumed that predation did not occur. We hypothesized that differences in mountain lion abundance and predation between Mazatzal Mountains and reference areas potentially represented a factor influencing desert bighorn sheep demographic changes, recognizing that demographic patterns of ungulates on those areas might be confounded by other factors.

### Rainfall

We obtained rainfall data between 1976 and 2003 from weather stations maintained by Salt River Project at Mormon Flat and Stewart Mountain dams on the Salt River (located at southern boundary of the study area) for Mazatzal Mountains and for Kofa Mine station and Bouse for Kofa and Plomosa Mountains, respectively (Western Regional Climate Center; <http://www.wrcc.dri.edu/summary/climsmaz.html>). We defined drought (Thurrow and Taylor 1999) as rainfall less than about 75% of the 1976 to 1999 average for Mazatzal Mountains and 1988 to 1998 averages for reference areas.

### Population Surveys

Arizona Game and Fish Department personnel conducted standardized helicopter surveys of desert bighorn sheep (Hervert et al. 1998; McKinney et al. 2001, 2003) during autumn in Mazatzal Mountains from 1989 through 2003 and on reference areas between 1989 and 1997 (Kofa) and 1989 and 2003 (Plomosa Mountains) to estimate abundance (total counted), production (lambs), productivity (lambs:100 females), and recruitment (yearlings). We computed total animals, males, females, lambs, and yearlings counted/hour of survey flight time and productivity to index population parameters during these years. We were unable to evaluate detectability in surveys, although sighting probability estimates on reference areas with similar habitat (i.e., vegetation type) to Mazatzal Mountains did not differ among years and averaged 0.46 (90% CI = 0.37–0.55; Hervert et al. 1998). We assumed that detectability was similar among study areas, although terrain ruggedness and area of escape terrain were lower and estimated long-term (1989 to 2001) densities of desert bighorn sheep higher in Mazatzal Mountains than on reference areas (McKinney et al. 2003). We conducted ground surveys continually in Mazatzal Mountains during January–July from 2000 through 2003 to estimate periodicity of lambing.

### Disease Exposure

We captured adult desert bighorn sheep in the Mazatzal Mountains (Fig. 2) using a net gun between June 2000 and October 2002, attached motion-sensitive radio collars (MOD-500, Telonics, Mesa, Arizona) and numbered ear tags at initial capture, and released animals on-site on completion of processing. We collected blood samples from each animal during each capture via jugular venipuncture and monitored seroconversions by repeated sampling of individual animals. We examined captured animals for clinical signs of disease and collected deep nasal and pharyngeal samples using sterile swabs that were placed in transport media (Becton-Dickenson Culturette II®). We also collected samples of ear debris using sterile swabs and collected ectoparasite and fecal samples. We kept all samples cool following collection and during transport within 24 hours to the Arizona Veterinary Diagnostic Laboratory (College of Agriculture, University of Arizona, Tucson) for analysis.

We used standard materials and methods for aerobic bacterial cultures, fecal examinations, and serology and scored serological results from individual desert bighorn sheep as positive or negative for each pathogen based on presence or absence of antibodies. We referred to animals with positive test results as “exposed” and defined multiple exposure as presence of antibodies against  $\geq 2$  disease agents. Nasal and pharyngeal swabs were cultured aerobically, and ear swab specimens were processed by maceration in warm aqueous potassium hydroxide solution, flotation in saturated sucrose solution, and microscopic examination for presence of ear mites (*Psoroptes* spp.). Fecal samples were tested for nematode parasites using flotation (Fecalyzer®). We performed the agar gel immunodiffusion (AGID) test on serum samples to detect antibodies against bluetongue (BT) and epizootic hemorrhagic disease (EHD). Sera that were AGID positive were referred to the National Veterinary Services Laboratory (Ames, Iowa) for serum neutralization (SN) testing to determine BT and EHD serotype-specific antibody. We used the SN test to detect

antibodies against parainfluenza-3 virus (PI-3), infectious bovine rhinotracheitis virus (IBR), bovine virus diarrhea (BVD), and bovine respiratory syncytial virus (BRV). We measured antibody titers of *Chlamydia* spp. and contagious ecthyma virus (CE) using complement fixation. Antibody to *Leptospira* spp. was determined using the microscopic agglutination (MA) test, with lowest dilution = 1:100. Serovars tested were *L. canicola*, *L. grippotyphosa*, *L. hardjo*, *L. icterohemorrhagiae*, *L. pomona*, *L. bratislavia*, and *L. szwajizak*.

### Nutritional Status

**Vegetation.**—We randomly hand-clipped samples in Mazatzal Mountains from July 2000 through June 2001 from forages potentially eaten by desert bighorn sheep based on review of literature (McKinney and Noon 2002). Sample collections, handling, and analyses for Ca, Cu, Fe, K, Mg, Mn, Na, P, Se, and Zn followed procedures described previously (Fox et al. 2000, McKinney and Noon 2002). We composited forage samples quarterly (July–September, October–December, January–March, April–June) for mineral analyses. We reanalyzed data and calculated means of mineral concentrations in vegetation sampled on the study area between July 1999 and June 2000 (McKinney and Noon 2002) and compared them with mean concentrations of minerals in vegetation collected during 2000–2001 during the same seasonal periods. Plant names follow Kearney and Peebles (1973).

We randomly established 17 sampling sites stratified within the range of desert bighorn sheep distribution (Fig. 2) in Mazatzal Mountains, each consisting of 6 parallel (100-m) line transects developed systematically at 10-m intervals along a random bearing (Heady et al. 1959, Hanley 1978, Anderson et al. 1979, Butler and McDonald 1983, Ratti and Garton 1994). We assigned the following categorical rankings for use of browse and forbs on each 100-m line transect: no hedging, moderate hedging, or heavy hedging (Patton and Hall 1966). We established 33.3-m line-intercept transects systematically within each 100-m line transect to determine structural composition of bare ground, browse, forbs, and grasses (Dodd 1989, Miller and Gaud 1989, Wakeling and Miller 1989, Holt et al. 1992). We estimated use of browse and forbs during August–September 1999 and February–March 2000 and measured structural composition of bare ground and vegetation during August–September and February–March 1999–2001.

**Fecal Indices.**—We collected fresh fecal samples (about 10 pellets from each of 10 individual groups) during the middle of each month from adult (adult-yearling) desert bighorn sheep in Mazatzal Mountains from July 1999 through June 2002 and composited samples collected during 2-month periods for analysis. We also collected fresh fecal pellets monthly in this manner from lambs during February–July from 2001 through 2003 and composited groups monthly for analysis. We placed fecal samples in plastic bags and froze them until analyzed by the Wildlife Habitat and Nutrition Laboratory (Washington State University, Pullman) to determine percent diet composition and dry-weight concentrations of FN, FDAPA, neutral detergent fiber (FNDF), Ca, K, Mg, Na, and P. Percent diet composition for each composited sample was determined using epidermal fragment cover as the sampling criterion, based on 25 views for each of 8

slides/sample, and all plants possible were identified. Fecal N, FDAPA, and FNDF were determined using procedures previously reported (Hodgman et al. 1996). Fecal samples (1 g) were ashed overnight at 500°C, cooled, and digested in an acid medium (10 ml 1.0 N HCl, diluted to 50 ml with H<sub>2</sub>O), and fecal mineral determinations were made using standard procedures of inductively coupled plasma emission spectroscopy. We used primary production, concentration of minerals in vegetation, composition of diets, and concentrations of FN, FDAPA, FNDF, and fecal minerals to index diet quality and evaluate nutritional status of desert bighorn sheep.

### Predators

**Mountain Lion Reduction.**—We incorporated mountain lion reduction as an experimental element of perturbation in the Mazatzal Mountains study area. The bag limit for mountain lions statewide in Arizona from 1971 through 1999 was 1/hunter/year (July 1–June 30 season). Annual harvest on the study area was not limited, but beginning July 1999, regulations permitted hunters to take a maximum of 12 animals annually from the study area using multiple tags to encourage predator reduction via sport hunting; a single hunter or combination of hunters might take the total harvest. We determined mountain lion harvest data based on mandatory reporting of kills by sport hunters.

**Track Surveys.**—We established transects in Mazatzal Mountains (Fig. 2) averaging 4.6 km (range 2.0–7.7 km) along 11 dry washes and 2 4-wheel-drive roads on ridge tops to monitor mountain lion track counts between 1999 and 2003. Number, length, and location of routes were limited by known associations of mountain lion tracks with topographic and other habitat features and availability of suitable substrate (i.e., dust, mud, or sand) for track detection and identification (Smallwood 1994, Smallwood and Fitzhugh 1995, Beier and Cunningham 1996). Transects in washes did not extend into upstream areas with poorly developed scour zones that might affect track detectability (Beier and Cunningham 1996). We assumed that track detectability did not differ between seasonal sampling periods, transects, or years (Van Sickle and Lindzey 1992, Smallwood 1994, Harveson et al. 1999).

One or 2 persons conducted track surveys on foot following  $\geq 5$  days free of precipitation (Beier and Cunningham 1996) during November–January (winter) and March–May (spring) each year from December 1998 to January 2004. We controlled for observer differences by using the same observer or observers on given routes each survey (Morrison et al. 2001). Completion of winter surveys and inception of spring surveys were at least 90 days apart. We completed surveys within about 4 hours during mornings, counted single tracks or sets comprised of contiguous multiple tracks believed made by the same individual, recorded data as presence/absence of tracks or track sets (Smallwood 1994, Beier and Cunningham 1996), and calculated tracks/km to index relative abundance of mountain lions.

**Diets.**—We collected mountain lion scats in Mazatzal Mountains from 1999 through 2003 while searching throughout the study area, primarily along dry washes, ridges, saddles, and canyon bluffs and slopes (Logan and Irwin 1985, Smallwood and Fitzhugh 1995, Cunningham et al. 1999). We plotted locations where mountain lion scats were collected on a topographic map to

ensure that sampling efforts represented the entire study area. We collected bobcat and coyote scats in Mazatzal Mountains from January 2000 through December 2003 following a similar sampling approach but also collected scats along livestock trails and occasionally while driving limited wilderness access roads (total length driven <20 km).

We identified feces to species by size and form of scats and presence of tracks and scrapes (Murie 1954, Danner and Dodd 1982, Cunningham et al. 1999). We further distinguished mountain lion feces by collecting only scats  $\geq 30$ -mm diameter, which we assumed excluded most bobcat and coyote feces (Weaver and Fritz 1979, Johnson et al. 1984, Cunningham et al. 1999). We placed mountain lion scats in plastic bags and froze them, except we air-dried fresh scats at ambient temperatures for  $\geq 1$  month before freezing. We handled fresh bobcat and coyote scats similarly but often examined remains in feces without freezing and while in the field. We thoroughly hand-dissected scats (Spaulding et al. 2000) and identified prey remains macro- and microscopically by comparing scat contents to a reference collection of mammalian bone, hair, and tooth fragments developed by AGFD and following Moore et al. (1974). We identified bird and reptile remains based on feathers, skin remnants, or claws.

**Desert Bighorn Sheep Mortalities.**—We monitored telemetry signals from radio-collared desert bighorn sheep on Mazatzal Mountains between June 2000 and December 2003 twice weekly from the ground and twice monthly using fixed-wing aircraft. We continually and in response to mortality signals from radio collars searched as soon as possible for desert bighorn sheep carcasses between 2000 and 2003 to determine cause of death. We also continually searched opportunistically for carcasses of desert bighorn sheep from 1999 through 2003 to estimate cause of death. We identified mountain lion predation as cause of death based on evidence observed at carcass sites, including attack and drag lines, canine tooth punctures and tissue damage, feeding patterns, presence of tracks, feces, scrapes, hair plucked from prey carcasses, caching of prey, and other indicators (Rominger and Weisenberger 1999, Hayes et al. 2000, Logan and Sweanor 2001, Rominger et al. 2004) and trail strikes at kill sites by trained hounds.

We also retrospectively evaluated mortalities between 1995 and 1998 of 15 desert bighorn sheep captured by net gun in the Mazatzal Mountains study area by AGFD personnel in November 1995, fitted with motion-sensitive radio collars, and released on-site. Arizona Game and Fish Department biologists identified mortalities due to mountain lion predation during 1995 to 1998 as in the present study, except they did not use trail strikes by hounds.

## Data Analyses

We determined relationships between rainfall, relative desert bighorn sheep population abundance, production, and yearling recruitment and diet and other nutritional indices using general linear regression models and assessed temporal trends of population indices and adult diets using Spearman's rank correlation. We differentiated mean fecal indices, forage mineral levels, mountain lion track counts, and seasonal rainfall using 90% confidence intervals (CIs; Yoccoz 1991, McBride et al. 1993, Johnson 1999).

We calculated annual percent occurrence (no. of occurrences of each food item as % of no. of occurrences of all food items) and frequency of occurrence (% of total scats in which a particular food item was found) of prey remains in mountain lion scats. We used annual frequency of occurrence of prey remains in scats to estimate relative percent of biomass and number of prey eaten by mountain lions, using established conversion factors and procedures (Ackerman et al. 1984, Cunningham et al. 1999, Logan and Sweanor 2001). We used a correction factor (C) for each prey species to estimate mass of prey consumed/scat ( $C = 1.98 \times 0.035B$ ; Ackerman et al. 1984), where C = mass of prey consumed/scat and B = estimated mean live weight of individual prey consumed. We used previously reported mean live mass of individual prey, including 50 kg for desert bighorn sheep (Cunningham et al. 1999), in estimating proportional biomass and numbers of prey eaten by mountain lions. We computed proportional biomass (D) of each prey consumed ( $D = [A \times C] / \Sigma[A \times C]$ ), where A = frequency of occurrence and relative number of individuals (E) of each prey consumed ( $E = [D \times B] / \Sigma[D/B]$ ).

In addition to analyses of individual prey categories, we placed prey remains found in scats into 4 categories and summed D and E separately within categories to compare relative consumption of prey biomass and numbers by mountain lions among years: small prey (e.g., lagomorphs, rodents), large prey (e.g., cattle, deer, desert bighorn sheep, collared peccary), cattle, and large wild prey. We used chi-square contingency tables, incorporating only expected cell frequencies  $\geq 5$ , to test for differences in mountain lion diet (% occurrence) and predation of desert bighorn sheep among years and to compare occurrence of large and small prey categories (Siegel and Castellan 1988, Zar 1996). We calculated diet diversity indices ( $\beta$ ) for mountain lions based on percent occurrence of prey remains in scats, following Litvaitis and Harrison (1989):

$$\beta = (\Sigma p^2)^{-1}$$

where  $p$  = unweighted use of a particular food resource. Value of  $\beta$  varies from 1 to  $n$ , where  $n$  = number of food categories.

## RESULTS

### Rainfall

**Mazatzal Mountains.**—Long-term rainfall (1976–1999) averaged 37.9 cm annually (January–December: 90% CI = 32.7–43.1 cm), and mean rainfall (Table 1) was greater during winter (November–April 1976–1999: 90% CI = 19.2–27.7 cm) than during summer (July–September 1976–1999: 90% CI = 8.9–13.1

**Table 1.** Mean long-term (1976–1999;  $\pm$ SD) and 1999–2003 summer (July–September) and winter (November–April) rainfall (cm), Mazatzal Mountains, Arizona, USA.

| Year      | Summer            | Winter             |
|-----------|-------------------|--------------------|
| 1976–1999 | 11.0 ( $\pm$ 5.9) | 23.4 ( $\pm$ 12.1) |
| 1999      | 12.7              | 10.8               |
| 2000      | 4.1               | 9.8                |
| 2001      | 5.4               | 20.3               |
| 2002      | 5.6               | 5.7                |
| 2003      | 3.4               | 18.9               |

**Table 2.** Percentage changes in total desert bighorn sheep and lambs observed/hour and winter (November–April) rainfall and estimated proportions of populations removed by sport hunting and translocation, primary and reference study areas, Arizona, USA, 1994–1997.

| Population <sup>a</sup> | Total/hour | Lambs/hour | WIN <sup>b</sup> | Removal <sup>c</sup> |
|-------------------------|------------|------------|------------------|----------------------|
| MM                      | –75.1%     | –80.0%     | –37.7%           | 4.7%                 |
| Kofa NWR                | –31.8%     | –14.3%     | –56.3%           | 6.3%                 |
| PM                      | –17.5%     | –13.6%     | –53.4%           | 9.6%                 |

<sup>a</sup> MM = Mazatzal Mountains; Kofa NWR = Kofa National Wildlife Refuge; and PM = Plomosa Mountains.

<sup>b</sup> WIN = winter rainfall.

<sup>c</sup> Removal = estimated proportions of populations removed by sport hunting and translocation.

cm). Mean annual long-term rainfall during July–June between 1976 and 1999 was 38.0 cm (SD = 14.4, 90% CI = 33.0–43.1%). Rainfall between July 1999 and June 2000, July 2000 and June 2001, and July 2001 and June 2002 was 64% (24.5 cm), 98% (37.0 cm), and 30% (11.5 cm) of the mean long-term level for July to June, respectively.

Rainfall during winter (Table 1) exceeded that in summer for all periods examined, and drought conditions prevailed in summers between 2000 and 2003 and in winters during 1999, 2000, and 2002 (Table 1). Winter rainfall declined between 1994 and 1997 (Table 2) from 19.1 to 11.9 cm. Winter precipitation in 1995 (26.9 cm) and 1998 (33.6 cm) was higher than the long-term winter average, but drought occurred in the winters of 1996 (7.4 cm) and 1997 (11.9 cm). Winter rainfall in Mazatzal Mountains during 1999, 2000, and 2002 was less than half the long-term winter average and was about 85% and 79% of long-term average in 2001 and 2003, respectively, whereas summer rainfall was about 115% of long-term average in 1999 but less than half of long-term average from 2000 to 2003 (Table 1). Winter drought conditions occurred during 4/7 years between 1994 and 1999 compared to 2/4 years between 2000 and 2003.

**Reference Areas.**—Long-term annual rainfall between 1988 and 1998 in Kofa averaged 16.9 cm (90% CI = 12.8–21.0 cm) and in Plomosa Mountains between 1989 and 2003 averaged 13.5 cm (90% CI = 10.3–16.7 cm). Long-term winter rainfall in Kofa averaged 10.2 cm (90% CI = 5.6–14.7 cm) and in Plomosa Mountains averaged 8.4 cm (90% CI = 5.8–11.0 cm) for the same respective periods; winter rainfall declined on these areas between 1994 and 1997 (Table 2) from 8.0 to 3.5 cm and 8.8 to 4.1 cm,

respectively. Winter rainfall declined more on reference areas than in Mazatzal Mountains between 1994 and 1997 (Table 2). Long-term summer rainfall in Kofa and Plomosa Mountains averaged about 5.5 cm (90% CI = 3.4–7.6 cm) and 4.3 cm (90% CI = 1.8–6.7 cm), respectively. Drought occurred in Plomosa Mountains in 2000 and 2002, and winter rainfall in successive years between 1999 and 2003 was 7.5, 0.7, 9.1, 1.6, and 8.4 cm, respectively, below levels in Mazatzal Mountains during this period (Table 1).

### Population Surveys

**Mazatzal Mountains.**—Flight time during surveys in Mazatzal Mountains averaged about 4.3 min/km<sup>2</sup>, higher than average flight times/km<sup>2</sup> in Kofa (0.6 min/km<sup>2</sup>) and Plomosa Mountains (1.0 min/km<sup>2</sup>) reference areas. The desert bighorn sheep population in Mazatzal Mountains essentially was stable during 1989–1994, but the population declined between 1994 and 1999; observation rates for total animals, lambs, and yearlings and productivity all declined  $\geq 50\%$  during 1995–1999 compared to 1989–1994 (McKinney et al. 2001). Observation rates during annual aerial surveys of the Mazatzal Mountains desert bighorn sheep population declined between 1994 and 1997, and indices indicated relatively stable population abundance and low production and productivity during 1998–1999 (Tables 2, 3). Between 1994 and 1997, observation rates (Table 3) declined 75% for total desert bighorn sheep, 72% for females, 68% for males, and 80% for lambs, whereas productivity declined 23% (from 26 to 20). Total, adult, and yearling desert bighorn sheep observed/hour declined from 1999 through 2000, then equaled or exceeded 2000 levels from 2001 through 2003.

In comparison, production and productivity exceeded 1999 levels each year during 2000 through 2003. Between 2000 and 2003, observation rates about doubled for total desert bighorn sheep and males and increased about 180% and 48% for lambs and females, respectively (Table 3). Productivity increased from 0 in 1999 to between 23 and 73 between 2000 and 2003 and was 35 in 2003. Production was higher in 2000 than in 1999, although winter drought was comparable between the years; apparent desert bighorn sheep population growth lagged production by 1 year during 2000–2003 (Tables 1, 3). Production in 2001–2003 tended to vary with winter rainfall, but production remained above the 1999 level in the particularly severe drought during winter of 2002 (Tables 1, 3). Winter drought occurred with similar frequencies between 1994 and 1999, prior to mountain lion reductions and when the desert bighorn sheep population declined, and between

**Table 3.** Desert bighorn sheep observed/hour and flight hours during annual October helicopter surveys, Mazatzal Mountains, Arizona, USA, 1994–2003.

| Year              | Total/hour | Males/hour | Females/hour | Lambs/hour | Yearlings/hour | Flight hours |
|-------------------|------------|------------|--------------|------------|----------------|--------------|
| 1994              | 18.1       | 5.6        | 7.8          | 2.0        | 2.7            | 6.4          |
| 1995              | 10.1       | 3.7        | 4.5          | 0.9        | 1.1            | 6.5          |
| 1996              | 9.4        | 3.7        | 4.7          | 0.3        | 0.7            | 6.8          |
| 1997              | 4.5        | 1.8        | 2.2          | 0.4        | 0              | 6.7          |
| 1998              | 6.6        | 2.1        | 4.2          | 0.2        | 0.2            | 6.2          |
| 1999              | 6.7        | 1.7        | 4.1          | 0          | 0.9            | 6.4          |
| 2000 <sup>a</sup> | 4.0        | 1.1        | 2.1          | 0.5        | 0.3            | 6.2          |
| 2001              | 5.4        | 1.2        | 2.2          | 1.6        | 0.4            | 6.9          |
| 2002              | 9.1        | 2.3        | 4.1          | 1.3        | 0.8            | 6.4          |
| 2003              | 7.9        | 2.2        | 4.0          | 1.4        | 0.3            | 5.8          |

<sup>a</sup> Mountain lion reduction began.

2000 and 2003, when the population showed upward demographic trends.

Total desert bighorn sheep ( $F_{1,13} = 7.02$ ,  $r^2 = 0.3505$ ,  $P = 0.02$ ,  $b = 0.59$ ), males ( $F_{1,13} = 7.35$ ,  $r^2 = 0.3612$ ,  $P = 0.018$ ,  $b = 0.60$ ), females ( $F_{1,13} = 4.88$ ,  $r^2 = 0.2728$ ,  $P = 0.046$ ,  $b = 0.52$ ), and lambs ( $F_{1,13} = 7.05$ ,  $r^2 = 0.3517$ ,  $P = 0.02$ ,  $b = 0.59$ ) observed/hour in Mazatzal Mountains during 1989–2003 were positively correlated with November–April rainfall in the same year, but observation rates were independent of summer precipitation ( $F_{1,13} \leq 0.55$ ,  $P \geq 0.47$ ). During 1989–2003, yearlings observed/hour ( $F_{1,13} = 20.44$ ,  $r^2 = 0.7818$ ,  $P < 0.004$ ,  $b = 0.78$ ) and yearlings:100 females ( $F_{1,13} = 9.62$ ,  $r^2 = 0.6522$ ,  $P = 0.008$ ,  $b = 0.65$ ) were positively correlated with winter rainfall the previous year. Lambs and yearlings observed/hour during 1989–2003 were positively correlated ( $F_{1,13} \geq 21.07$ ,  $r^2 \geq 0.7864$ ,  $P < 0.001$ ,  $b \geq 0.79$ ) with total desert bighorn sheep observed/hour. Production also was positively correlated with recruitment ( $F_{1,13} = 16.41$ ,  $r^2 = 0.5776$ ,  $P < 0.002$ ,  $b = 0.76$ ) during this period. Ground surveys indicated that lambing occurred primarily between January and March between 2000 and 2003. However, most lambing occurred during January–February in 2000, 2001, and 2002, but most lambs were born during late February through March in 2003.

Coefficient of variation (CV) for lambs surveyed/hour (0.84) between 1989 and 2003 was about double that for total desert bighorn sheep (0.48), adults (0.41), males (0.49), and females (0.44) and comparable to that for yearlings (0.78). Group size declined between 1989 and 2003 ( $\bar{x} = 4.6$ ,  $CV = 0.24$ ,  $r = -0.6726$ ,  $P = 0.006$ ) but was independent of total desert bighorn sheep observed/hour ( $P = 0.215$ ). Mean group size was highest during 1989–1994 ( $\bar{x} = 5.4$ , 90% CI = 4.4–6.4), and was lower during 1995–1999 ( $\bar{x} = 4.3$ , 90% CI = 3.5–4.0) and was not different between 1995 and 1999 and between 2000 and 2003 ( $\bar{x} = 3.9$ , 90% CI = 3.4–4.9).

**Reference Areas.**—We omitted statistical analyses of temporal trends in desert bighorn sheep survey results for Kofa because surveys were not conducted in 6/15 years (i.e., 1993, 1995, 1996, 1998, 1999, and 2001). In comparison, surveys in Plomosa Mountains were conducted during 12/15 years (i.e., omitted in 1998, 2000, and 2001), and we analyzed temporal trends statistically for 1989–2003. Total desert bighorn sheep observed/hour in Plomosa Mountains declined ( $r = -0.7795$ ,  $P = 0.008$ ) during 1989–1999, but lambs/hour showed no temporal trend ( $r = -0.3149$ ,  $P = 0.35$ ). Observation rates increased between 1999 and 2003 in Plomosa Mountains for total desert bighorn sheep (10.0–18.0/hour), lambs (0.4–1.6/hour), and productivity (7–16). Coefficients of variation in Plomosa Mountains for lambs (0.64) and yearlings (0.68) surveyed/hour during 1989–2003 were higher than that for total desert bighorn sheep (0.23), and CVs for these groups were lower than for the Mazatzal Mountains population. During 1989–2003, lambs observed/hour in Plomosa Mountains in year  $n$  were positively correlated with total desert bighorn sheep ( $F_{1,9} = 5.23$ ,  $r^2 = 0.6063$ ,  $P = 0.048$ ,  $b = 0.61$ ) and yearlings ( $F_{1,9} = 6.22$ ,  $r^2 = 0.4088$ ,  $P = 0.034$ ,  $b = 0.64$ ) observed/hour in year  $n + 1$ . Mean group size in Plomosa Mountains ( $\bar{x} = 2.4$ , 90% CI = 2.2–2.5) showed no trend and was smaller than on the primary study area.

Total desert bighorn sheep observed/hour (Table 2) declined

during 1994–1997 in Kofa from 8.8 to 6.0 and in Plomosa Mountains from 11.4 to 9.4. Lambs observed/hour (Table 2) decreased during 1994–1997 in Kofa from 0.7 to 0.6 and in Plomosa Mountains from 2.2 to 1.9. Comparing survey results in 1994 and 1997, productivity increased from 13 to 20, respectively, in Kofa but showed no change in Plomosa Mountains (41 and 41, respectively). Estimated proportional declines of desert bighorn sheep on primary study and reference areas during 1994–1997 were independent of animals removed by sport hunting and translocations (Table 2).

During 1989–1999, total desert bighorn sheep ( $F_{1,8} = 16.22$ ,  $r^2 = 0.6697$ ,  $P < 0.004$ ,  $b = 0.82$ ) and yearlings ( $F_{1,8} = 6.93$ ,  $r^2 = 0.4641$ ,  $P = 0.030$ ,  $b = 0.68$ ) observed/hour during surveys in Plomosa Mountains and yearlings observed in Kofa ( $F_{1,4} = 15.59$ ,  $r^2 = 0.7958$ ,  $P = 0.017$ ,  $b = 0.89$ ) were positively correlated with winter (November–April) rainfall. Total desert bighorn sheep, lambs, and yearlings observed/hour on reference areas were independent of summer precipitation ( $P \geq 0.08$ ).

Between 1994 and 1997, observation rates of total desert bighorn sheep and lambs declined more rapidly in Mazatzal Mountains than in Kofa and Plomosa Mountains despite greater decreases in winter rainfall on reference areas (Table 2). Total desert bighorn sheep observed/hour declined between 1994 and 1997 from 18.1 to 4.5 in Mazatzal Mountains, 8.8 to 6.0 in Kofa, and 11.4 to 9.4 in Plomosa Mountains. Lambs observed/hour on these respective areas decreased between 1994 and 1997 from 2.0 to 0.4, 0.7 to 0.6, and 2.2 to 1.9. Between 1999 and 2003, observation rates of total desert bighorn sheep (1999 = 10.0/hour, 2003 = 18.0/hour) and lambs (1999 = 0.4/hour, 2003 = 1.6/hour) and productivity (1999 = 7, 2003 = 16) increased in Plomosa Mountains.

## Disease Exposure

We collected blood (Table 4) and other samples from 20 adult desert bighorn sheep (11 females, 9 males) during 51 captures of individual animals between June 2000 and October 2002. Sample sizes in any given year ranged from 30% to 87% of adult desert bighorn sheep counted during helicopter surveys in respective years. Males and females did not differ in evidence of disease exposure (Yates adjusted chi-square:  $\chi^2 \leq 1.91$ ,  $df = 1$ ,  $P \geq 0.17$ ), and we combined sexes to analyze results of disease testing. We observed no clinical signs of disease in any captured animal, and animals appeared to be healthy and in good condition based on external examinations.

**Table 4.** Seroprevalence (calculated only from test results that could be evaluated; no. animals with positive titers/no. of animals sampled) of selected disease agents in samples collected from desert bighorn sheep, Mazatzal Mountains, Arizona, USA, 2000–2002.

| Date         | LEP <sup>a</sup> | CE <sup>a</sup> | BT <sup>a</sup> | EHD <sup>a</sup> | BRSV <sup>a</sup> |
|--------------|------------------|-----------------|-----------------|------------------|-------------------|
| June 2000    | 0/6              | 4/4             | 3/6             | 4/6              | 6/6               |
| April 2001   | 4/5              | 4/4             | 1/5             | 1/5              | 3/5               |
| October 2001 | 1/15             |                 | 6/15            | 9/15             | 14/15             |
| April 2002   | 11/12            | 7/7             | 5/12            | 7/12             | 4/12              |
| October 2002 | 7/13             | 7/8             | 8/13            | 9/13             | 5/13              |

<sup>a</sup> LEP = leptospirosis; CE = contagious ecthyma; BT = bluetongue; EHD = epizootic hemorrhagic disease; BRSV = bovine respiratory syncytial virus.

**Table 5.** Mean seasonal mineral concentrations (ppm dry wt) and Ca:P ratios of desert bighorn sheep forage classes, Mazatzal Mountains, Arizona, USA, July 2000–June 2001.

| Forage  | Months           | Minerals |      |       |        |       |      |      |       |      |      |      |
|---------|------------------|----------|------|-------|--------|-------|------|------|-------|------|------|------|
|         |                  | Ca       | Cu   | Fe    | K      | Mg    | Mn   | Na   | P     | Se   | Zn   | Ca:P |
| Browse  | July–September   | 18,524   | 8.93 | 126.1 | 15,459 | 3,237 | 59.8 | 81.5 | 1,462 | 0.16 | 23.8 | 12.7 |
|         | October–December | 18,871   | 7.95 | 151.6 | 13,859 | 3,154 | 59.9 | <50  | 1,865 | 0.14 | 21.1 | 10.1 |
|         | January–March    | 18,418   | 7.85 | 118.3 | 13,510 | 2,726 | 58.3 | 57   | 1,957 | 0.13 | 21.8 | 9.4  |
|         | April–June       | 19,096   | 8.32 | 138.8 | 15,190 | 2,891 | 61.6 | 59.8 | 1,621 | 0.16 | 24.9 | 11.8 |
| Forbs   | July–September   | 13,523   | 7.49 | 152.3 | 15,650 | 2,128 | 48.3 | <50  | 1,488 | 0.14 | 27.7 | 9.1  |
|         | October–December | 21,433   | 9.86 | 277.3 | 15,967 | 3,027 | 78.5 | <50  | 2,220 | 0.14 | 29.0 | 9.7  |
|         | January–March    | 18,033   | 7.52 | 135.3 | 17,393 | 2,157 | 82.2 | <50  | 2,107 | 0.13 | 26.7 | 8.6  |
|         | April–June       | 13,463   | 7.60 | 151.0 | 16,293 | 2,033 | 51.3 | <50  | 1,643 | 0.19 | 27.4 | 8.2  |
| Grasses | July–September   | 2,977    | 4.47 | 337.7 | 8,227  | 1,031 | 74.5 | <50  | 727   | 0.12 | 16.6 | 4.1  |
|         | October–December | 2,927    | 5.78 | 171.6 | 8,620  | 1,138 | 46.7 | <50  | 983   | 0.12 | 21.0 | 0.3  |
|         | January–March    | 3,300    | 21.0 | 384.7 | 6,777  | 1,066 | 87.9 | <50  | 962   | 0.08 | 21.0 | 3.4  |
|         | April–June       | 3,103    | 4.33 | 257.0 | 7,107  | 1,156 | 83.2 | <50  | 758   | 0.09 | 14.5 | 4.1  |

**Serology.**—Seroprevalence of antibodies against viruses varied with respect to disease agents (Table 4). We tested 50 serum samples for antibody to CE and 51 samples for antibodies against other disease organisms during 2000–2002 (Table 4). Results were reported anticomplementary or nonspecific for 27 samples tested for CE. Nine desert bighorn sheep and 22 samples had complement-fixing antibody titers to CE, ranging from 1:5 to 1:10. Sera from 9 desert bighorn sheep and 20 samples had serum-neutralizing antibody to BT virus (serotypes 2, 10, 11, 13, and 17); titers ranged from 1:10 to  $\geq$ 1:80. Fourteen animals and 23 samples had serum-neutralizing antibody to EHD (serotypes 1 and 2); titers ranged from 1:40 to  $\geq$ 1:80. Fifteen desert bighorn sheep and 32 samples had serum-neutralizing antibody to BRSV; titers ranged from 1:4 to 1:32. Fifteen animals sampled and 23 samples had low levels of antileptospiral antibody at the lowest dilutions (1:100). Reactive leptospiral serovars were *L. icterohemorrhagiae* (15/23), followed by *L. bratislava* (8/23), *L. szwajizak* (7/23), and *L. canicola* (1/23); *L. szwajizak* antibody first appeared in animals captured October 2002, when it was the only serovar found.

Seroprevalence of antibodies against CE, BRSV, and EHD viruses tended to be higher than for other diseases (Table 4), and there were no detectable levels of antibody to BVD, IBR, or PI-3 viruses. Fifteen desert bighorn sheep were negative to detectable antibody to chlamydia during 2000–2001, but 11 of 13 desert bighorn sheep tested in 2002 had antibody titers ranging from 1:4 to 1:8. Sera from 17 of 20 (85%) individual desert bighorn sheep had antibody to multiple diseases.

**Bacteriology.**—Nasal and pharyngeal swab samples from 20 desert bighorn sheep were cultured aerobically. Aerobic bacteria were isolated from nasal swabs of 7 (35%) animals, including *Mannheimia haemolytica* ( $n = 4$ ; formerly *Pasteurella haemolytica*; Miller 2001), *Pasteurella multocoda* ( $n = 1$ ), and *Staphylococcus aureus* ( $n = 2$ ). Aerobic bacteria were isolated from pharyngeal swabs of 12 of 16 (75%) animals, including *M. haemolytica* ( $n = 3$ ), *Pasteurella* spp. ( $n = 3$ ), and *S. aureus* ( $n = 9$ ).

**Parasites.**—Ear swab samples were negative for *Psoroptes* spp., and ear ticks were found only in October. Light infestations of *Dermacentor hunteri* were found in ears of 10 of 15 (67%) and 11 of 13 (85%) desert bighorn sheep captured in 2001 and 2002, respectively (Fisher exact test,  $df = 1$ ,  $P = 0.39$ ). Fecal samples

collected from 16 desert bighorn sheep were negative for nematode eggs.

### Nutritional Status

**Vegetation.**—Browse analyzed for mineral concentrations included mesquite (*Prosopis glandulosa*), coursetia (*Coursetia glandulosa*), brittlebush (*Encelia farinosa*), catclaw (*Acacia greggii*), Mormon tea (*Ephedra* spp.), little-leaf paloverde (*Parkinsonia microphylla*), wild buckwheat (*Erigonum fasciculatum*), desert lavender (*Hyoptis emoryi*), white ratany (*Krameria grayi*), creosotebush (*Larrea tridentata*), jojoba (*Simmondsia chinensis*), ocotillo (*Fouquieria splendens*), turpentine brush (*Aplopappus* spp.), and fairy duster (*Calliandra eriophylla*). Forbs analyzed included ditaxis (*Argythamnia lanceolata*), mallow (*Abutilon* spp.), spurge (*Euphorbia* spp.), and globe mallow (*Sphaeralcea ambigua*); grasses included three-awn (*Aristida* spp.), tanglehead (*Heteropogon contortus*), and sideoats grama (*Bouteloua curtipendula*). Numbers of forb and grass species sampled were restricted by our inability to obtain quantitative representative samples during various months.

Mineral concentrations of browse, forbs, and grasses (Table 5) varied, and most in general appeared to be higher between autumn and spring. Concentration of P in browse ( $\bar{x} = 1,337$  ppm, 90% CI = 1,210–1,464 ppm) was greater than in forbs ( $\bar{x} = 628$  ppm, 90% CI = 341–914 ppm) and grasses ( $\bar{x} = 560$  ppm, 90% CI = 476–645 ppm) during the drier sampling periods of 1999–2000 (rainfall = 24.5 cm). In comparison, levels of P in browse ( $\bar{x} = 1,726$  ppm, 90% CI = 1,460–1,952 ppm) and forbs ( $\bar{x} = 1,865$  ppm, 90% CI = 1,448–2,281 ppm) did not differ during the wetter sampling periods of 2000–2001 (rainfall = 41.7 cm). Mean concentration of P in browse during 2000–2001 ( $\bar{x} = 1,726$  ppm, 90% CI = 1,460–1,992 ppm) tended to be higher than in 1999–2000 ( $\bar{x} = 1,337$  ppm, 90% CI = 1,210–1,464 ppm). Mean concentrations of P in forbs ( $\bar{x} = 1,865$  ppm, 90% CI = 1,448–2,281 ppm) and grasses ( $\bar{x} = 858$  ppm, 90% CI = 700–1,015 ppm) in 2000–2001 exceeded levels in forbs ( $\bar{x} = 628$  ppm, 90% CI = 34–914 ppm) and grasses ( $\bar{x} = 560$  ppm, 90% CI = 476–645 ppm) in 1999–2000.

Mean concentration of Ca in forbs was higher during 2000–2001 ( $\bar{x} = 16,613$  ppm, 90% CI = 12,070–21,156 ppm) than in 1999–2000 ( $\bar{x} = 7,514$  ppm, 90% CI = 5,524–9,504 ppm). Mean concentrations of Ca in browse during 1999–2000 ( $\bar{x} = 18,686$  ppm,

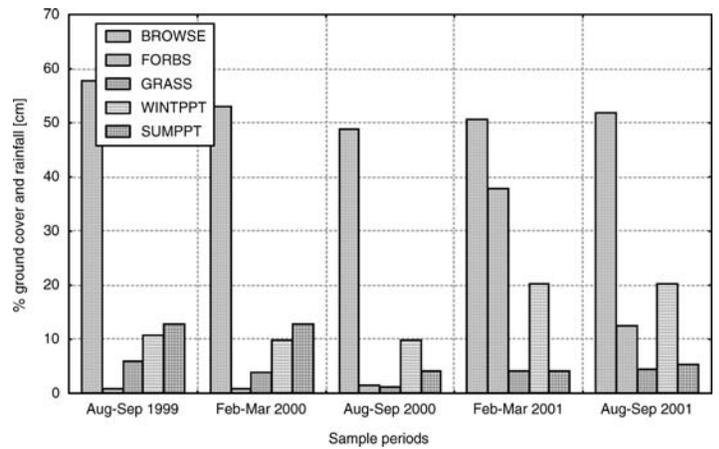
90% CI = 17,098–19,474 ppm) and 2000–2001 ( $\bar{x}$  = 18,727 ppm, 90% CI = 18,359–19,095 ppm) did not differ. Levels of Ca in browse ( $\bar{x}$  = 18,286 ppm, 90% CI = 17,098–19,474 ppm) exceeded levels in forbs ( $\bar{x}$  = 7,514 ppm, 90% CI = 5,524–9,504 ppm) in 1999–2000, but levels of Ca in browse ( $\bar{x}$  = 18,727 ppm, 90% CI = 18,359–19,085 ppm) and forbs ( $\bar{x}$  = 16,613 ppm, 90% CI = 12,070–21,156) did not differ in 2000–2001. Mean concentrations of Ca in grasses during 1999–2000 ( $\bar{x}$  = 4,116 ppm, 90% CI = 1,385–6,847 ppm) and 2000–2001 ( $\bar{x}$  = 3,077 ppm, 90% CI = 2,881–3,272 ppm) did not differ.

Ratios of Ca:P were narrower for forbs than browse in each sampling period and were narrower for grasses than for browse and forbs. Ratios of Ca:P tended to be narrower between winter and spring for browse and forbs and narrower for grasses during autumn. Ratios of Ca:P for browse ( $\bar{x}$  = 11.0, 90% CI = 9.2–12.8) and forbs ( $\bar{x}$  = 8.9, 90% CI = 8.1–9.7) did not differ in 2000–2001. Mean Ca:P ratio of forbs during 2000–2001 ( $\bar{x}$  = 8.8, 90% CI = 8.1–9.7) was narrower than the ratio in 1999–2000 ( $\bar{x}$  = 15.3, 90% CI = 11.7–18.9). The Ca:P ratio of browse in 2000–2001 ( $\bar{x}$  = 11.0, 90% CI = 9.2–12.8) was narrower than in 1999–2000 ( $\bar{x}$  = 15.7, 90% CI = 14.0–17.3). Mean Ca:P ratios for grasses in 2000–2001 ( $\bar{x}$  = 3.0, 90% CI = 0.8–5.1) and 1999–2000 ( $\bar{x}$  = 5.3, 90% CI = 4.6–6.1) did not differ.

Mean concentrations of K in browse (1999–2000  $\bar{x}$  = 14,064 ppm, 90% CI = 12,692–15,436 ppm; 2000–2001  $\bar{x}$  = 14,693 ppm, 90% CI = 13,162–16,203 ppm), forbs (1999–2000  $\bar{x}$  = 13,378 ppm, 90% CI = 10,946–15,810 ppm; 2000–2001  $\bar{x}$  = 16,275 ppm, 90% CI = 13,461–19,089 ppm), and grasses (1999–2000  $\bar{x}$  = 6,588 ppm, 90% CI = 4,870–8,306 ppm; 2000–2001  $\bar{x}$  = 6,259 ppm, 90% CI = 4,923–7,595 ppm) did not differ within forage classes between 1999–2000 and 2000–2001. Ratios of K:Ca for browse ( $\bar{x}$  = 0.77, 90% CI = 0.62–0.92) and forbs ( $\bar{x}$  = 0.83, 90% CI = 0.68–0.97) were lower than for grasses ( $\bar{x}$  = 2.46, 90% CI = 1.56–3.35) during 1999–2000, and did not differ from those of browse ( $\bar{x}$  = 0.77, 90% CI = 0.71–0.83), forbs ( $\bar{x}$  = 0.76, 90% CI = 0.22–1.30), and grasses ( $\bar{x}$  = 2.51, 90% CI = 2.03–2.99) in 2000–2001.

Mean concentrations of Na in browse, forbs, and grasses during 1999–2000 were 100.9 ppm (90% CI = 81.5–140.3 ppm), 40.8 ppm (90% CI = 29.3–52.2), and 27.8 ppm (90% CI = 20.6–35.1 ppm), respectively. Sodium concentrations for forage classes during 2000–2001 were reported by the laboratory as  $\leq 50$  ppm or concentrations measured at higher levels, precluding direct comparisons between years of Na levels and Na:K ratios. However, proportion of browse species with Na concentrations  $< 50$  ppm was lower in 1999–2000 (45.3%) than in 2000–2001 (89.1%;  $\chi^2 = 26.16$ ,  $P < 0.001$ ). Proportion of forb species with Na levels  $< 50$  ppm tended to be higher in 2000–2001 than in 1999–2000 (1999–2000 = 66.7% vs. 2000–2001 = 100%; Yates adjusted chi-square:  $\chi^2 = 2.83$ ,  $P = 0.09$ ), but proportion of grass species with Na levels  $< 50$  ppm was 100% both years.

During 2000–2001, levels of Se in browse ( $\bar{x}$  = 0.15 ppm, 90% CI = 0.13–0.17 ppm), and Zn in forbs ( $\bar{x}$  = 27.7 ppm, 90% CI = 26.6–28.8 ppm) and grasses ( $\bar{x}$  = 18.3 ppm, 90% CI = 14.4–22.1 ppm) were higher than Se levels in browse ( $\bar{x}$  = 0.12 ppm, 90% CI = 0.11–0.13 ppm), and concentrations of Zn in forbs ( $\bar{x}$  = 21.4 ppm, 90% CI = 19.0–23.8 ppm) and grasses ( $\bar{x}$  = 12.7 ppm, 90%



**Figure 3.** Percent ground cover of browse, forbs, and grass, and seasonal rainfall (WINTPPT = November–April; SUMPPT = July–September), Mazatzal Mountains, Arizona, USA, August–September (Aug–Sept) 1999, 2000, and 2001 and February–March (Feb–March) 2000 and 2001.

CI = 11.7–13.6 ppm) than in 1999–2000. Mean concentration of Fe in browse was lower in 2000–2001 ( $\bar{x}$  = 133.7 ppm, 90% CI = 116.5–150.9 ppm) than in 1999–2000 ( $\bar{x}$  = 200.8 ppm, 90% CI = 163.3–238.4 ppm). Mean levels of Cu, Mg, and Mn in browse, forbs, and grasses did not differ between forage classes or between years within forage classes.

Occurrences of moderate (range = 0.5–4.2%) and heavy (range = 0–0.9%) hedging on all sites were similar during August–September 1999 and February–March 2000 and were apparent on only about 2% of 6,499 individual browse or forb plants for combined sampling periods. Aboveground portions of grasses generally were dead during sampling periods, and we were unable to estimate levels of use. Ground cover of forbs and grass tended to increase primarily with higher winter rainfall, whereas ground cover of browse appeared to be independent of rainfall levels (Fig. 3). Coverage of bare ground ranged from a high of 52.4% in August–September 2000 (90% CI = 47.4–57.5%) to a low of 31.4% in February–March 2001 (90% CI = 25.3–37.4%).

**Diets.**—Diets of adults (Table 6) based on analyses of feces were dominated by browse between the summer of 1999 (July–August) and the winter of 2000 (January–February), followed by forbs, grass, and sedges-lichens-moss-berries-seeds-nuts. However, forbs exceeded browse and browse continued to exceed grass in diets from the spring of 2000 (March–April) through the summer of 2002 (May–June). Percentages of forbs in adult diets increased between July–August 1999 and May–June 2002 ( $r = 0.5336$ ,  $P = 0.023$ ), whereas percentages of browse ( $r = -0.5199$ ,  $P = 0.027$ ) declined. Percentage of forbs in diets tended to be lower within sampling years in July–August 1999 and 2000, September–October 2001, and March–June 2002. In comparison, percentage of browse peaked in January–February 2000 and exhibited other seasonal increases in July–August 2000, January–February 2001, and March–June 2002.

Mean annual (July–August to May–June) consumption (indexed by % composition in feces) of forbs during 2001–2002 ( $\bar{x}$  = 63.58%, 90% CI = 53.81–73.36%) was greater than in 1999–2000 ( $\bar{x}$  = 30.08%, 90% CI = 24.68–51.49%), whereas mean annual consumption of browse in 2001–2002 ( $\bar{x}$  = 24.97%, 90%

**Table 6.** Percent fecal neutral detergent fiber (FNDF), forbs, browse, grass, and other forages<sup>a</sup> for adult desert bighorn sheep, Mazatzal Mountains, Arizona, USA, 1999–2002.

| Years | Months            | FNDF | Forbs | Browse | Grass | Other <sup>a</sup> |
|-------|-------------------|------|-------|--------|-------|--------------------|
| 1999  | July–August       | 62.9 | 22.4  | 39.1   | 32.2  | 6.3                |
|       | September–October | 53.1 | 33.1  | 47.5   | 16.7  | 2.9                |
|       | November–December | 53.0 | 27.7  | 52.9   | 12.3  | 7.3                |
| 2000  | January–February  | 55.4 | 28.7  | 62.9   | 1.5   | 6.9                |
|       | March–April       | 56.1 | 53.6  | 43.9   | 1.5   | 0.5                |
|       | May–June          | 57.5 | 63.0  | 28.8   | 4.5   | 4.2                |
| 2001  | July–August       | 53.3 | 39.6  | 42.2   | 8.6   | 8.6                |
|       | September–October | 57.3 | 53.5  | 27.7   | 14.7  | 14.7               |
|       | November–December | 52.6 | 58.7  | 33.1   | 8.0   | 8.0                |
|       | January–February  | 57.4 | 49.8  | 39.6   | 9.2   | 9.2                |
|       | March–April       | 49.9 | 62.7  | 29.3   | 4.3   | 4.3                |
|       | May–June          | 57.1 | 62.7  | 28.3   | 4.5   | 4.5                |
| 2002  | July–August       | 53.3 | 57.7  | 20.9   | 14.7  | 7.3                |
|       | September–October | 57.0 | 55.0  | 26.5   | 13.2  | 5.7                |
|       | November–December | 52.2 | 75.3  | 19.6   | 4.0   | 1.1                |
| 2002  | January–February  | 57.8 | 80.9  | 17.3   | 1.0   | 0.8                |
|       | March–April       | 49.8 | 61.5  | 27.1   | 7.9   | 3.5                |
|       | May–June          | 57.8 | 51.1  | 38.4   | 2.3   | 8.2                |

<sup>a</sup> Sedges, lichens, moss, and berries, seeds, and nuts.

CI = 18.69–31.25%) was lower than in 1999–2000 ( $\bar{x}$  = 48.85, 90% CI = 36.23–55.47%). Percentages of browse and forbs in the adult diet were negatively correlated ( $F_{1, 16} = 39.72$ ,  $r^2 = 0.7128$ ,  $P < 0.001$ ,  $b = -0.84$ ), and number of forbs identified that comprised  $\geq 5\%$  of adult diets was positively correlated with total rainfall during 2 months prior to diet sampling ( $F_{1, 16} = 5.29$ ,  $r^2 = 0.2484$ ,  $P = 0.035$ ,  $b = 0.50$ ).

Percentage of grass in adult diets tended to be higher during summer to autumn 1999–2001 than through winter to early summer but increased in March–April 2002 and declined ( $r = -0.4829$ ,  $P = 0.042$ ) during 1999–2002. Percentages of sedges, lichens, moss, berries, seeds, and nuts in adult diets evidenced little clear annual or seasonal trend (Table 6). Grasses comprised similar proportions of desert bighorn sheep diets during 1999–2000 ( $\bar{x}$  = 11.5%, 90% CI = 1.7–21.2%), 2000–2001 ( $\bar{x}$  = 8.2%, 90% CI = 5.1–11.4%), and 2001–2002 ( $\bar{x}$  = 7.2%, 90% CI = 2.5–11.9%). Mean percentages of sedges, lichens, moss, berries, seeds, and nuts as a forage group in adult diets did not differ among years (1999–2000  $\bar{x}$  = 4.7%, 90% CI = 2.5–6.9%; 2001–2002  $\bar{x}$  = 4.4%, 90% CI = 1.9–7.0%), although the mean was nearly 2-fold higher during 2000 to 2001 ( $\bar{x}$  = 8.2%, 90% CI = 5.1–11.4%). Adult desert bighorn sheep ate 33–37 plant species each year between July–August and May–June sampling periods. Number of species comprising  $\geq 5\%$  of the diet each year (8–9) included 3–6 forbs and 1–4 browse. The number of grass species comprising  $\geq 5\%$  of the diet increased to a maximum of 2 only during the wetter summer of 1999.

Forbs predominated in lamb diets (based on analyses of feces) each year during 2001 through 2003, followed by browse, grass, and combined sedges, lichens, moss, berries, seeds, and nuts (Table 7). Percentages of sedges, lichens, moss, berries, seeds, and nuts tended to be similar in adult and lamb diets (Tables 6, 7). Mean percentage of this food group eaten by lambs did not differ among years (2001  $\bar{x}$  = 9.0%, 90% CI = 2.2–15.8%; 2002  $\bar{x}$  = 4.6%, 90% CI = 0.23–8.9%; 2003  $\bar{x}$  = 6.4%, 90% CI = 5.0–7.8%). Lambs ate 35–45 plant species each year, and 3–5 each of

**Table 7.** Percent fecal neutral detergent fiber (FNDF), forbs, browse, grass, and other forages<sup>a</sup> for desert bighorn sheep lambs, Mazatzal Mountains, Arizona, USA, 2001–2003.

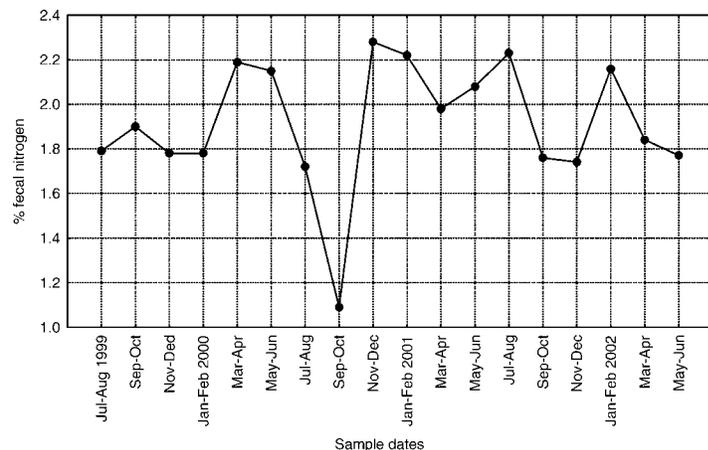
| Years | Months   | FNDF | Forbs | Browse | Grass | Other <sup>a</sup> |
|-------|----------|------|-------|--------|-------|--------------------|
| 2001  | March    | 45.2 | 49.1  | 28.1   | 19.7  | 2.1                |
|       | April    | 51.6 | 55.5  | 40.3   | 1.8   | 2.4                |
|       | May      | 45.2 | 55.0  | 37.4   | 4.9   | 2.7                |
| 2002  | June     | 51.6 | 58.0  | 28.1   | 3.8   | 10.1               |
|       | February | 50.5 | 60.2  | 33.6   | 1.2   | 5.0                |
|       | March    | 51.8 | 48.1  | 31.0   | 15.5  | 5.4                |
|       | April    | 57.0 | 55.1  | 31.1   | 5.4   | 8.4                |
|       | May      | 57.3 | 60.7  | 30.0   | 5.0   | 4.3                |
|       | June     | 57.2 | 53.0  | 35.1   | 3.8   | 8.1                |
| 2003  | July     | 57.5 | 37.4  | 53.6   | 1.7   | 7.3                |
|       | April    | 62.5 | 58.8  | 20.9   | 14.3  | 4.8                |
|       | May      | 64.3 | 51.9  | 42.0   | 2.9   | 3.2                |
|       | June     | 64.6 | 43.8  | 38.0   | 4.7   | 13.5               |
| July  | 61.8     | 47.6 | 36.2  | 1.8    | 14.4  |                    |

<sup>a</sup> Sedges, lichens, moss, and berries, seeds, and nuts.

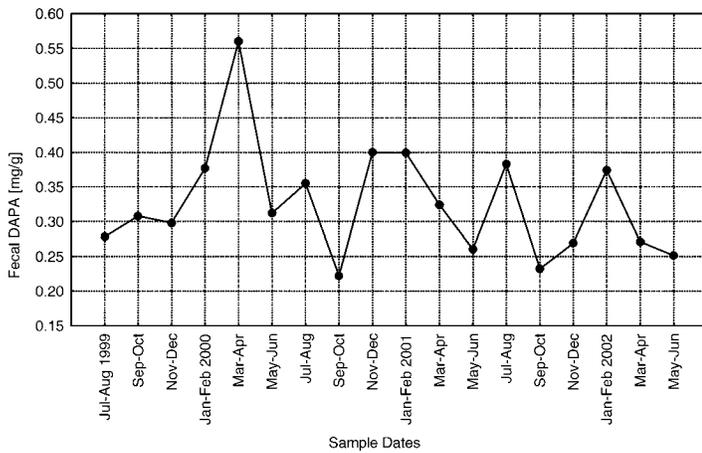
forbs and browse species comprised  $\geq 5\%$  of diets in any month. Lambs ate more grass during spring (February–April) than during other months, and grass consumption by lambs in spring exceeded that by adults (Tables 6, 7).

**Fecal Nutrients.**—Levels of nitrogen (Fig. 4) and DAPA (Fig. 5) in feces of adult desert bighorn sheep showed differences corresponding with winter but not summer rainfall. Mean concentrations of FN and FDAPA (Table 8) also did not differ among years for the July–August to May–June sampling periods. Fecal nitrogen levels increased during winter to spring each year, but differences in durations of higher concentrations corresponded with winter rainfall. During lower winter rainfall in 2000 (41% of long-term average), highest concentrations of FN extended from March–April to May–June, whereas during lowest winter rainfall in 2002 (24% of long-term average), highest levels of FN occurred only in January–February. In contrast, highest concentrations of FN extended from November–December 2000 through July–August 2001, corresponding with highest winter rainfall during our study, a level that neared long-term average (Table 1).

Compared to FN, concentrations of FDAPA less clearly showed trends corresponding to levels of winter rainfall (Figs. 5, 6;



**Figure 4.** Fecal nitrogen concentrations (%) for adult desert bighorn sheep, Mazatzal Mountains, Arizona, USA, July–August 1999 to May–June 2002.



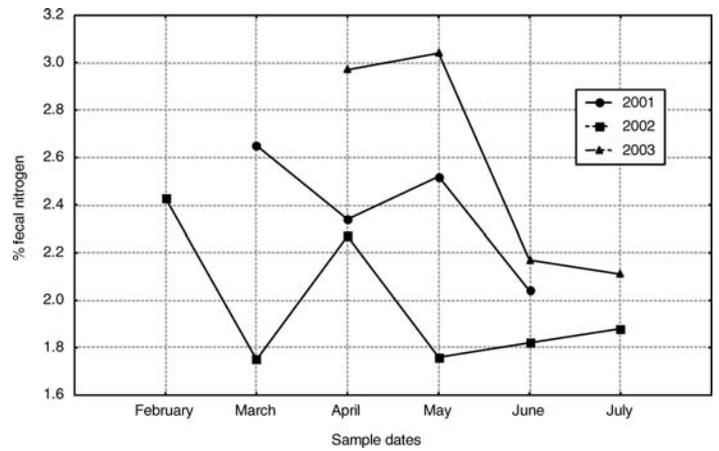
**Figure 5.** Fecal 2,6-diaminopimelic acid (DAPA) concentrations (mg/g) for adult desert bighorn sheep, Mazatzal Mountains, Arizona, USA, July–August 1999 to May–June 2002.

Table 1), but positive correlation of these variables with each other ( $F_{1, 16} = 10.55$ ,  $r^2 = 0.3973$ ,  $P = 0.005$ ,  $b = 0.63$ ) supported similarity of trends. Concentrations of FDAPA increased during winter and summer and were lowest in autumn, and highest levels were more prolonged in the wettest year of 2001, compared to drier years of 1999 and 2002. Although adult FN and FDAPA concentrations showed patterns associated with winter rainfall, total rainfall during and 1 or 2 months prior to fecal sampling periods did not correlate ( $F_{1, 16} \leq 2.3$ ,  $P \geq 0.14$ ) with concentrations of FN, FDAPA, FNDF, or % browse, forbs, grasses, and combined sedges-lichens-moss-berries-seeds-nuts in the diet (Table 6).

Percent FNDF (Table 6) appeared to vary without clear pattern (1999–2000: 56.3%, 90% CI = 53.3–59.4%; 2000–2001: 54.6%, 90% CI = 52.0–57.2%; 2001–2002: 54.7%, 90% CI = 51.9–57.4%) and was independent of rainfall in either season (Table 1). Fecal N and FDAPA were positively correlated for adults, whereas neither FN nor FDAPA were correlated with FNDF ( $P \geq 0.76$ ). Concentrations of FDAPA and FNDF were not correlated ( $F_{1, 16} \leq 1.54$ ,  $r^2 \leq 0.10$ ,  $P \geq 0.20$ ) with percentages of browse, forbs, or combined sedges, lichens, moss, berries, seeds, and nuts in the adult diet. Concentrations of FN were negatively correlated ( $F_{1, 16} = 5.45$ ,  $r^2 = 0.2541$ ,  $P = 0.033$ ,  $b = -0.50$ ) with percentage of combined sedges, lichens, moss, berries, seeds, and nuts in the diet, but were not correlated ( $F_{1, 16} \leq 1.43$ ,  $P \geq 0.24$ ) with percentages of browse, forbs, or grasses in the diet.

**Table 8.** Mean (90% CI in parentheses) concentrations of fecal nitrogen (FN; %) and 2,6-diaminopimelic acid (FDAPA; mg/g) of desert bighorn sheep adults and lambs, Mazatzal Mountains, Arizona, USA, July–June 1999–2002 (adults) and 2001–2003 (lambs).

|        | Year      | FN               | FDAPA            |
|--------|-----------|------------------|------------------|
| Adults | 1999–2000 | 1.93 (1.77–2.09) | 56.3 (53.3–59.4) |
|        | 2000–2001 | 1.90 (1.53–2.26) | 54.6 (52.0–57.2) |
|        | 2001–2002 | 1.92 (1.74–2.10) | 54.7 (51.9–57.4) |
| Lambs  | 2001      | 2.39 (2.08–2.70) | 0.41 (0.20–0.61) |
|        | 2002      | 1.99 (1.75–2.22) | 0.34 (0.20–0.49) |
|        | 2003      | 2.57 (1.98–3.16) | 0.38 (0.27–0.49) |



**Figure 6.** Fecal nitrogen concentrations (%) for desert bighorn sheep lambs, Mazatzal Mountains, Arizona, USA, 2001–2003.

Specifically, FN was not correlated with diet composition of browse ( $F_{1, 16} = 0.22$ ,  $r^2 = 0.0135$ ,  $P = 0.65$ ) or forbs ( $F_{1, 16} = 1.43$ ,  $r^2 = 0.0823$ ,  $P = 0.25$ ), but fecal phosphorus (FP) tended to increase with FN ( $F_{1, 16} = 3.86$ ,  $r^2 = 0.1945$ ,  $P = 0.067$ ,  $b = 0.44$ ). Fecal DAPA ( $F_{1, 16} \leq 1.76$ ,  $r^2 \leq 0.10$ ,  $P \geq 0.20$ ), FNDF ( $F_{1, 16} \leq 2.09$ ,  $r^2 \leq 0.12$ ,  $P \geq 0.17$ ), and FP ( $F_{1, 16} \leq 1.62$ ,  $r^2 \leq 0.09$ ,  $P \geq 0.22$ ) concentrations were independent of percentage diet composition of forage classes. Number of forb species comprising  $\geq 5\%$  of adult diets was positively correlated with FP ( $F_{1, 16} = 15.85$ ,  $r^2 = 0.4976$ ,  $P = 0.001$ ,  $b = 0.71$ ) and was negatively correlated with FNDF ( $F_{1, 16} = 4.91$ ,  $r^2 = 0.2347$ ,  $P = 0.042$ ,  $b = -0.48$ ).

Mineral concentrations in feces of adults (Table 9) exhibited different trends and apparent associations with rainfall throughout the study (Table 1). Mineral levels in adult feces evidenced few and weak relationships only between % browse and forbs in diets. Fecal concentrations of Na and K tended to increase with % forbs in diets ( $F_{1, 16} \leq 6.19$ ,  $r^2 \leq 0.28$ ,  $P \leq 0.03$ ,  $b \leq 0.53$ ). Fecal concentrations of Mg tended to increase ( $F_{1, 16} = 6.14$ ,  $r^2 = 0.2772$ ,  $P = 0.02$ ,  $b = 0.53$ ), whereas levels of fecal K tended to decline ( $F_{1, 16} = 4.62$ ,  $r^2 = 0.2240$ ,  $P < 0.05$ ,  $b = -0.47$ ), with higher % browse in diets. Mean level of Mg in adult feces did not differ in 1999–2000 ( $\bar{x} = 0.74\%$ , 90% CI = 0.61–0.87%), 2000–2001 ( $\bar{x} = 0.54\%$ , 90% CI = 0.46–0.61%), or 2001–2002 ( $\bar{x} = 0.67\%$ , 90% CI = 0.59–0.74%), although the mean tended to be higher in 1999–2000 than 2000–2001.

Mean concentrations of fecal Ca were comparable in 1999–2000 ( $\bar{x} = 3.32\%$ , 90% CI = 3.00–3.63%) and 2000–2001 ( $\bar{x} = 3.55\%$ , 90% CI = 2.81–4.29%), but mean fecal Ca level in 2001–2002 ( $\bar{x} = 4.25\%$ , 90% CI = 3.69–4.81%) was higher than in 1999–2000. Mean fecal concentrations of K were similar in 1999–2000 ( $\bar{x} = 0.19\%$ , 90% CI = 0.15–0.23%) and 2001–2002 ( $\bar{x} = 0.28\%$ , 90% CI = 0.23–0.34%), but mean concentration in 2000–2001 ( $\bar{x} = 0.38\%$ , 90% CI = 0.25–0.50%) was higher than in 1999–2000. Mean fecal Na concentration increased more than 4-fold during 2001–2002 compared to 1999–2000 and 2000–2001 (1999–2000  $\bar{x} = 0.028\%$ , 90% CI = 0.026–0.030%; 2000–2001  $\bar{x} = 0.047\%$ , 90% CI = 0.024–0.069%; 2001–2002  $\bar{x} = 0.217\%$ , 90% CI = 0.102–0.331%), clearly indicating greater excretion of

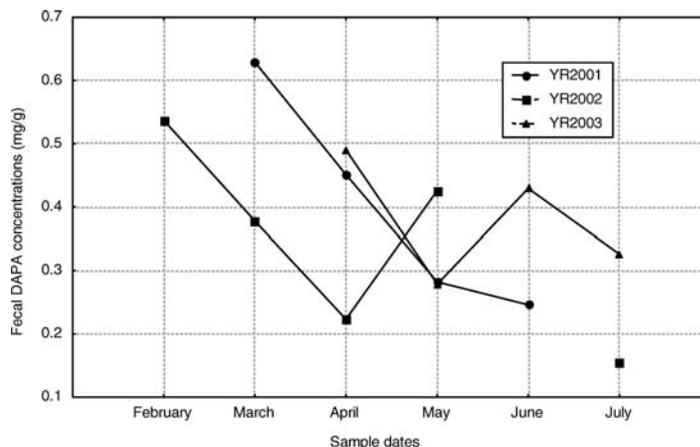
**Table 9.** Concentrations of fecal minerals (% dry wt) for adult desert bighorn sheep, Mazatzal Mountains, Arizona, USA, 1999–2002.

| Years | Months            | Ca   | K    | Mg   | Na    | P    |
|-------|-------------------|------|------|------|-------|------|
| 1999  | July–August       | 2.80 | 0.19 | 0.61 | 0.030 | 0.24 |
|       | September–October | 3.80 | 0.18 | 0.70 | 0.032 | 0.27 |
|       | November–December | 3.50 | 0.14 | 0.81 | 0.025 | 0.19 |
| 2000  | January–February  | 3.60 | 0.14 | 0.97 | 0.028 | 0.19 |
|       | March–April       | 3.20 | 0.24 | 0.80 | 0.028 | 0.23 |
|       | May–June          | 3.00 | 0.26 | 0.53 | 0.027 | 0.30 |
|       | July–August       | 2.64 | 0.33 | 0.52 | 0.063 | 0.18 |
|       | September–October | 3.81 | 0.17 | 0.57 | 0.020 | 0.25 |
| 2001  | November–December | 4.25 | 0.48 | 0.63 | 0.032 | 0.33 |
|       | January–February  | 4.82 | 0.28 | 0.64 | 0.031 | 0.39 |
|       | March–April       | 3.15 | 0.58 | 0.44 | 0.038 | 0.48 |
|       | May–June          | 2.62 | 0.41 | 0.41 | 0.095 | 0.25 |
|       | July–August       | 3.27 | 0.40 | 0.59 | 0.042 | 0.31 |
| 2002  | September–October | 4.14 | 0.22 | 0.56 | 0.032 | 0.22 |
|       | November–December | 4.59 | 0.26 | 0.66 | 0.297 | 0.21 |
|       | January–February  | 4.69 | 0.31 | 0.80 | 0.299 | 0.26 |
|       | March–April       | 5.22 | 0.28 | 0.71 | 0.313 | 0.24 |
|       | May–June          | 3.77 | 0.22 | 0.67 | 0.317 | 0.20 |

Na associated with the driest year of the study. Fungi might provide high dietary sources of Na (Weeks and Kirkpatrick 1976), but we found no correlation between % fungi and Na concentrations for either adults or lambs ( $F_{1, 16} \leq 0.235$ ,  $P \geq 0.62$ ). Mean concentrations of FP did not differ for 1999–2000 ( $\bar{x} = 0.25\%$ , 90% CI = 0.20–0.31%), 2000–2001 ( $\bar{x} = 0.30\%$ , 90% CI = 0.21–0.38%), and 2001–2002 ( $\bar{x} = 0.24\%$ , 90% CI = 0.21–0.23%). However, concentrations of FP during January–April were about 2-fold higher during the wetter year of 2001 than during the drier years of 2000 and 2002.

Mean ratio of fecal Ca:P of adults also was wider during lower rainfall in July 2001–June 2002 ( $\bar{x} = 18.3$ , 90% CI = 14.9–21.7%) than during higher rainfall in July 2000–June 2001 ( $\bar{x} = 12.1$ , 90% CI = 9.5–14.6%). Mean ratio of fecal Ca:P during the wetter period of July 2000–June 2001 did not differ compared to the mean for the drought year of July 1999–June 2000 ( $\bar{x} = 14.5$ , 90% CI = 11.6–17.4%). Mean fecal Na:K ratio in 2001–2002 ( $\bar{x} = 0.82$ , 90% CI = 0.36–1.28%) was higher than in 1999–2000 ( $\bar{x} = 0.16$ , 90% CI = 0.12–0.19%) and 2000–2001 ( $\bar{x} = 0.13$ , 90% CI = 0.08–0.19%). Fecal K levels were not correlated with fecal Na ( $F_{1, 16} < 0.001$ ,  $P > 0.98$ ) or Na:K ratios ( $F_{1, 16} = 0.31$ ,  $P > 0.58$ ). In comparison, fecal Na was positively correlated with Na:K ratios ( $F_{1, 16} = 357.8$ ,  $r^2 = 0.9572$ ,  $P < 0.001$ ,  $b = 0.98$ ). Rainfall during and 1–2 months prior to sampling periods did not correlate with adult FN, FDAPA, FNDF, or fecal mineral concentrations other than FP; concentrations of FP tended to increase with total rainfall 2 months prior to sampling ( $F_{1, 16} = 3.37$ ,  $r^2 = 0.1740$ ,  $P = 0.085$ ,  $b = 0.42$ ).

Concentrations of N and DAPA in lamb feces early during lactation exceeded levels in adult feces and declined to about adult levels by summer between 2001 and 2003, as maturation progressed (Figs. 4–7). In contrast, FNDF concentrations for lambs were below adult levels early in lactation and increased to about adult levels as maturation progressed (Tables 6, 7). Winter rainfall (Table 1) also influenced lamb fecal indices (Tables 7, 10; Figs. 6, 7). Mean concentrations of FN and FDAPA of lambs did not differ among sampling periods (Table 8). However, concen-



**Figure 7.** Fecal 2,6-diaminopimelic acid (DAPA) concentrations (mg/g) for desert bighorn sheep lambs, Mazatzal Mountains, Arizona, USA, 2001–2003.

trations of FN and FDAPA during early to mid-lactation appeared to be lower during lower winter rainfall in 2002, compared with during higher winter rainfall in 2001 and 2003. Mean FNDF of lambs in 2003 increased about 26% above the mean in 2001 and about 16% above the mean in 2002 (2001  $\bar{x} = 50.2\%$ , 90% CI = 46.3–54.0%; 2002  $\bar{x} = 54.8\%$ , 90% CI = 51.6–58.0%; 2003  $\bar{x} = 63.3\%$ , 90% CI = 61.6–64.9%).

Fecal mineral concentrations for lambs tended to vary with respect to maturation and in most instances approached adult levels by early summer (Tables 9, 10). Concentrations of K in lamb feces consistently declined during maturation, but concentrations of fecal Ca and Mg showed no clear trends. Mean concentrations of most lamb fecal minerals showed few differences in relation to rainfall levels between years. Mean fecal concentrations of K (2001  $\bar{x} = 0.33\%$ , 90% CI = 0.24–0.41%; 2002  $\bar{x} = 0.36\%$ , 90% CI = 0.22–0.50%; 2003  $\bar{x} = 0.27\%$ , 90% CI = 0.10–0.44%), Mg (2001  $\bar{x} = 0.48\%$ , 90% CI = 0.41–0.54%; 2002  $\bar{x} = 0.54\%$ , 90% CI = 0.47–0.61%; 2003  $\bar{x} = 0.54\%$ , 90% CI = 0.41–0.66%), and Na (2001  $\bar{x} = 0.05\%$ , 90% CI = 0.02–0.08%; 2002  $\bar{x} = 0.04\%$ , 90% CI = 0.03–0.04%; 2003  $\bar{x} = 0.03\%$ , 90% CI = 0.01–0.05%) did not differ among years.

In comparison, concentrations of Na in feces tended to increase as lambs matured in wetter years of 2001 and 2003 but not in the

**Table 10.** Concentrations of fecal minerals (% dry wt) for desert bighorn sheep lambs, Mazatzal Mountains, Arizona, USA, 2001–2003.

| Years | Months   | Ca   | K    | Mg   | Na    | P    |
|-------|----------|------|------|------|-------|------|
| 2001  | March    | 3.51 | 0.42 | 0.49 | 0.029 | 0.58 |
|       | April    | 2.17 | 0.33 | 0.43 | 0.047 | 0.31 |
|       | May      | 2.17 | 0.28 | 0.43 | 0.048 | 0.29 |
|       | June     | 2.60 | 0.27 | 0.55 | 0.085 | 0.23 |
| 2002  | February | 4.24 | 0.56 | 0.58 | 0.030 | 0.24 |
|       | March    | 3.25 | 0.45 | 0.47 | 0.036 | 0.20 |
|       | April    | 3.90 | 0.33 | 0.46 | 0.048 | 0.24 |
|       | May      | 4.04 | 0.24 | 0.63 | 0.037 | 0.21 |
|       | July     | 3.52 | 0.22 | 0.57 | 0.027 | 0.20 |
| 2003  | April    | 2.52 | 0.48 | 0.58 | 0.019 | 0.42 |
|       | May      | 2.57 | 0.17 | 0.54 | 0.020 | 0.47 |
|       | June     | 2.82 | 0.27 | 0.39 | 0.025 | 0.55 |
|       | July     | 3.58 | 0.16 | 0.64 | 0.057 | 0.28 |

drier year of 2002. Fecal Ca and P concentrations tended to be higher and lower, respectively, during the drier winter of 2002 compared to winters 2001 and 2003. Mean fecal Ca concentrations in 2001 and 2003 were lower than in 2002 (2001  $\bar{x}$  = 2.61%, 85% CI = 2.00–3.22%; 2002  $\bar{x}$  = 3.79%, 85% CI = 3.47–4.11%; 2003  $\bar{x}$  = 2.87%, 85% CI = 2.40–3.34%). Mean fecal P concentration in 2003 exceeded that in 2002 (2001  $\bar{x}$  = 0.35%, 90% CI = 0.17–0.54%; 2002  $\bar{x}$  = 0.22%, 90% CI = 0.20–0.24%; 2003  $\bar{x}$  = 0.43%, 90% CI = 0.30–0.56%). Mean Ca:P ratio in 2002 ( $\bar{x}$  = 17.4, 90% CI = 16.2–18.5%) was wider than in 2001 ( $\bar{x}$  = 8.0, 90% CI = 5.2–18.5%) and 2003 ( $\bar{x}$  = 7.6, 90% CI = 2.7–12.4%). Concentrations of fecal K and Na were not correlated ( $F_{1, 11} = 0.86, P > 0.37$ ), and mean Na:K ratios did not differ in 2001 ( $\bar{x}$  = 0.13, 90% CI = 0.05–0.29%), 2002 ( $\bar{x}$  = 0.11, 90% CI = 0.07–0.15%), and 2003 ( $\bar{x}$  = 0.15, 90% CI = –0.01–0.32%). However, ratios of Na:K were positively correlated with Na levels ( $F_{1, 11} = 21.17, r^2 = 0.6581, P < 0.001, b = 0.81$ ) in lamb feces; in contrast to results for adults, Na:K ratios were negatively correlated with concentrations of K ( $F_{1, 11} = 7.75, r^2 = 0.4133, P < 0.02, b = -0.64$ ) in lamb feces.

### Predators

**Mountain Lion Reduction.**—Sport hunters harvested a mean of 0.8 mountain lions/year (range 0–2) on the Mazatzal Mountains study area between 1989 and 1999 (AGFD, unpublished data). Sport hunters killed 13 mountain lions within the study area between the winters of 1999–2000 and 2003–2004 (Table 11); 12 were harvested after 1999, including 6 in 2000, 3 in 2001, 2 in 2002, and 1 in 2003. Hunters killed 3 mountain lions within the known distribution of desert bighorn sheep (Fig. 2); the remainder were initially trailed by hounds within but killed outside that range or were initially encountered and killed by hunters outside that range (AGFD, unpublished data).

Based on an estimated initial population size of 16 resident adult mountain lions on the study area (AGFD, unpublished data), sport hunters prior to the 2003 desert bighorn sheep survey might have killed about half the 1999 resident adult population. Of 11 adults harvested during 2000–2003, 5 were males and 6 were females, consistent with a likely 50:50 population sex ratio (Cunningham et al. 2001a). Mean mountain lion track counts,

**Table 11.** Mean track counts (90% CI) during winter (November–January) and spring (March–May) and cumulative number of sport harvested mountain lions, Mazatzal Mountains, Arizona, USA, 1998–1999 to 2003–2004.

| Survey period                 | Tracks/km | 90% CI    | Cumulative harvest |
|-------------------------------|-----------|-----------|--------------------|
| Winter 1998–1999              | 0.37      | 0.09–0.64 | 0                  |
| Spring 1999                   | 0.55      | 0.33–0.77 | 0                  |
| Winter 1999–2000 <sup>a</sup> | 0.44      | 0.17–0.71 | 2                  |
| Spring 2000                   | 0.19      | 0.06–0.32 | 5                  |
| Winter 2000–2001              | 0.09      | 0.03–0.16 | 10                 |
| Spring 2001                   | 0.18      | 0.18–0.29 | 10                 |
| Winter 2001–2002              | 0.14      | 0.03–0.25 | 11                 |
| Spring 2002                   | 0.18      | 0.05–0.31 | 12                 |
| Winter 2002–2003              | 0.13      | 0.04–0.22 | 12                 |
| Spring 2003                   | 0.18      | 0.08–0.27 | 12                 |
| Winter 2003–2004              | 0.22      | 0.08–0.37 | 13                 |

<sup>a</sup> Mountain lion reduction began.

compared to the spring 1999 survey, were lower each spring between 2000 and 2003, but mean track counts during the winters of 1999–2004 did not clearly indicate differences among sampling periods (Table 11).

**Diets.**—We analyzed 171 mountain lion scats collected between 1999 and 2003 for prey remains (Table 12). We found 1.0–1.2 prey items/mountain lion scat collected during this period. Mountain lion diet differed among years during 1999–2003 ( $\chi^2 = 38.97, P < 0.001$ ) and the index of diet diversity declined >50% after 2000 following cattle removal and as mountain lion reductions continued. Occurrence of cattle remains in scats declined following cattle removal (Yates adjusted chi-square:  $\chi^2 = 30.22, P < 0.001$ ), but occurrence of collared peccary remains increased more than 3-fold (Yates adjusted chi-square:  $\chi^2 = 6.83, P < 0.01$ ). We found 60% ( $n = 103$ ) of scats within the range of desert bighorn sheep distribution (Fig. 2) and 40% ( $n = 68$ ) of scats outside this area. Occurrence of desert bighorn sheep remains in scats collected within their range of distribution (1999 = 5.0%, 2000 = 26.3%, 2001 = 12.5%, 2002 = 9.5%, 2003 = 9.4%), as well as throughout the study area (Table 12), increased between 1999 and 2000 and declined in subsequent years to nearer 1999 levels. We identified no desert bighorn sheep remains in 321 bobcat and 621 coyote scats examined during 2000–2003.

Occurrences of large and small prey in scats collected between 1999 and 2003 differed among years ( $\chi^2 = 16.5, P < 0.005$ ). Relative consumption of large wild prey biomass more than doubled between 1999 and 2003, as consumption of cattle biomass declined and mountain lion reductions continued, whereas consumption of small prey biomass fell more than 75%. Relative biomass of large prey eaten exceeded that of small prey during all years and increased from about 70% in 1999 to from 84% to 92% in following years because of greater relative consumption of large wild prey (Table 13). Desert bighorn sheep comprised 3.7%, 19.1%, 10.0%, 6.9%, and 8.2% of biomass consumed by mountain lions during successive years between 1999 and 2003, respectively.

**Table 12.** Percent occurrence of prey remains in scats collected throughout the study area, and indices of diet diversity for mountain lions, Mazatzal Mountains, Arizona, USA, 1999–2003.

| Prey                 | Years |                   |                   |      |      |
|----------------------|-------|-------------------|-------------------|------|------|
|                      | 1999  | 2000 <sup>a</sup> | 2001 <sup>b</sup> | 2002 | 2003 |
| Deer                 | 8.9   | 18.2              | 11.1              | 12.5 | 15.1 |
| Collared peccary     | 15.6  | 13.6              | 51.9              | 57.5 | 60.4 |
| Cattle               | 13.3  | 13.6              | 7.4               | 2.5  | 0    |
| Bighorn sheep        | 2.2   | 22.7              | 7.4               | 5.0  | 5.7  |
| Lagomorph            | 33.3  | 18.2              | 14.8              | 22.5 | 9.4  |
| Rodent               | 8.9   | 9.1               | 0                 | 0    | 5.7  |
| Bird                 | 6.7   | 0                 | 3.7               | 0    | 0    |
| Reptile              | 2.2   | 4.5               | 0                 | 0    | 3.8  |
| Coyote               | 4.4   | 0                 | 0                 | 0    | 0    |
| Common gray fox      | 0     | 0                 | 3.7               | 0    | 0    |
| Mountain lion        | 4.4   | 0                 | 0                 | 0    | 0    |
| No. food items       | 45    | 22                | 27                | 40   | 53   |
| No. scats examined   | 37    | 19                | 27                | 40   | 48   |
| Diet diversity index | 5.62  | 6.07              | 3.16              | 2.49 | 2.47 |

<sup>a</sup> Mountain lion reduction began.

<sup>b</sup> Cattle removed by February 2001.

**Table 13.** Frequency of occurrence (%), percent biomass (Biom.; kg), and percent of numbers eaten (Num.) for large (cattle, deer, desert bighorn sheep, collared peccary) and small (lagomorphs, rodents) prey, cattle, and large wild prey in mountain lion diets, Mazatzal Mountains, Arizona, USA, 1999–2003.

| Year              | n <sup>a</sup> | Large prey |       |      |       |       |       |        |       |           |      |  |
|-------------------|----------------|------------|-------|------|-------|-------|-------|--------|-------|-----------|------|--|
|                   |                | Small prey |       |      | Total |       |       |        |       |           |      |  |
|                   |                | %          | Biom. | Num. | %     | Biom. | Num.  | Cattle |       | Wild prey |      |  |
|                   |                |            |       |      |       |       | Biom. | Num.   | Biom. | Num.      |      |  |
| 1999              | 37             | 51.4       | 30.4  | 95.5 | 48.6  | 69.5  | 4.7   | 33.9   | 0.9   | 35.6      | 3.8  |  |
| 2000 <sup>b</sup> | 19             | 21.1       | 7.7   | 87.2 | 78.9  | 92.3  | 12.8  | 31.2   | 1.8   | 61.1      | 11.0 |  |
| 2001 <sup>c</sup> | 27             | 19.2       | 10.8  | 77.4 | 80.8  | 89.2  | 22.6  | 14.7   | 1.1   | 74.5      | 21.5 |  |
| 2002              | 40             | 22.5       | 16.3  | 83.2 | 77.5  | 83.7  | 16.8  | 5.1    | 0.3   | 78.6      | 16.5 |  |
| 2003              | 48             | 16.7       | 7.5   | 71.8 | 89.7  | 92.6  | 28.1  | 0      | 0     | 92.6      | 28.1 |  |

<sup>a</sup> No. scats analyzed.

<sup>b</sup> Mountain lion reduction began.

<sup>c</sup> Cattle removed by February 2001.

Converting frequency of occurrence of prey remains in scats to estimated relative numbers of prey eaten (Table 13), 95% of individuals consumed by mountain lions during 1999 were small prey, and this declined to about 83% by 2002. Greater relative numbers of small compared to large prey were eaten throughout the study. Relative numbers eaten of all large prey combined and large wild prey increased more than 2-fold and 3-fold, respectively, between 1999 and 2003, whereas estimated relative number of cattle eaten declined more than 66% during this period.

**Desert Bighorn Sheep Mortalities.**—Mountain lion predation was identified as cause of death for 10 (5 males, 5 females) radio-collared desert bighorn sheep in Mazatzal Mountains between 1995 and 1998 (AGFD, unpublished data). Between 2000 and 2003, 7 radio-collared desert bighorn sheep died, and mountain lion predation was indicated in 5 deaths (3 males, 2 females). Mortalities of radio-collared animals due to mountain lion predation were lower between 2000 and 2003 than between 1995 and 1998 ( $\chi^2 = 4.49$ ,  $P = 0.034$ ), and mortality rates were higher during 1995–1998 (3.3/yr) than during 2000–2003 (1.3/year). We also found carcasses of 14 desert bighorn sheep (13 adults, 1 lamb) without radio collars between 1999 and 2003 and were able to determine mountain lions killed 4 of them. Of 21 carcasses of desert bighorn sheep (12 males, 5 females, 3 uncertain sex or age, 1 lamb) we found between 1999 and 2003 that died from causes other than sport hunting, we concluded that mountain lion predation was cause of death in 9 instances.

## DISCUSSION

Evaluation of factors potentially affecting trends and persistence of desert bighorn sheep populations can provide valuable perspective to resource managers addressing questions of management intervention (Van Ballenberghe and Ballard 1994; Ballard et al. 2001, 2003; McKinney et al. 2003; Laundré 2005). Declines and extirpations, particularly of small desert bighorn sheep populations, present concerns to wildlife management agencies (Bleich et al. 1996, Berger 1999, Kamler et al. 2002, McKinney et al. 2003, Rominger et al. 2004), and numerous factors have been suggested to influence persistence and population dynamics. Predator management and research represent a complex matrix of biological and sociopolitical challenges (Ballard et al. 2001, 2003; Treves and Karanth 2003). Opposition by special interest

groups (McKinney et al. 2000) compromised present study design and hampered captures of desert bighorn sheep for evaluation of disease exposure and causes of mortalities during 1999–2001.

In summary, we identified 2 proximate factors that likely acted or interacted to affect demographic characteristics of the desert bighorn sheep population in Mazatzal Mountains: nutritional status (winter rainfall [ultimate factor] was associated with differences in quality and availability of forages and quality of diets) and predation by mountain lions. We considered these variables to be limiting factors, defined as any factors that might operate to cause changes in loss or production of animals and thus contribute to the upper limit a population can reach in an environment (Messier 1991, Ballard et al. 2001, Logan and Sweanor 2001).

Our findings suggested associations between winter rainfall and indicators of nutritional status, including primary production, mineral content of vegetation, composition of diets, fecal nutrients, and demographic changes of the desert bighorn sheep population. Associations also were apparent between reductions of mountain lion abundance and predation and demographic attributes of the population. Observation rates of total desert bighorn sheep and lambs or yearlings were positively correlated with winter rainfall in Mazatzal Mountains and on the Plomosa Mountains reference area, where mountain lions were presumed absent. Winter rainfall (Table 1) likely influenced nutritional status of desert bighorn sheep in Mazatzal Mountains. Production of forbs (Fig. 3), concentrations of minerals in vegetation (Table 5), and consumption of forages by and nutritional status of desert bighorn sheep adults and lambs (Figs. 4–7; Tables 6, 7, 9, 10) were associated with patterns of winter rainfall, except that diets of lambs (Table 7) appeared to be independent of differences in rainfall (Table 1). Concentrations of Na, P, and ratios of Ca:P in forages (Table 5) in particular were associated with patterns of rainfall (Table 1). Fecal concentrations, particularly of N, DAPA, and P, of adults and lambs (Figs. 4–7, Tables 9, 10) also showed positive associations with winter rainfall (Table 1). Fecal ratios of Ca:P and concentrations of Ca were and narrower and lower, respectively, for adults and lambs when winter precipitation was higher (Tables 1, 9, 10), supporting the notion of better nutritional status with higher rainfall.

Concentrations of Na in feces of adults also increased dramatically during late autumn through spring in a year of

severe drought (Tables 1, 9). In comparison, concentrations of Na in feces of lambs tended to increase during spring to summer in wetter years but showed no clear trend during severe drought (Tables 1, 10). Although concentrations of FN for adults and lambs (Figs. 4, 6) consistently were higher than a level likely indicating absolute dietary deficiency (Irwin et al. 1993), higher winter rainfall (Table 1) positively influenced concentrations of FN as well as FDAPA (Figs. 4–7), suggesting that moderate deficiencies of dietary protein and energy were associated with drought conditions during winter to spring. Mean concentrations of FN and FDAPA did not differ during sampling periods (Table 8), but concentrations showed longer durations of seasonally higher levels for adults (Figs. 4, 5), and higher levels especially during winter to early spring for lambs (Figs. 6, 7), during wetter periods (Table 1).

Indices of nutritional quality of forages (Table 5) and consumption of forbs by adults (Table 6) were associated with winter precipitation (Table 1; % forbs in diets also was positively correlated with incremental increases in rainfall throughout the study), and corresponding differences were apparent in concentrations of macronutrients and minerals in diets (Figs. 4, 5; Table 9). Feces of lambs tended to reflect patterns of nutrient concentrations (Figs. 6, 7; Table 10) similar to those for adults, even though composition of diets of lambs (Table 7) appeared to be comparable during wetter and drier years (Table 1).

Thus, our findings support a hypothesis that linkages occur between winter rainfall, quality and quantity of available forages (Fig. 3; Table 5; particularly production of forbs and concentrations of P and ratios of Ca:P), other indicators of nutritional status (composition of diets, concentrations of fecal macronutrients [FN, FDAPA], and minerals [Tables 9, 10; particularly concentrations of P and ratios of Ca:P]), and production and productivity (Table 3) of the desert bighorn sheep population. We suggest that concentrations, particularly ratios of Ca:P in forages and concentrations of N, DAPA, and P and ratios of Ca:P in feces during periods of winter drought, likely reflect moderate dietary deficiencies that correspond with lower nutritional status of desert bighorn sheep adults and lambs and lower production and productivity.

Nutritional requirements of desert bighorn sheep are poorly understood, but we observed apparently moderate nutritional deficiencies of desert bighorn sheep adults and lambs that corresponded with drought conditions and lower production and productivity of the population. Considerable research has addressed estimated deficiencies and limiting levels in concentrations of nutrients in forages and feces of free-ranging, wild ruminants, providing a limited, qualitative basis for comparison with our results and assessments of apparent nutritional deficiencies in desert bighorn sheep. Numerous researchers have suggested that concentrations of P in forages in the southwestern United States might be limiting for deer. Difficulties in evaluating P as a limiting factor arise from interactions of concentrations of P in forages with factors such as other minerals, N, and digestibility of forages (Grasman and Hellgren 1993). Generally, concentrations of P in diets and forages of  $\geq 0.25\%$  might meet requirements of wild ruminants (Irvine 1969, Urness et al. 1971, Ullrey et al. 1975, Schwartz et al. 1977). However, western deer

may require concentrations of P  $< 0.25\%$  (Dietz 1965), and dietary requirements of deer for P might be as low as 0.14–0.19% (Grasman and Hellgren 1993). High concentrations of Ca interfere with metabolism of P, and ratios of Ca:P  $< 5:1$  may indicate adequate nutritional quality for deer (Dietz 1965, Urness et al. 1971). Concentrations of P  $< 0.19\%$  in selected forages of desert bighorn sheep also might indicate nutrient deficiency (Irvine 1969). Concentrations of P in browse, forbs, and grass in our study were  $\leq 0.20\%$ ,  $\leq 0.22\%$ , and  $\leq 0.10\%$ , respectively, and ratios of Ca:P in browse, forbs, and grass ranged from 9.4 to 12.7, 8.2 to 9.7, and 0.3 to 4.1, respectively (Table 5). Thus, concentrations of P in browse and forbs might indicate adequate availability of the mineral, but ratios of Ca:P  $> 5:1$  in browse and forbs, as well as in feces (Tables 9, 10), suggested potential interference of metabolism of P by Ca.

Concentrations of P in feces might correspond with dietary concentrations of P in ruminants (Mubanga et al. 1985). Concentrations of P in feces of adults and lambs in our study were  $< 0.25\%$  more often during drought than during wetter years, and ratios of Ca:P in feces of adults and lambs tended to be  $> 5:1$  during drier and wetter years (Tables 9, 10). Mean concentrations of P in feces of adults did not differ between wetter years and drought, but concentrations of P in feces of lambs were higher in wetter years than drought (Tables 1, 9, 10). Mean ratios of Ca:P in feces of adults were narrower in a wetter year than during drought in 2001–2002 but did not differ between the wetter year and drought in 1999–2000. Mean ratios of Ca:P in feces of lambs also were narrower in wetter years than during drought (Tables 1, 9, 10). Thus, ratios of Ca:P in browse and forbs and concentrations of P and ratios of Ca:P in feces of adults and lambs were consistent with a hypothesis of moderate dietary deficiency during winter drought. Ratios of Ca:P might provide a better indicator of relative nutritional adequacy than absolute concentrations of either mineral (Mayland and Shewmaker 2001).

Concentrations of FN and FDAPA, as indices of dietary nitrogen and energy, respectively (Osborn and Ginnett 2001), have been widely used by biologists as indicators of diet quality (Leslie et al. 1989, Irwin et al. 1993, Brown et al. 1995, Hodgman et al. 1996, Bleich et al. 1997, Osborn and Jenks 1998). Concentrations of FN of desert bighorn sheep adults (Fig. 4) peaked at about 2.2% during a wetter year from November–December 2000 to July–August 2001 and during a drier year between March–April and May–June 2000 and in January–February during the severe drought in 2002 (Table 1). Concentrations of FN of lambs (Fig. 6) reached lowest levels of about 2.1% during wetter years of 2001 and 2003 and about 1.7% in the drought year of 2002. Concentrations of FDAPA for adults and lambs tended to show patterns similar to those of FN (Figs. 5, 7). In comparison, concentrations of FN  $\leq 1.3\%$  might indicate nutritional deficiencies of Rocky Mountain bighorn sheep consuming low-tannin diets on winter ranges (Irwin et al. 1993), and FN levels  $< 1.7\%$  might indicate dietary nitrogen deficiencies in cattle (Wofford et al. 1985). Thus, we hypothesize that wider ratios of Ca:P in browse and forbs, shorter temporal durations of higher levels of FN and FDAPA of adults, lower concentrations of FN and FDAPA of lambs, and concentrations of some minerals, particularly ratios of Ca:P in feces of adults and

lambs, suggested moderate nutritional deficiencies during periods of winter drought that corresponded with poorer indices of desert bighorn sheep productivity.

Results also indicated that predation by mountain lions was a substantial mortality factor affecting the desert bighorn sheep population and likely influenced demographic patterns more prior to than following mountain lion reductions. Drought persisted on study areas between 1994 and 1997, and winter rainfall declined 38% in Mazatzal Mountains, compared to >53% on reference areas. Despite higher rainfall in Mazatzal Mountains, observation rates of total desert bighorn sheep and lambs during this period declined 75% and 80%, respectively (Table 2). In comparison, rainfall was lower on reference areas, and observation rates of total desert bighorn sheep and lambs between 1994 and 1997 declined less, from  $\leq 32\%$  and  $\leq 14\%$ , respectively (Table 2). Predation by mountain lions ostensibly provided an explanation for differential declines of desert bighorn sheep population parameters in Mazatzal Mountains, compared to reference areas, despite higher rainfall and lower decline of rainfall on the primary study area.

We initiated reductions of mountain lions in Mazatzal Mountains during 2000 and continued reductions through 2003 (Table 12), and drought occurred there during 3 of 5 years between 1999 and 2003 (Table 1). As mountain lions were harvested, observation rates of total and male desert bighorn sheep increased 18% and 29%, respectively, between 1999 and 2003, but observation rates of females showed less change (Table 3). Observation rates of lambs increased during this period from 0 to 1.4/hour, and productivity increased from 0 to  $\geq 35$  (Table 3) despite periods of drought, following demographic changes and patterns of rainfall similar to those observed in Plomosa Mountains. Moreover, predation of radio-collared desert bighorn sheep by mountain lions in Mazatzal Mountains declined with predator reductions between 2000 and 2003, compared to mountain lion predation between 1995 and 1998, prior to experimental predator reductions. We thus hypothesize that dynamics of desert bighorn sheep in Mazatzal Mountains were not driven entirely by fluctuations in winter rainfall and nutritional status and that predation by mountain lions was a mortality factor ostensibly acting or interacting with winter rainfall and nutritional status to have potential population-level impacts.

### Population Surveys

We employed annual, standardized surveys to index trends of desert bighorn sheep populations, a procedure widely used by natural resource agencies (Rabe et al. 2002). Indices of relative abundance present considerable practical and statistical challenges (Link and Nichols 1994, Stewart-Oaten et al. 1995, Thomas 1996, Reed and Blaustein 1997) but can be necessary and useful in evaluating trends of wildlife populations (Eberhardt 1978). Detectability during bighorn sheep surveys may vary, but we attempted to improve precision of counts by using experienced personnel, standardizing survey techniques (consistent survey hours, weather conditions, time of day, and attempting to avoid double counts), and surveying standardized habitat blocks on reference areas (Bodie et al. 1995, Hervert et al. 1998, Saether et al. 2002).

We assumed direct relationships between abundance of desert bighorn sheep and survey indices, measures that do not directly

yield density estimates but functionally are related to densities and dynamics of the desert bighorn sheep population, although accuracy of these relationships is uncertain (Eberhardt 1978). Recognizing limitations of indices, we believe annual survey results clearly indicated population declines in Mazatzal Mountains and reference areas between 1994 and 1997 (Tables 2, 3), and reflected increasing population demographic parameters in Mazatzal (Tables 2, 3) and Plomosa mountains between 1999 and 2003.

Habitat evaluations during the 1980s (Cunningham 1989) and in 1999 (McKinney et al. 2001) indicated little meaningful temporal change in desert bighorn sheep habitat quality despite extensive wildfire in 1996 on portions largely exclusive of desert bighorn sheep habitat in the Mazatzal Mountains study area (Cunningham et al. 2001b, 2003; McKinney et al. 2001). Moreover, overuse of forages likely was not a factor affecting forage availability in Mazatzal Mountains. Our review of literature suggested that overuse of forages by desert bighorn sheep likely occurs rarely, if at all; we found only 1 report of overuse of a browse species by penned bighorn sheep in British Columbia (Wikeem and Pitt 1987). Thus, some factor or factors other than overuse of forages likely were driving dynamics of desert bighorn sheep in Mazatzal Mountains.

Drought conditions persisted in Mazatzal Mountains during most years between 1994 and 2003 (Table 1; McKinney et al. 2001). Winter rainfall levels were below long-term levels in 1999, 2000, and 2002 but increased in 2001 and 2003 about 2-fold above levels during these previous 3 winters (Table 1). Winter rainfall in 2002 was the lowest in at least 27 years and was about half that in the winters of 1999 and 2000 and less than about 30% of 2001 and 2003 levels. Compared to Mazatzal Mountains, reference areas received lower rainfall, and drought conditions occurred on all study areas during 1994–1997, but proportional declines in winter rainfall during this period were greater on reference areas than in Mazatzal Mountains (Table 2).

Higher quantity and quality of forages, survival of preweaning young, and female fecundity among large herbivores often correspond with higher precipitation during winter to spring (Berger 1982, Leslie and Douglas 1982, Douglas and Leslie 1986, Wehausen et al. 1987, Douglas 2001, McKinney et al. 2001), presumably acting via lower forage quality or quantity. Production of newborn and weaned young generally is recognized as an important factor influencing growth and trends of large herbivore populations (Creeden and Graham 1997, Jorgenson et al. 1997, Gaillard et al. 2000), but viability of an endangered bighorn sheep population appeared to be more sensitive to changes in survival of adult females than to reproduction or survival of younger animals (Rubin et al. 2002a).

Production of lambs was positively correlated with winter rainfall in Mazatzal Mountains and likely was a driving variable influencing recruitment of yearlings and growth of desert bighorn sheep populations in Mazatzal and Plomosa mountains. Winter rainfall was positively correlated with observation rates of total desert bighorn sheep, lambs, and yearlings in Mazatzal Mountains and was positively correlated with yearlings in Kofa and Plomosa mountains. Moreover, observation rates of lambs, yearlings, and total desert bighorn sheep were positively correlated with each

other in Mazatzal and Plomosa mountains, suggesting importance of lamb production and recruitment on population growth. Despite lower rainfall and greater declines in winter rainfall during 1994–1997 on reference areas than in Mazatzal Mountains, total desert bighorn sheep and lambs observed in Mazatzal Mountains declined more than on reference areas during this period (Table 2). In comparison, observation rates of total desert bighorn sheep, lambs, and productivity tended to increase in both Mazatzal (Table 3) and Plomosa mountains between 2000 and 2003. Desert bighorn sheep total abundance and abundance of adults and lambs increased between 2000 and 2003 in Mazatzal Mountains despite drought conditions in 3 of 5 years (Tables 1, 3). During 1994–1999, desert bighorn sheep population parameters declined in Mazatzal Mountains (McKinney et al. 2001) when drought occurred in 3 of 6 years. Thus, results suggest that a factor or factors other than overuse of forages and in addition to drought were influencing population dynamics of the Mazatzal Mountains desert bighorn sheep population.

Productivity of desert bighorn sheep in Mazatzal Mountains (Table 3) between 2000 and 2003 neared or exceeded in all years an estimated level necessary to maintain a population (Remington 1989), even though drought occurred in 2000 and winter rainfall in 2002 was the lowest in at least a quarter century. Within parameters of our study, desert bighorn sheep population growth, production of lambs, and productivity tended to be higher during years with higher winter rainfall (Tables 1, 3). Amounts and patterns of precipitation and production of plants also may influence distribution of desert bighorn sheep or persistence of populations (Berger 1991, Oehler et al. 2003). Home ranges of desert bighorn sheep may be larger in association with lower rainfall and availability and quality of forage (Oehler et al. 2003), and abundance of mule deer in deserts likely is lower in areas with lower abundance of plants and lower rainfall (Leopold and Krausman 1991).

Our findings indicated that forage quantity and quality, quality of diets, and productivity of desert bighorn sheep were factors positively associated with winter rainfall. Lower survival or production of desert bighorn sheep lambs also were postulated as likely in other areas of Arizona during years of drought that yield low forage availability and quality (Seegmiller and Ohmart 1982, Holt et al. 1992). Although availability of forage (based on estimate of overuse) likely was not a limiting factor in Mazatzal Mountains, quality of available forage and associated moderate dietary deficiencies appeared to correspond with lower productivity of desert bighorn sheep during periods of drought. Positive associations between winter rainfall, forb production, and mule deer fawn:doe ratios also were found on our study area, but forage production other than following years of extreme winter drought likely did not limit fawn survival (Smith and LeCount 1979). In comparison, neither forage availability nor quality were believed to limit desert bighorn sheep in southern Arizona (Mazaika et al. 1992).

### Disease Exposure

We found no indication that disease or exposure to disease agents was a factor affecting survival of radio-collared adult desert bighorn sheep in the Mazatzal Mountains population. Evidence of bacterial and viral activity persisted throughout the study

(Table 4) and was unremarkable in comparison to results of studies of other desert bighorn sheep populations (Turner and Payson 1982, Clark et al. 1985, Dunbar et al. 1985, deVos 1989, Elliott et al. 1994, DeForge et al. 1997). Despite persistent exposure to disease agents, we observed no clinical symptoms or temporal differences in disease exposure during 2000–2002 (Table 4). We also found no differences between males and females regarding evidence of disease exposure.

Occurrences of disease exposure among populations may correspond poorly with demographic trends (Clark et al. 1985, Ward et al. 1997). Exposure to a large number of pathogenic agents may have contributed to downward trends in regional bighorn sheep populations in California, but interpreting seroprevalence of pathogen exposure as causative in population declines merits caution in the absence of a demonstrated link to demographic processes (Elliott et al. 1994). In comparison with our findings, neither habitat suitability nor disease likely caused a bighorn sheep population to decline in California's San Gabriel Mountains (Holl et al. 2004). Consistent with results of DeForge et al. (1997), we found no evidence that exposure to multiple infectious agents operated to affect adult desert bighorn sheep. Eighty-five percent of animals examined showed exposure to multiple disease agents, comparable to exposure of individuals to multiple disease agents at similar latitude in California (Elliott et al. 1994). Small sample sizes can be problematic in evaluating absence/presence of disease in bighorn sheep populations (Wehausen 1987), but we sampled between 30% and 87% of adult desert bighorn sheep observed during annual surveys.

### Nutritional Status

**Vegetation.**—Rainfall that is highly variable from year to year is a primary factor affecting forage resources in deserts (Marshall et al. 2002, 2005) and in our study ostensibly influenced desert bighorn sheep nutritional status. Our findings support the notion that differences in winter rainfall among years (Table 1) influenced production of forbs (Fig. 3), mineral levels in forages (Table 5), composition of diets (Tables 6, 7), and other indicators of nutritional status (Figs. 4–7; Tables 9, 10) of desert bighorn sheep adults and lambs. Compared to 2000, higher winter rainfall in 2001 clearly was associated with increased seasonal production of forbs, consistent with other studies reporting positive associations between precipitation and forage production in desert regions (Herbel et al. 1972, Beatley 1974, Goldberg and Turner 1986, Ernest et al. 2000, Marshall et al. 2005). Increasing winter rainfall also supported higher spring production of forbs, but spring grass yield was independent of winter precipitation in previous research on our primary study area (Smith and LeCount 1979). Relationship between seasonal rainfall and production of browse and grasses was less clear than for forbs (Fig. 3), but drought conditions during most years likely corresponded with reduced cover and production of forbs (Fig. 3; Smith and LeCount 1979) and grasses (Herbel et al. 1972, Cable 1975).

Concentrations of protein, NDF, and moisture and digestibility of forages eaten by desert bighorn sheep vary widely among plant species and seasons (Morgart et al. 1986, Krausman et al. 1989, Seegmiller et al. 1990, Bleich et al. 1997). Protein content is generally higher in forbs than in browse and grasses, although location, interspecific, and seasonal variables may affect protein

content (Seegmiller et al. 1990, Mazaika et al. 1992, Bleich et al. 1997). Differences in forage quality might occur among years because of differences in annual rainfall and growing-season temperatures (Bleich et al. 1992), but little is known about variables potentially influencing temporal variations in desert bighorn sheep forage quality. Selective foraging likely enhances maintenance of diet nutritional quality by ruminants (Provenza 1995, Hanley 1997).

Soils of the general area of Mazatzal Mountains study are poorly developed and shallow over stony decomposed granites, with low levels of N, P, and Se that might contribute to forage deficiencies (Urness et al. 1971, Sprinkle et al. 2000). Compared to dietary requirements of domestic sheep (Puls 1994), browse, forbs, and grasses (Table 5) tended to be deficient or marginally deficient in ratios of Ca:P and concentrations of K, P (except for forbs during a wetter period between October 2000 and March 2002), Se, and Zn, but concentrations tended to be adequate in all forages for concentrations of Fe, Mg, Mn, and possibly Na. A population of Rocky Mountain bighorn sheep in Alberta, Canada, consistently had high lamb production, high survival, and young age at first estrus despite very low levels of blood Se (Samson et al. 1989).

Differences in winter rainfall were associated with differences in concentrations of some minerals between and within forage categories in our study. Higher winter rainfall (Table 1) corresponded with higher levels of Ca, P, Na, and Se and lower levels of Fe in browse; higher levels of Ca, Na, P, and Zn in forbs; and higher concentrations of P and Zn in grasses (Table 5). Concentrations of Ca and P also varied widely among seasons and species for bighorn sheep forages in northwestern Arizona (Morgart et al. 1986). Winter moisture levels and whether dead or live plant tissues are evaluated both might affect concentrations of minerals in forages (Greene et al. 1987, Grings et al. 1996, Sprinkle et al. 2000).

Mean Ca:P ratios of browse and forbs were about 30% and 43% narrower, respectively, during the wetter year of July 2000–May 2001 than in the drier year of July 1999–May 2000 (Table 5). Moreover, mean fecal Ca:P ratios of adults (Table 9) were about 20% wider in drier years of July 1999–June 2000 and July 2001–June 2002 than during the wetter year of July 2000–June 2001. Similarly, ratios of Ca:P in feces of lambs (Table 10) were >2-fold wider during the drier year of 2002 than in wetter years of 2001 and 2003. Concentrations of P in feces of adults and lambs (Tables 9, 10) were >29% and 59% to 95% higher, respectively, during wetter than in drier years. Thus, results support a hypothesis of linkages between rainfall, forb production, mineral concentrations in forages, and diet quality.

Dietary requirements of minerals for wild ruminants are poorly understood (Robbins et al. 1985, Grasman and Hellgren 1993, Krausman et al. 1999), and wildlife biologists often have employed the questionable practice of using requirements of domestic animals to evaluate the mineral status of wild ungulates (Robbins et al. 1985, Samson et al. 1989, Robbins 1992). Mineral requirements of domestic ruminants have been studied widely (Puls 1994, National Research Council 1996), but mineral requirements of wild ungulates tend to be a fraction of requirements of domestic animals (Robbins et al. 1985, Samson et al. 1989). Nonetheless, P is considered one of the most limiting

minerals affecting growth and reproduction of large mammalian herbivores worldwide (Grasman and Hellgren 1993), and concentrations of Ca in forages usually are high on western ranges and might be high enough to adversely affect metabolism of P (Dietz 1965). However, wild ungulates likely are more tolerant than domestic ungulates of wider Ca:P ratios in feed and diets (Jones and Weeks 1985, Urness et al. 1971, Puls 1994). Phosphorus deficiency or wider Ca:P ratios in ungulates might correspond with reduced feed intakes, milk yield, and conception rate and weaker young, suppressed estrus, or other abnormalities (Dietz 1965, Puls 1994).

**Diets.**—Male and female desert bighorn sheep adults tend to segregate during an approximate October–June nonbreeding season (Lenarz 1979, Leslie and Douglas 1979, Bleich et al. 1997), and surveys in Mazatzal Mountains indicated comparatively few yearlings (Table 3), suggesting that adult fecal samples we collected in this period likely represented primarily females. Moreover, diets of female and male desert bighorn sheep may tend to be similar (Krausman et al. 1989; but see Bleich et al. 1997), and fecal concentrations of crude protein tend to exhibit similar trends for the sexes throughout the year (Bleich et al. 1997). However, adult females often consume more forbs than do males (Krausman et al. 1989, Bleich et al. 1997), and precipitation patterns may influence consumption of grasses and shrubs by females (Oehler et al. 2003).

Diets of adult desert bighorn sheep in Arizona's Sonoran Desert are diverse and vary spatially and temporally. Seasonally, browse often tends to dominate diets during much of the year, but forbs tend to be consumed more frequently during winter and summer, whereas grasses may be more prevalent in diets during summer (Halloran and Crandell 1953, Dodd and Brady 1988, Krausman et al. 1989, Miller and Gaud 1989, Holt et al. 1992). Browse dominated diets of adults initially in our study during the summer of 1999 to the early winter of 2000. Contrary to our expectation, because winter drought conditions occurred in 2000 and 2002 (Table 1), forbs predominated over browse in adult diets from the early spring of 2000 into the early summer of 2002 (Table 6), but composition of forbs in diets of adults throughout our study increased with increasing increments of rainfall. Ratios of Ca:P of forbs consistently were narrower than those of browse, and higher percent of forbs in diets throughout our study corresponded with declining percentages of browse. In comparison, consumption of forbs and browse by desert mule deer increased and declined, respectively, when forb production was high because of increased winter precipitation (Krausman et al. 1997). Grass in diets of adults tended to increase during summer to autumn (Table 6), likely reflecting increased production associated with summer monsoons (Cable 1975). Relative proportions of forage classes eaten by adults and lambs appeared to be comparable as lambs matured, except that lambs tended to eat more grass than adults did during early spring (Tables 6, 7).

**Fecal Nutrients.**—Differences in FN, FDAPA, and fecal minerals that ostensibly influenced nutritional status of adults and lambs were associated with demographic changes in the desert bighorn sheep population (Figs. 4–7; Tables 3, 9, 10). Correlations between FN and FDAPA and dietary protein and energy (Brown et al. 1995, Hodgman et al. 1996), as well as other

findings (Leslie and Starkey 1985, Leslie et al. 1989, Irwin et al. 1993, Bleich et al. 1997, Osborn and Ginnett 2001, Blanchard et al. 2003), suggest that FN and FDAPA can provide useful indices of diet quality and nutritional status of bighorn sheep. Seasonal measures of FN might be particularly useful indices of bighorn sheep nutritional status in environments such as deserts and other habitats that have higher variability in forage production (Blanchard et al. 2003). In comparison, FN and FDAPA were poor predictors of indices of physical condition and population parameters for a migratory herd of mule deer (Kucera 1997).

Presence of secondary compounds in forages potentially reduces digestible protein (Hanley et al. 1992) and elevates FN (Leslie and Starkey 1987, Robbins et al. 1987, Osborn and Ginnett 2001). Tannin levels might not influence concentrations of FP and FDAPA (Mubanga et al. 1985, Osborn and Ginnett 2001), and it appears that forages high in tannins must comprise about 25–33% of the ruminant diet before the relationship between fecal and dietary N is affected (Hodgman et al. 1996). Compared to average foods available, ruminants also tend to consume diets higher in nutrients and lower in toxins, and diets of browsers likely are influenced by homeostatic mechanisms of food selection, digestion, and an acceptable body phenolic burden determined by rate of detoxification and elimination (Robbins et al. 1987, Provenza 1995, Hanley 1997). Female bighorn sheep might compensate for decreased forage quality by increasing dietary intake or modifying their strategy of resource allocation (Berger 1991, Blanchard et al. 2003).

Correlations between FN and FDAPA and FN and FP in our study suggested comparatively low dietary concentrations of plant secondary compounds and usefulness of FN and FDAPA as indices of relative dietary quality (Leslie et al. 1989, Osborn and Jenks 1998, Osborn and Ginnett 2001). Weak positive correlation between FN and FP tended to support this conclusion (Osborn and Jenks 1998). Moreover, FN, FNDF, and FP were not correlated with % composition of browse, forbs, or grasses in desert bighorn sheep diets. Browse and forb leaves may contain tannins (Hanley et al. 1992), and lack of correlation between fecal indices and composition of forage classes in diets indicated that tannins had little effect in increasing FN levels (Bleich et al. 1997). Crude protein levels in desert bighorn sheep feces also tended to correspond with seasonal changes in percent protein and in vitro dry matter digestibility of forages eaten, particularly browse and forbs (Bleich et al. 1997). Moreover, patterns of precipitation might influence in vitro dry matter digestibility and protein content of forages (Oehler et al. 2003), and dietary energy and protein (Holt et al. 1992).

Nutritional deficiencies of adults might contribute to lower survival of juvenile ungulates (Robinette et al. 1973, Brady et al. 1978, Flueck 1994). Preweaning survival of large herbivores often increases with higher forage quality and quantity, possibly through improved milk quality and yield (Murphy and Coates 1966, Robinson and Forbes 1968, Hudson and Adamczewski 1990, Gaillard et al. 2000). Inadequate nutrition may have caused increased mortality of late-born bighorn sheep lambs in Alberta, Canada (Festa-Bianchet 1988a). Fecal crude protein concentrations did not correspond with survival of kids to weaning in mountain goats (*Oreamnos americanus*) but was positively asso-

ciated with survival of females to 1 year (Côté and Festa-Bianchet 2001). Higher levels of rainfall in more xeric regions generally are associated with improved production and productivity in populations of large herbivores (Coe et al. 1976, Smith and LeCount 1979, Leopold and Krausman 1991, Fynn and O'Connor 2000), including desert bighorn sheep (Douglas and Leslie 1986, Wehausen et al. 1987, McKinney et al. 2001). Positive associations occurred between winter rainfall, forb production, and mule deer fawn:doe ratios on our study area and forage condition other than during years of extreme winter drought likely did not limit fawn survival (Smith and LeCount 1979).

Our findings are consistent with the notion that improved nutritional status of lambs and adults and higher survival of young correspond with relatively higher winter rainfall (McCutchen 1988, Krausman et al. 1989). Improved nutritional status of adults and higher production (Figs. 4, 5; Tables 3, 9) were associated with higher winter rainfall levels (Table 1), suggesting positive associations among winter rainfall, nutritional status, and population dynamics. Although increased levels of N and DAPA occurred in feces of adults during each winter–spring, effects of higher winter rainfall were particularly evident in more prolonged duration of elevated levels of these nutritional indices in wetter winters (Figs. 4, 5; Table 1), likely corresponding with higher primary production (Fig. 3). Higher winter rainfall in 2001 was associated with greater forb production and increased consumption of forbs by adult desert bighorn sheep, although percentage of forbs in their diets remained high during winter 2002 despite low winter rainfall and ostensibly low forb production that year (Fig. 3; Tables 1, 6). In comparison, an index of FN for adult Rocky Mountain bighorn sheep was positively correlated with rainfall in the summer growing season (Blanchard et al. 2003).

Fecal NDF concentrations for adults among sampling periods (Table 6) and lack of correlation between FNDF and FN or FDAPA indicated that FNDF was independent of diet quality, although NDF levels in forages may affect dietary intake (Mubanga et al. 1985, Baker and Hobbs 1987, Krausman et al. 1988). In contrast, FNDF alone was a suitable index of diet quality for penned mule deer fed diets derived from diverse mixtures of wild-grown forages (Hodgman et al. 1996). Higher forage concentrations of NDF adversely affect digestibility, but deer and, to a lesser extent, bighorn sheep may be able to some degree to regulate dietary intake in relation to relative digestibility of forages and meet energy needs (Ammann et al. 1973, Baker and Hobbs 1987, Krausman et al. 1988). Bighorn sheep may digest fiber relatively efficiently (Baker and Hobbs 1987), but digestibility may correspond negatively with dietary NDF levels (Krausman et al. 1988). Penned desert bighorn sheep fed native forages ad libitum varied consumption seasonally, with highest dietary intake between January and June (Mazaika et al. 1992), but factors affecting seasonal dietary intake are uncertain.

Despite numerous studies, temporal breeding patterns of desert bighorn sheep remain poorly understood (Lenarz 1979, Rubin et al. 2000). Rutting activity by desert bighorn sheep in southwestern Arizona is believed to occur primarily during July–September (Russo 1956), suggesting a lambing season primarily during January–March (Turner and Hansen 1980). Most desert bighorn sheep lambs in the Peninsular Ranges of California were born

between February and March (Rubin et al. 2000). Consistent with other findings (Russo 1956, Brown et al. 1976, Turner and Hansen 1980, Seegmiller and Ohmart 1982), we observed that lambing occurred primarily during late December into March, and lambs apparently began foraging to some extent within a few weeks of birth (Table 7). Birth of most lambs in our study likely was delayed in 2003, compared to between 2000 and 2002, suggesting that lower winter rainfall and marginal or deficient nutritional status during severe drought in 2002 (Figs. 4, 5; Tables 1, 9) retarded breeding and perhaps affected gestation the following year. Regardless, nutritional status of adults in 2003 (Figs. 4, 5; Tables 1, 9) likely remained adequate to support production, productivity, and stability or growth of the desert bighorn sheep population (Table 3; Remington 1989). Factors influencing periods of peak parturition within the birthing season of desert bighorn sheep populations seldom have been studied (Rubin et al. 2000).

Moderate undernutrition may delay onset of estrus in ungulates, with minimal effect on pregnancy rates, whereas severe nutritional deficiencies might delay mating, lengthen gestation, reduce productivity and growth and survival of young, and cause complete cessation of reproductive activity (Verme 1965, Murphy and Coates 1966, Cook et al. 2001). Female ungulates of several species, when in poor body condition, also may tend to give birth later than females in better condition (Côté and Festa-Bianchet 2001). Compared to females receiving adequate diet, quantitative diet restriction of penned white-tailed deer was associated with delayed onset of mating, extended gestation, and lower fawn production (Verme 1965). Survival of fawns in penned white-tailed deer also was reduced by lower levels of protein in rations provided to adult females (Murphy and Coates 1966). Concentrations of N in feces of adults in Mazatzal Mountains during all sampling periods except September–October 2000 generally were  $\geq 1.7\%$  and were within ranges reported for other desert bighorn sheep populations (Bleich et al. 1997; Rubin et al. 2000, 2002*b*; Oehler et al. 2003).

Nutritional status of adults and lambs during our study appeared adequate to sustain productivity and population growth, but increased productivity corresponded with higher winter rainfall, compared to drier winters, suggesting associations between nutritional status, productivity, and winter precipitation. Assuming that more prolonged and comparatively higher concentrations of FN and FDAPA in our study corresponded to higher and more available dietary nitrogen and digestible protein and energy (Irwin et al. 1993, Wehausen 1995, Hodgman et al. 1996), nutritional status of females during pregnancy and lactation in wetter years likely corresponded with enhanced milk yield and better condition and growth of lambs (Thomson and Thomson 1953, Robinson and Forbes 1968, Robbins 1992). Differences in female nursing or lamb suckling behavior or qualitative and quantitative aspects of milk production (Russo 1956, McCutchen 1988) likely are key variables affecting lamb nutritional status negatively in particularly dry periods during winter to spring.

Our results suggested that behavioral or physiological homeostatic mechanisms influenced diet composition, nutritional status, and mineral metabolism of adults and lambs. Concentrations of forbs in diets of desert bighorn sheep were comparatively high

during drought, when production of forbs likely was low, suggesting forage selection. Highest concentrations of FN and FDAPA diminished in duration during drier winters but nonetheless reached levels indicating at least brief periods of adequate nutrition. Homeostatic behavioral and physiological mechanisms operative for desert bighorn sheep might reflect only some increasing tendency, although rapid changes in mechanisms might occur, often making quantitative inferences difficult (Blair-West et al. 1968, Provenza 1995, Hanley 1997). Pattern and amount of precipitation and subsequent primary production also may affect diets, distribution, and home range size of female desert bighorn sheep (Berger 1991, Oehler et al. 2003).

Active homeostatic mechanisms undoubtedly are involved with mineral metabolism in ruminants (Robbins 1992) and contribute to forage selection associated with differences in nutrient concentrations, enhancing positive nutrient and mineral balances (Weeks and Kirkpatrick 1976, Grasman and Hellgren 1993, Provenza 1995, Hanley 1997). Concentrations of protein, available energy, and minerals in diets, feces, or forages might be affected by rainfall levels and reflect differences between drought and wetter years that possibly influence desert bighorn sheep nutritional status and lamb survival (Jones et al. 1967, Urness et al. 1971, Weeks and Kirkpatrick 1976, Jones and Weeks 1985, Holt et al. 1992, Puls 1994).

Apparent associations of rainfall with concentrations of some fecal minerals in our study suggested homeostatic mechanisms were associated with temporal variability in diet quality and relationships between precipitation and dietary intake of minerals or metabolic processes in adults and lambs. Mineral concentrations in feces of ungulates may be affected by variables other than dietary intake, including absorption, tissue storage, interactions among minerals, and homeostatic mechanisms involved in mineral metabolism (Weeks and Kirkpatrick 1976, Grasman and Hellgren 1993, Mayland and Shewmaker 2001). Awareness of mineral requirements of forages and herbivores is essential to understanding complex interactions among dietary mineral elements (Mayland and Shewmaker 2001). Desert bighorn sheep in the Sonoran Desert forage on most plant species we analyzed for mineral content (present data, Krausman et al. 1989, Seegmiller et al. 1990, Holt et al. 1992), but during the present and previous (McKinney and Noon 2002) studies, they did not eat all forages analyzed, perhaps limiting comparisons of and inferences regarding minerals in feces and forages.

Among adults, FP increased and fecal ratios of Ca:P narrowed in association with higher rainfall (Tables 1, 9), paralleling changes of these indices in forages (Tables 1, 5). Concentrations of Ca in forbs and levels of Ca in feces of adults were higher in a wetter year, consistent with higher dietary use and production of forbs in wetter years (Fig. 3; Tables 1, 6, 9). In comparison, concentrations of Ca in feces of lambs tended to increase and concentration of fecal P to decrease during the low rainfall year of 2002 as compared to wetter years, and wider ratios of Ca:P in feces paralleled trends in forages during a drier year (Tables 1, 5, 10). Concentrations of Na in feces of adults were higher during severe drought in 2002 (Tables 1, 9, 10), although Na levels in browse and forbs appeared to decline with lower rainfall (Tables 1, 5). In general, levels of K and Na in feces of adults increased with

percent forbs in diets and concentrations of fecal Mg increased, but concentrations of fecal K declined, in relation to % browse in diets (Tables 6, 9).

Higher productivity and concentrations of FN, FDAPA, and FP for lambs tended to correspond with higher winter rainfall, whereas lower productivity and higher concentrations of NDF, Ca, and Mg in feces of lambs tended to associate with lower winter precipitation (Figs. 6, 7; Tables 1, 3, 7, 10). Concentrations of fecal minerals of lambs tended to decline during maturation, nearing adult levels in early summer (Tables 9, 10), as lambs likely nursed progressively less and approached weaning (McCutchen 1988). Patterns of declining FN and FDAPA and increasing concentrations of FNDF during maturation also tended to characterize feces of lambs (Figs. 6, 7; Table 7), likely reflecting development of the alimentary tract and dietary shifts from milk to solid food (Cook et al. 1994). In contrast to declining concentrations of FN with maturation of lambs, protein content of milk produced by females during lactation might be expected to increase as lambs mature (Cook et al. 1970, Mueller and Sadler 1977). Concentrations of Na in feces of lambs (Table 9) tended to decline during maturation in wetter years (Table 1) but did not decline during the driest year of our study. Further, feces of lambs tended to have lower concentration of Ca, higher concentration of P and narrower ratios of Ca:P in wetter years, but concentrations of K and Na and ratios of Na:K were independent of winter rainfall (Tables 1, 10). In comparison with adults (Table 9), ratios of Na:K in lamb feces were positively correlated (also positively correlated for adults) and negatively correlated (not correlated for adults) with concentrations of Na and K, respectively (Table 10), suggesting possible inhibitory influence of K on retention of Na by lambs (Weeks and Kirkpatrick 1976). However, concentrations of Na and ratios of Na:K in feces of adults and lambs likely did not indicate dietary deficiencies of Na (Weeks and Kirkpatrick 1976).

Comparatively little research has addressed mineral requirements and utility of using indices of fecal mineral concentrations to assess diet quality of wild ungulates. Desert bighorn sheep may ingest soil and use mineral licks, but little is known about their mineral requirements (Krausman et al. 1999). Linkages may occur between indices of diet quality and fecal minerals for wild ruminants. Positive relationships between dietary and fecal phosphorus of wild ruminants suggest utility of fecal P in monitoring diet quality (Leslie and Starkey 1985, Mubanga et al. 1985, Howery and Pfister 1990, Osborn and Jenks 1998). Positive linear relationships occurred between estimated dietary intake and concentrations of Ca and K but not levels of Mg or P in feces of free-ranging fallow (*Dama dama*), roe (*Capreolus capreolus*), and sika (*Cervus nippon*) deer in South Africa (Putman and Hemmings 1986). Levels of K and Na in feces of white-tailed deer increased during spring, when percentages particularly of forbs in their diet increased (Weeks and Kirkpatrick 1976), and concentration of Na in feces of mountain goats increased when diets were changed from sun-cured to succulent forage (Hebert and Cowan 1971).

Excessive levels of dietary and fecal K might contribute to high loss of Na in feces, but behavioral and physiological mechanisms may allow maintenance of positive Na balance in white-tailed deer (Weeks and Kirkpatrick 1976). However, lack of correlation in our study between fecal Na and K and between fecal K and ratios

of Na:K and positive correlation between fecal Na and ratios of Na:K, provided evidence that excess K did not influence increased levels of Na that we observed in feces of adult desert bighorn sheep during severe drought. Mean concentration of Na in feces of adults clearly was highest in our study between November 2001 and June 2002 (Table 9), when rainfall during July–June was less than half that during the same period in previous years, possibly reflecting higher dietary intake of the mineral or active homeostatic physiological mechanisms (Jones et al. 1967, Weeks and Kirkpatrick 1976).

Higher concentrations of Na in barrel cactus (*Ferrocactus* spp.) might help explain consumption of the plant by desert bighorn sheep (McKinney and Noon 2002), but they may supplement water demands by eating the cacti during hottest, driest seasons (Warrick and Krausman 1989). Inadequate winter rainfall and correspondingly reduced forb production might contribute to deficiencies of P in deer on chaparral and desert ranges (Urness et al. 1971), but behavioral and physiological mechanisms may allow maintenance of positive balances of K, Na, and P (Weeks and Kirkpatrick 1976, Grasman and Hellgren 1993). Bighorn sheep are concentrate selectors, eating primarily browse tips, forbs, and new growth of grasses (Hobbs et al. 1983). Forage selection possibly reduces susceptibility to potential deficiencies in dietary P through relative consumption of forbs, browse, and grasses, which successively decline in concentrations of P (Urness 1973, Grasman and Hellgren 1993, Mayland and Shewmaker 2001, McKinney and Noon 2002). Phosphorus and Na are essential to many body functions in animals, but little is known regarding adaptive mechanisms by which herbivores maintain positive balance of minerals (Weeks and Kirkpatrick 1976, Robbins 1992, Grasman and Hellgren 1993).

### Predators

Several lines of evidence suggested that mountain lion predation potentially was a substantial mortality factor affecting the Mazatzal Mountains desert bighorn sheep population, particularly prior to predator reductions, and that predator reductions diminished this mortality factor. Following a protracted period of apparently declining abundance, productivity, production, and recruitment of the desert bighorn sheep population between 1994 and 1999 (Table 3; McKinney et al. 2001), indices of abundance, production, and productivity ostensibly increased between 2000 and 2003 (Table 3), when mountain lions were experimentally removed (Table 11). Mortalities and mortality rates of radio-collared desert bighorn sheep due to mountain lion predation were  $\geq 2$ -fold higher between 1995 and 1998, when there was no experimental predator removal, compared to the period of experimental predator reductions between 2000 and 2003. Winter drought occurred on the primary study area with similar frequencies during these periods, suggesting that apparent changes in population parameters were not associated with differences in occurrence of inadequate rainfall. Drought occurred during 2 of 4 years in 1995 to 1998, and observation rates of total desert bighorn sheep and lambs declined about 35% and 78%, respectively. Drought also occurred during 2 of 4 years between 2000 and 2003 (Table 1), but observation rates of total desert bighorn sheep, males, females, and lambs increased about 98%, 100%, 90%, and

180%, respectively, and productivity increased  $\geq 33\%$  during this period (Table 3).

We attempted further to factor out the potential role of mountain lion predation on dynamics of the Mazatzal Mountains desert bighorn sheep population by comparisons between population parameters and winter rainfall on the primary study area and 2 reference areas during 1994–1997 (Fig. 1; Table 2) and comparison of population parameters and winter rainfall between the primary study area and Plomosa Mountains during 1999–2003. Mountain lions are believed to be absent on reference areas (Germaine et al. 2000, Arizona Game and Fish Department 2005). Relative abundance of desert bighorn sheep was positively correlated with winter rainfall in Mazatzal Mountains and reference areas, and winter rainfall was higher in Mazatzal Mountains but declined less there than on reference areas between 1994 and 1997. In contrast, abundance of desert bighorn sheep between 1994 and 1997 declined  $>2$  to  $>5$  times more in Mazatzal Mountains than on reference areas (Table 2), leading us to suspect that mountain lion predation in Mazatzal Mountains was a variable influencing the desert bighorn sheep population. Moreover, increasing patterns of desert bighorn sheep population parameters and patterns of winter rainfall were similar in both Mazatzal and Plomosa mountains between 1999 and 2003 (in contrast to magnitude of negative trends apparent between 1994 and 1997), suggesting that higher population parameters in Mazatzal Mountains between 2000 and 2003 ostensibly were associated with predator reductions (Table 11) and lower mountain lion predation.

Compared to 1999, survey observations of total desert bighorn sheep males, females, and yearlings during drought in 2000 declined 40%, 35%, 49%, and 67%, respectively, whereas production and productivity increased from 0 to 0.5 and 24, respectively (Tables 1, 3), coincident with harvest of mountain lions (Table 11) and higher occurrence of desert bighorn sheep remains in mountain lion scats (Table 12). Observation rates of total desert bighorn sheep males, females, and lambs, as well as productivity, then increased between 2001 and 2003 (Table 3), coincident with lower occurrence of remains of the ungulate, compared to occurrence in 2000, in mountain lion scats, continued mountain lion reductions, and lower indices of abundance of the predator (Tables 11, 12). Results suggested association between mountain lion predation and continued harvest of the predator, even though some continued predation was apparent between 2000 and 2003. Although 90% of mountain lion scats containing desert bighorn sheep remains in east-central Arizona indicated consumption of lambs or young (Cashman et al. 1992), we found no discernible evidence of remains of young desert bighorn sheep in mountain lion scats and no clear evidence of predation on lambs or yearlings.

Visual characteristics of scats have been widely used to identify predator species and assign prey items eaten by species, but inaccuracies of this approach may have affected our assessments of predator diets (Johnson et al. 1984, Farrell et al. 2000, Davison et al. 2002, Reed et al. 2004). Nonetheless, experience and training likely are major factors affecting accurate visual identifications of carnivore feces (Zuercher et al. 2003), and we suggest that bias in scat identification likely had little meaningful effect on our

conclusions (Johnson et al. 1984, Cunningham et al. 1999, Thornton et al. 2004).

Given large expected home ranges of mountain lions in desert habitats (Cunningham et al. 1995, Logan and Sweanor 2001) and the known range of desert bighorn sheep distribution on the primary study area (Fig. 2), mountain lions indexed during track surveys (Table 11) likely were potential predators of the Mazatzal Mountains desert bighorn sheep population. Track surveys, particularly during spring (Table 11), indicated effectiveness of mountain lion reductions in lowering predator abundance and suggested little likelihood that movements other than seasonally during winter influenced postremoval abundance. We speculate that more variable mountain lion track densities during winter than during spring (Table 11) were associated with prebreeding (Anderson 1983, Logan and Sweanor 2001) movement patterns, particularly by males. Consistent with our findings, mountain lion track densities also were higher during autumn than spring in southeastern Arizona (Cunningham et al. 1995). Decline of spring track counts after cattle removal (Tables 11, 12) suggested that earlier obliteration of mountain lion tracks on transects by cattle (Beier and Cunningham 1996) was not meaningful, and transects on roads received little vehicle traffic that might have obliterated mountain lion tracks.

Extensive mountain lion habitat was contiguous with our study area (Arizona Game and Fish Department 2003) and transient animals might have been expected to replace harvested residents (Hemker et al. 1984, Laing and Lindzey 1993, Beier 1995). However, lower mean track counts (particularly during spring surveys), coincident with increased sport harvest of mountain lions (Table 11), indicated that there likely was little, if any, population recovery. In comparison, removal of about half of adult mountain lions from a study area in New Mexico was followed by recovery of the population in about 31 months (Logan and Sweanor 2001). Abundance of resident adult mountain lions in a Utah population returned to pretreatment levels in about 9 months following removal of 42% of that population segment (Lindzey et al. 1992). In contrast, harvest of mountain lions at a rate greater than in our study in southern Arizona, where cattle, deer, and collared peccary were abundant, was not associated with decline in abundance of the predator (Cunningham et al. 1995, 1999, 2001a).

Predation by coyotes occurs in some bighorn sheep populations (Hass 1989, Cunningham and deVos 1992, Bleich 1999) and bobcats and coyotes may scavenge carcasses of prey killed by other predators (Major and Sherburne 1987, Koehler and Hornocker 1991, Arjo et al. 2002), but we found no evidence that bobcats and coyotes preyed on or scavenged desert bighorn sheep. In contrast, carcasses identified as kills and prey remains in scats (Table 12) indicated some continual predation of desert bighorn sheep by mountain lions in Mazatzal Mountains between 1999 and 2003.

Predation by mountain lions on bighorn sheep is sporadic (Ross et al. 1997, Logan and Sweanor 2001, Sawyer and Lindzey 2002), consistent with variability we observed among years in frequency of desert bighorn sheep remains in scats (Table 12). Population-level impacts of predation on bighorn sheep can be particularly severe if mountain lions kill substantial numbers of reproductive females and their young (Gaillard et al. 1998, Hayes et al. 2000). However, studies of prey selection by mountain lions have yielded

conflicting results regarding bighorn sheep (Mooring et al. 2004). Females with lambs may facilitate predator evasion by selecting particularly rugged escape terrain, and mountain lions may kill adult males more often than adult females (Festa-Bianchet 1988*b*, Bleich et al. 1997, Ross et al. 1997, Schaefer et al. 2000, Mooring et al. 2004).

Conversely, mountain lions selected lambs in a population of Rocky Mountain bighorn sheep and prey-class vulnerability might be largely a function of behavior of individual mountain lions (Ross et al. 1997). Male desert bighorn sheep often were observed in less rugged areas than female or mixed groups, ostensibly exposing males more than females to predation by mountain lions (Bleich et al. 1997, Mooring et al. 2004). However, rugged terrain might not be very effective in deterring predation by stalking predators like mountain lions (Creeden and Graham 1997, Ross et al. 1997, Sawyer and Lindzey 2002, Mooring et al. 2004). In comparison, escape terrain deters predation of bighorn sheep by cursorial predators, such as coyotes (Bleich 1999). Limited availability of escape terrain and restricted spatial distribution of the bighorn sheep population in Mazatzal Mountains (Fig. 2; McKinney et al. 2001, 2003) might have been factors influencing mountain lion predation (Cunningham 1989, Skogland 1991).

Mountain lion predation in some circumstances likely can affect growth and stability of bighorn sheep populations (Wehausen 1996, Creeden and Graham 1997, Ross et al. 1997, Hayes et al. 2000, Sawyer and Lindzey 2002) and hamper reintroduction efforts (Krausman et al. 1999, Rominger and Weisenberger 1999, Kamler et al. 2002, Rominger et al. 2004). Potential population-level effects of mountain lion predation appear to be greatest for small ( $\leq 100$ ) populations inhabiting desert habitats (Sawyer and Lindzey 2002). Predation by individual mountain lions, likely reflecting learned behavior, may impact bighorn sheep populations independently of mountain lion density (Hoban 1990, Ross et al. 1997, Rominger and Weisenberger 1999, Logan and Sweanor 2001), and harvest of individuals that targeted desert bighorn sheep may have been a factor in our study. However, removal of a few mountain lions each year, whether targeted or not for individual predation behavior, might in some instances benefit growth, productivity, and persistence of small, isolated bighorn sheep populations (Wehausen 1996, Ernest et al. 2002). About 29% of lambs, 44% of females, and 50% of males killed by mountain lions in a population of Rocky Mountain bighorn sheep exhibited anatomical or behavioral disabilities just prior to mortality (Ross et al. 1997), but we found no clear evidence indicating that abnormalities influenced predation.

Annual surveys suggested statewide deer populations declined during 1989–2002 (Arizona Game and Fish Department 2003, Kamler et al. 2002), and lower abundance of deer on our study area during drought (Anthony 1976, Rominger and Weisenberger 1999) might have contributed to higher mountain lion predation of desert bighorn sheep (Branch et al. 1996, Logan and Sweanor 2001, Kamler et al. 2002, Rosas-Rosas et al. 2003). Mule deer are believed to be primary prey—and bighorn sheep alternative prey—for mountain lions (Anderson 1983, Schaefer et al. 2000), and the predator might switch to alternative prey, including bighorn sheep, following a mule deer decline (Leopold and Krausman 1986, Logan and Sweanor 2001, Kamler et al. 2002, Holl et al.

2004). Occurrence of deer remains in mountain lion scats in our study was generally less than about half of levels often reported for the western United States (Iriarte et al. 1990, Cashman et al. 1992, Cunningham et al. 1999, Logan and Sweanor 2001).

We hypothesize increased relative availability of ungulate prey/mountain lion was associated with predator reductions and influenced behavior as well as diets (Tables 12, 13) of mountain lions. Although results might suggest increased per capita consumption rate of wild ungulate prey following predator reductions (i.e., presumably fewer mountain lions ate greater relative biomass and numbers of wild prey), we were unable to quantify functional response (per capita rate of prey consumption; Abrams 1997). Relative roles of prey-dependent (per capita kill rate increases with prey density) and ratio-dependent (kill rate dependent on ratio of prey to predator) predator kill rates have been controversial in developing models of predator–prey relationships (Arditi and Ginzburg 1989, Arditi and Akçakaya 1990, Abrams 1997, Abrams and Ginzburg 2000, Vucetich et al. 2002). A ratio-dependent model (Vucetich et al. 2002) greatly outperformed a prey-dependent model of wolf (*Canis lupus*) predation of moose (*Alces alces*). However, predator functional responses in natural systems are unlikely to be either purely prey or purely ratio dependent (Abrams and Ginzburg 2000, Vucetich et al. 2002).

We have no data from which to infer behavioral patterns of mountain lions or large ungulate prey during our study but speculate that behavioral dynamics (Arditi and Ginzburg 1989, Arditi and Akçakaya 1990, Brown et al. 1999, Skalski and Gilliam 2001) possibly contributed to differences we observed in predation by mountain lions between 1995–1998 and 2000–2003 and in composition and diversity of mountain lion diets (Tables 12, 13). An extensive empirical and theoretical literature indicates that predation is a function of relative abundances of predator and prey and is influenced by differences in predator interference (direct encounters among predators) and prey behavior across predator abundances (Brown et al. 1999, Skalski and Gilliam 2001, Alonso et al. 2002). Variation in social organization in relation to prey availability is typical of many carnivores (Pierce et al. 2000), and density-related behavioral dynamics of predator–prey interactions might influence predation by mountain lions (Brown et al. 1999).

Mountain lions may prey heavily on locally abundant small and medium-sized prey when large prey are not available or are less vulnerable (Iriarte et al. 1990). Differences in abundance of large ungulate and small prey per se between years prior to and following predator removal in our study did not appear to explain initially high occurrence and biomass of small prey in mountain lion diets (Tables 12, 13). Cattle were removed from the study area by early 2001 (Table 12), but surveys suggested there likely was little change in total relative abundance of wild ungulates between 1999 and 2003 (Arizona Game and Fish Department 2004). Differences in winter rainfall between 1999 and subsequent years (Table 1) suggested little probability of overall declines during this period in abundance of wild large or small prey; winter drought prevailed during 1999, 2000, and 2002, and normal winter precipitation occurred in 2001 and 2003. Winter rainfall in desert regions generally corresponds positively with productivity and recruitment of desert bighorn sheep (present data, McKinney et al. 2001) and mule deer (Smith and LeCount 1979, Leopold

and Krausman 1991, Marshal et al. 2002) as well as primary production and relative availability of small prey (Beatley 1969, Reichman and Van De Graaff 1975, Jones and Smith 1979, Ernest et al. 2000, Marshal et al. 2005).

Although annual sample sizes for scats in our study were comparatively small (Núñez et al. 2000), we believe that data sufficiently reflected valid trends in mountain lion diets that were independent of winter rainfall levels. Occurrence of small prey remains in mountain lion scats in 1999 (Table 12) was nearly double the highest occurrence reported in most other studies, but occurrence of small prey after implementation of predator reductions was more similar to ranges reported previously. Occurrence of small prey in studies of mountain lion diets generally ranged from about 0% to 27% (Robinette et al. 1959, Ackerman et al. 1984, Iriarte et al. 1990, Cashman et al. 1992, Cunningham et al. 1999). In comparison, occurrence of small prey in mountain lion scats in Mexico in deciduous dry forest habitat (Núñez et al. 2000) was similar to our results in 1999. Occurrences of small prey in mountain lion scats generally are lower in Mexico and North America than in more southern latitudes (Yáñez et al. 1986, Branch et al. 1996). Small prey in mountain lion scats differed little prior to and following a deer decline (Leopold and Krausman 1986).

Lower diet diversity following mountain lion reductions (Tables 11, 12) is consistent with the hypothesis that reduced intraspecific interference corresponded with lower abundance of the predator (Baker et al. 2001). Interference among mountain lions likely would increase (Skalski and Gilliam 2001)—and mountain lions may become comparatively inefficient predators—as their population densities increase (Arditi and Akçakaya 1990, Brown et al. 1999), possibly influencing prey selection. Prey appear to assess and behaviorally control their risk of predation (Lima and Dill 1990), and vigilance of ungulates increases at higher mountain lion densities but declines at lower densities (Brown et al. 1999). Moreover, mutual interference between predators may produce nonuniform spatial distributions of predator and prey (Alonso et al. 2002). Vigilance and potential exposure of desert bighorn sheep to predation likely are lower and higher, respectively, when group size is  $<5$  (Mooring et al. 2004), and mean group size in our study was below this level from 1995 through 2003 (present data, McKinney et al. 2001). We thus speculate that changes in social behavior of predator and prey and predator/prey ratio influenced mountain lion diets, as well as predation of desert bighorn sheep, during predator reductions and comparatively low overall abundance of ungulate prey in Mazatzal Mountains.

## MANAGEMENT IMPLICATIONS

Identifying potential limiting factors represents a continual challenge for wildlife biologists and resource managers (McNamara and Houston 1987, Ballard et al. 2001). Limiting factors might be of interest primarily if responsible for major year-to-year population fluctuations (Sinclair 1991). Unpredictable, density-independent events such as drought can correspond with ungulate population declines and challenge conservation strategies (Bleich and Taylor 1998). Mortality of desert bighorn sheep lambs may be influenced by multiple variables acting within the same time frame (DeForge and Scott 1982, McNamara and Houston 1987,

Gaillard et al. 1998, Logan and Sweanor 2001). Inadequate forage resources and predation occur within the same time frame and should not be considered independently as alternative limiting factors (McNamara and Houston 1987, Sinclair 1991).

During the past quarter century, results of several studies suggested that predation by mountain lions might be an important mortality factor associated with bighorn sheep population declines, and small, isolated populations appear more vulnerable to population-level effects of mountain lion predation (Sawyer and Lindzey 2002). Removal of resident adult mountain lions in New Mexico by translocation was ineffective in reducing desert bighorn sheep losses to mountain lion predation or preventing decline of a desert bighorn sheep population (Logan and Sweanor 2001). Results of other studies indicated that lethal mountain lion removals likely would benefit bighorn sheep populations (Hoban 1990, Wehausen 1996, Ernest et al. 2002).

Factors affecting mountain lion predation of bighorn sheep are poorly understood but might involve numerous abiotic and biotic variables, including drought, disabilities or diseases, habitat changes (Hoban 1990, Creeden and Graham 1997, Ross et al. 1997, Rominger and Weisenberger 1999, Logan and Sweanor 2001), and availability of primary or alternative prey (Leopold and Krausman 1986, Schaefer et al. 2000, Logan and Sweanor 2001). Limited, herd-specific, short-term lethal removal of mountain lions may under some circumstances provide a management tool, particularly to benefit small, isolated desert bighorn sheep populations (Schaefer et al. 2000, Ernest et al. 2002, Kamler et al. 2002, Holl et al. 2004, Rominger et al. 2004).

Biologists in the western United States recently have been concerned over mountain lion predation of bighorn sheep (Wehausen 1996, Creeden and Graham 1997, Ross et al. 1997, Rominger and Weisenberger 1999, Hayes et al. 2000, Kamler et al. 2002), but predator control, particularly to benefit game species, remains controversial (McKinney et al. 2000; Ballard et al. 2001, 2003). Predator-prey dynamics of mountain lions and desert bighorn sheep vary widely among populations and years, and mountain lion reductions designed to benefit prey populations should be implemented specific to spatial and temporal variables and based on assessments of biological relevance (Ballard et al. 2001, 2003). Translocation of mountain lions may result in high risk of death and likely is of limited value as a management tool (Ruth et al. 1998).

Adaptive natural resources management is a learning process where actions are complex and uncertain and is difficult to conduct from a scientific viewpoint but potentially promotes rigor and objectivity in the management of natural resources (Morrison et al. 2001). Deliberate experimentation may benefit adaptive management efforts but cannot answer with scientific certainty the question of how much better (or worse) a system performed in response to a treatment than if the treatment had not been implemented (Walters and Green 1997). Ecological field experiments seldom meet criteria for modern experimental design (Eberhardt and Thomas 1991). Inferences we derived generally are limited to the primary study area, but broader inference derives from results of different investigations in different areas at different times (Sinclair 1991, Johnson 1999), ostensibly benefiting adaptive resources management. Resource managers need to understand

how abiotic and biotic variables influence mountain lions, their prey, and predator–prey relationships (McNamara and Houston 1987; Ballard et al. 2001, 2003; Logan and Sweanor 2001).

## SUMMARY

We identified 2 proximate factors that likely acted or interacted within the same time frame to affect demographic patterns of the desert bighorn sheep population in Mazatzal Mountains: nutritional status (winter rainfall patterns [ultimate factor] were associated with differences in primary production, concentrations of minerals in forages, and quality of desert bighorn sheep diets) and predation by mountain lions. We were unable to distinguish clearly the relative impacts of these factors operating to affect population parameters, but these variables likely were destabilizing elements for the population. Understanding relationships between desert bighorn sheep populations and habitat variables is fundamental to nutritional ecology. However, researchers may have focused less on the role of density-independent factors, such as quality and quantity of available food, than on the role of predation as limiting factors for ungulate populations (Saether 1997). Within parameters of our study, we hypothesize that unpredictable winter rainfall influenced primary production particularly of forbs, forage nutritional quality, and nutritional quality of diets and demographic attributes of the population of desert bighorn sheep in Mazatzal Mountains.

It appears unlikely that intermittent drought contributes to catastrophic declines in desert bighorn sheep abundance in the absence of potentially interacting mortality factors that might have population-level impacts, such as disease, overgrazing by domestic livestock, and predation. However, prolonged drought may correspond with downward trends in desert bighorn sheep abundance associated with relatively poorer forage production and quality and poorer nutritional status and lower productivity or

survival of lambs. We postulate that desert bighorn sheep incorporate homeostatic behavioral and physiological mechanisms that tend to promote maintenance of dietary nutritional quality and quantity and positive balance of some minerals under conditions of unpredictable rainfall characteristic of desert habitats.

Lethal removals of mountain lions in Mazatzal Mountains between 2000 and 2003 were associated with dietary changes of the predator, lower indices of mountain lion abundance and lower predation of desert bighorn sheep, and increased indices of growth, production, and productivity of the desert bighorn sheep population despite successive years of drought. As a result, we hypothesize that both nutritional status and mountain lion predation likely influenced demographic parameters of the desert bighorn sheep population in Mazatzal Mountains and that short-term removal of mountain lions by lethal harvest contributed to higher growth and productivity of the small, isolated population, even during periods of drought.

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## LITERATURE CITED

- Abrams, P. 1997. Anomalous predictions of ratio-dependent models of predation. *Oikos* 80:163–171.
- Abrams, P. A., and R. Ginzburg. 2000. The nature of predation: prey dependent, ratio dependent or neither? *Trends in Ecology and Evolution* 15: 337–341.
- Ackerman, B. B., F. G. Lindzey, and T. P. Hemker. 1984. Cougar food habits in southern Utah. *Journal of Wildlife Management* 48:147–155.
- Aldredge, M. W., J. M. Peek, and W. A. Wall. 2002. Nutritional quality of forages used by elk in northern Idaho. *Journal of Range Management* 55: 253–259.
- Alonso, D., F. Bartumeus, and J. Catalan. 2002. Mutual interference between predators can give rise to Turing spatial patterns. *Ecology* 83:28–34.
- Ammann, A. P., R. L. Cowan, C. L. Mothershead, and B. R. Baumgardt. 1973. Dry matter and energy intake in relation to digestibility in white-tailed deer. *Journal of Wildlife Management* 37:195–201.
- Anderson, A. E. 1983. A critical review of literature on puma (*Felis concolor*). Colorado Division of Wildlife Special Report No. 54, Denver, USA.
- Anderson, C. R., and F. G. Lindzey. 2003. Estimating cougar predation rates from GPS location clusters. *Journal of Wildlife Management* 67:307–316.
- Anderson, D. R., J. L. Laake, B. R. Crain, and K. P. Burnham. 1979. Guidelines for line transect sampling of biological populations. *Journal of Wildlife Management* 43:70–78.
- Animal Care and Use Committee. 1998. Guidelines for the capture, handling, and care of mammals as approved by the American Society of Mammalogists. *Journal of Mammalogy* 79:1416–1431.
- Anthony, R. G. 1976. Influence of drought on diets and numbers of desert deer. *Journal of Wildlife Management* 40:140–144.
- Arditi, R., and L. R. Ginzburg. 1989. Coupling in predator-prey dynamics: ratio-dependence. *Journal of Theoretical Biology* 139:311–326.
- , and H. R. Akçakaya. 1990. Underestimation of mutual interference of predators. *Oecologia* 83:358–361.
- Arizona Game and Fish Department. 2003. Hunt Arizona—2003 edition. Arizona Game and Fish Department, Phoenix, USA.
- . 2004. Hunt Arizona—2004 edition. Arizona Game and Fish Department, Phoenix, USA.
- . 2005. Hunt Arizona—2005 edition. Arizona Game and Fish Department, Phoenix, USA.
- Arjo, W. M., D. H. Pletscher, and R. R. Ream. 2002. Dietary overlap between wolves and coyotes in northwestern Montana. *Journal of Mammalogy* 83: 754–766.
- Baker, D. L., and N. T. Hobbs. 1987. Strategies of digestion: digestive efficiency and retention time of forage diets in montane ungulates. *Canadian Journal of Zoology* 65:1978–1984.
- Baker, L. A., R. J. Warren, D. R. Diefenbach, W. E. James, and M. J. Conroy. 2001. Prey selection by reintroduced bobcats (*Lynx rufus*) on Cumberland Island, Georgia. *American Midland Naturalist* 145:80–93.
- Ballard, W. B., D. Lutz, T. W. Keegan, L. H. Carpenter, and J. C. deVos Jr. 2001. Deer-predator relationships: a review of recent North American studies with emphasis on mule and black-tailed deer. *Wildlife Society Bulletin* 29:99–115.
- , ———, ———, ———, and ———. 2003. Deer-predator relationships. Pages 177–218 in J. C. deVos Jr., M. R. Conover, and N. E. Hedrick,

- editors. Mule deer conservation: issues and management strategies. Berryman Institute Press, Utah State University, Logan, USA.
- Beatley, J. C. 1969. Dependence of desert rodents on winter annuals and precipitation. *Ecology* 50:721–724.
- . 1974. Phenological events and their environmental triggers in Mojave Desert ecosystems. *Ecology* 55:856–863.
- Beier, P. 1995. Dispersal of juvenile cougars in fragmented habitat. *Journal of Wildlife Management* 59:228–237.
- , and S. C. Cunningham. 1996. Power of track surveys to detect changes in cougar populations. *Wildlife Society Bulletin* 24:540–546.
- Berger, J. 1982. Female breeding and lamb survival in desert bighorn sheep (*Ovis canadensis*). *Mammalia* 46:183–190.
- . 1990. Persistence of different-sized populations: an empirical assessment of rapid extinctions in bighorn sheep. *Conservation Biology* 4:91–98.
- . 1991. Pregnancy incentives, predation constraints and habitat shifts: experimental and field evidence for wild bighorn sheep. *Animal Behaviour* 41:61–67.
- . 1999. Intervention and persistence in small populations of bighorn sheep. *Conservation Biology* 13:432–434.
- Blair-West, J. R., J. P. Coghlan, D. A. Denton, J. F. Nelson, E. Orchard, B. A. Scoggins, R. D. Wright, K. Myers, and C. L. Junqueira. 1968. Physiological, morphological and behavioural adaptation to a sodium deficient environment by wild native Australian and introduced species of animals. *Nature* 217: 922–928.
- Blanchard, P., M. Festa-Bianchet, J. Gaillard, and J. T. Jorgenson. 2003. A test of long-term fecal nitrogen monitoring to evaluate nutritional status in bighorn sheep. *Journal of Wildlife Management* 67:477–484.
- Bleich, V. C. 1999. Mountain sheep and coyotes: patterns of predator evasion in a mountain ungulate. *Journal of Mammalogy* 80:283–289.
- , R. T. Bowyer, D. J. Clark, and T. O. Clark. 1992. An analysis of forage used by mountain sheep in the eastern Mojave Desert, California. *Desert Bighorn Council Transactions* 36:41–47.
- , ———, and J. D. Wehausen. 1997. Sexual segregation in mountain sheep: resources or predation? *Wildlife Monographs* 134:1–50.
- , and T. J. Taylor. 1998. Survivorship and cause-specific mortality in five populations of mule deer. *Great Basin Naturalist* 58:265–272.
- , J. D. Wehausen, and S. A. Holl. 1990. Desert-dwelling mountain sheep: conservation implications of a naturally fragmented distribution. *Conservation Biology* 4:383–390.
- , R. R. Ramey, and J. L. Rechel. 1996. Metapopulation theory and mountain sheep: implications for conservation. Pages 353–373 in D. R. McCullough, editor. *Metapopulations and wildlife conservation*. Island Press, Covelo, California, USA.
- Bodie, W. L., E. O. Garton, E. R. Taylor, and M. McCoy. 1995. A sightability model for bighorn sheep in canyon habitats. *Journal of Wildlife Management* 59:832–840.
- Brady, P. S., L. J. Brady, P. A. Whetter, D. E. Ullrey, and L. D. Fay. 1978. The effect of dietary selenium and vitamin E on biochemical parameters and survival of young among white-tailed deer (*Odocoileus virginianus*). *Journal of Nutrition* 108:1439–1448.
- Branch, L. C., M. Pessino, and D. Villarreal. 1996. Response of pumas to a population decline of the plains vizcacha. *Journal of Mammalogy* 77:1132–1140.
- Brown, D. E. 1984. The effects of drought on white-tailed deer recruitment in the arid southwest. Pages 7–12 in P. R. Krausman, and N. S. Smith, editors. *Deer in the Southwest: a workshop*. Arizona Cooperative Wildlife Research Unit and University of Arizona, Tucson, USA.
- . 1994. Biotic communities—southwestern United States and northwestern Mexico. University of Utah Press, Salt Lake City, USA.
- Brown, J. S., J. W. Laundré, and M. Gurung. 1999. The ecology of fear: optimal foraging, game theory, and trophic interactions. *Journal of Mammalogy* 80:385–399.
- Brown, K. W., R. M. Lee, and R. P. McQuivey. 1976. Observations on the food habits of desert bighorn lambs. *Desert Bighorn Council Transactions* 20:40–41.
- Brown, R. D., E. C. Hellgren, M. Abbott, D. C. Ruthven III., and R. L. Bingham. 1995. Effects of dietary energy and protein restriction on nutritional indices of female white-tailed deer. *Journal of Wildlife Management* 59:595–609.
- Butler, S. A., and L. L. McDonald. 1983. Unbiased systematic sampling plans for the line intercept method. *Journal of Range Management* 36:463–468.
- Cable, D. R. 1975. Influence of precipitation on perennial grass production in the semidesert Southwest. *Ecology* 56:981–986.
- Callan, R. J., T. D. Bunch, G. W. Workman, and R. E. Mock. 1991. Development of pneumonia in desert bighorn sheep after exposure to a flock of exotic wild and domestic sheep. *Journal of the American Veterinary Medical Association* 198:1052–1056.
- Cashman, J. L., M. Pierce, and P. R. Krausman. 1992. Diets of mountain lions in southwestern Arizona. *Southwestern Naturalist* 37:324–326.
- Cassirer, E. F., L. E. Oldenburg, V. L. Coggins, P. Fowler, K. Rudolph, D. L. Hunter, and W. J. Foreyt. 1998. Overview and preliminary analysis of a bighorn sheep dieoff, Hells Canyon 1995–1996. Biennial Symposium of the North American Wild Sheep and Goat Council 10:78–86.
- Clark, R. K., and D. A. Jessup. 1992. The health of mountain sheep in the San Andres Mountains, New Mexico. *Desert Bighorn Council Transactions* 36: 30–35.
- , ———, M. D. Kock, and R. A. Weaver. 1985. Survey of desert bighorn sheep in California for exposure to selected infectious diseases. *Journal of the American Veterinary Medical Association* 187:1175–1179.
- Coe, M. J., D. H. Cummings, and J. Phillipson. 1976. Biomass and production of large African herbivores in relation to rainfall and primary production. *Oecologia* 22:341–354.
- Cook, H. W., A. M. Pearson, N. M. Simmons, and B. E. Baker. 1970. Dall sheep (*Ovis dalli dalli*) milk. I. Effects of stage of lactation on the composition of the milk. *Canadian Journal of Zoology* 48:629–633.
- Cook, J. G., L. L. Irwin, L. D. Bryant, and J. W. Thomas. 1994. Fecal nitrogen and dietary quality relationships in juvenile elk. *Journal of Wildlife Management* 58:46–53.
- Cook, R. C., D. L. Murphy, J. G. Cook, P. Zager, and S. L. Monfort. 2001. Nutritional influences on breeding dynamics in elk. *Canadian Journal of Zoology* 79:845–853.
- Côté, S. D., and M. Festa-Bianchet. 2001. Birthdate, mass and survival in mountain goat kids: effects of maternal characteristics and forage quality. *Oecologia* 127:230–238.
- Creeden, P. J., and V. K. Graham. 1997. Reproduction, survival, and lion predation in the Black Ridge/Colorado National Monument desert bighorn herd. *Desert Bighorn Council Transactions* 41:37–43.
- Cunningham, S. C. 1989. Evaluation of bighorn sheep habitat. Pages 135–160 in R. M. Lee, editor. *The desert bighorn sheep in Arizona*. Arizona Game and Fish Department, Phoenix, USA.
- , W. B. Ballard, L. M. Monroe, M. J. Rabe, and K. D. Bristow. 2003. Black bear habitat use in burned and unburned areas, central Arizona. *Wildlife Society Bulletin* 31:786–792.
- , ———, and H. A. Whitlaw. 2001a. Age structure, survival, and mortality of mountain lions in southeastern Arizona. *Southwestern Naturalist* 46:76–80.
- , and J. C. deVos Jr. 1992. Mortality of mountain sheep in the Black Canyon area of northwest Arizona. *Desert Bighorn Council Transactions* 36: 27–29.
- , C. R. Gustavson, and W. B. Ballard. 1999. Diet selection of mountain lions in southeastern Arizona. *Journal of Range Management* 52:202–207.
- , L. A. Gustavson, C. R. Haynes, and D. D. Haywood. 1995. Evaluation of the interaction between mountain lions and cattle in the Aravaipa-Klondyke area of southeast Arizona. Technical Report 17, Arizona Game and Fish Department, Phoenix, USA.
- , L. M. Monroe, L. Kirkendall, and C. L. Ticer. 2001b. Effects of the catastrophic Lone Fire on low, medium, and high mobility wildlife species. Technical Guidance Bulletin No. 5, Arizona Game and Fish Department, Phoenix, USA.
- Danner, D. A., and N. L. Dodd. 1982. Comparison of coyote and gray fox scat diameters. *Journal of Wildlife Management* 46:240–241.
- Davison, A., J. D. S. Birks, R. C. Brookes, T. C. Braithwaite, and J. E. Messenger. 2002. On the origin of faeces: morphological versus molecular methods for surveying rare carnivores from their scats. *Journal of Zoology (London)* 257:141–143.
- DeForge, J. R., S. D. Ostermann, C. W. Willmott, K. B. Brennan, and S. G. Torres. 1997. The ecology of peninsular bighorn sheep in the San Jacinto Mountains, California. *Desert Bighorn Council Transactions* 41:8–25.
- , and J. E. Scott. 1982. Ecological investigations into high lamb mortality. *Desert Bighorn Council Transactions* 26:65–76.
- DePerno, C. S., J. A. Jenks, S. L. Griffin, and L. A. Rice. 2000. Female survival in a declining white-tailed deer population. *Wildlife Society Bulletin* 28:1030–1037.
- deVos, J. C. Jr. 1989. The role of disease in Arizona's desert bighorn sheep.

- Pages 30–62 in R. M. Lee, editor The desert bighorn sheep in Arizona. Arizona Game and Fish Department, Phoenix, USA.
- Dickson, B. G., J. S. Jenness, and P. Beier. 2005. Influence of vegetation, topography, and roads on cougar movement in southern California. *Journal of Wildlife Management* 69:264–276.
- Dietz, D. R. 1965. Deer nutrition research in range management. *North American Wildlife Conference* 30:274–285.
- Dodd, N. L. 1989. Dietary considerations. Pages 109–134 in R. M. Lee, editor. The desert bighorn sheep in Arizona. Arizona Game and Fish Department, Phoenix, USA.
- , and W. W. Brady. 1988. Dietary relationships of sympatric desert bighorn sheep and cattle. *Desert Bighorn Council Transactions* 32:1–6.
- Douglas, C. L. 2001. Weather, disease, and bighorn lamb survival during 23 years in Canyonlands National Park. *Wildlife Society Bulletin* 29:297–305.
- , and D. M. Leslie Jr. 1986. Influences of weather and density on lamb survival of desert mountain sheep. *Journal of Wildlife Management* 50:153–156.
- Dunbar, M. R., D. A. Jessup, J. F. Evermann, and W. J. Foreyt. 1985. Seroprevalence of respiratory syncytial virus in free-ranging bighorn sheep. *Journal of the American Veterinary Medical Association* 187:1173–1174.
- Eberhardt, L. L. 1978. Appraising variability in population studies. *Journal of Wildlife Management* 42:207–238.
- , and J. M. Thomas. 1991. Designing environmental studies. *Ecological Monographs* 6:53–73.
- Elliott, L. F., W. M. Boyce, R. K. Clark, and D. A. Jessup. 1994. Geographic analysis of pathogen exposure in bighorn sheep (*Ovis canadensis*). *Journal of Wildlife Diseases* 30:315–318.
- Ernest, H. B., E. S. Rubin, and W. M. Boyce. 2002. Fecal DNA analysis and risk assessment of mountain lion predation of bighorn sheep. *Journal of Wildlife Management* 66:75–85.
- Ernest, S. K. M., J. H. Brown, and R. R. Parmenter. 2000. Rodents, plants, and precipitation: spatial and temporal dynamics of consumers and resources. *Oikos* 88:470–482.
- Etchberger, R. C., and P. R. Krausman. 1999. Frequency of birth and lambing sites of a small population of mountain sheep. *Southwestern Naturalist* 44:354–360.
- Farrell, L. E., J. Roman, and M. E. Sunquist. 2000. Dietary separation of sympatric carnivores identified by molecular analysis of scats. *Molecular Ecology* 9:1583–1590.
- Festa-Bianchet, M. 1988a. Birthdate and survival in bighorn lambs (*Ovis canadensis*). *Journal of Zoology* 214:653–661.
- . 1988b. Seasonal range selection in bighorn sheep: conflicts between forage quality, forage quantity, and predator avoidance. *Oecologia* 75:580–586.
- Flueck, W. T. 1994. Effect of trace elements on population dynamics: selenium deficiency in free-ranging black-tailed deer. *Ecology* 75:807–812.
- Foreyt, W. J. 1989. Fatal *Pasteurella haemolytica* pneumonia in bighorn sheep after direct contact with clinically normal domestic sheep. *American Journal of Veterinary Research* 50:341–344.
- Fox, L. M., P. R. Krausman, M. L. Morrison, and T. H. Noon. 2000. Mineral content of Sonoran pronghorn forage. *California Fish and Game* 86:159–174.
- Fynn, R. W. S., and T. G. O'Connor. 2000. Effect of stocking rate and rainfall on rangeland dynamics and cattle performance in a semi-arid savanna, South Africa. *Journal of Applied Ecology* 37:491–507.
- Gaillard, J.-M., M. Festa-Bianchet, and N. G. Yoccoz. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. *Trends in Ecology and Evolution* 13:58–63.
- , ———, ———, A. Loison, and C. Toïgo. 2000. Temporal variation in fitness components and population dynamics of large herbivores. *Annual Review of Ecology and Systematics* 31:367–393.
- Germaine, S. S., K. D. Bristow, and L. A. Haynes. 2000. Distribution and population status of mountain lions in southwestern Arizona. *Southwestern Naturalist* 45:333–338.
- Goldberg, D. E., and R. M. Turner. 1986. Vegetation change and plant demography in perennial plots in the Sonoran Desert. *Ecology* 67:695–712.
- Grasman, B. T., and E. C. Hellgren. 1993. Phosphorus nutrition in white-tailed deer: nutrient balance, physiological responses, and antler growth. *Ecology* 74:2279–2296.
- Greene, L. W., W. E. Pinchak, and R. K. Heitschmidt. 1987. Seasonal dynamics of minerals in forages at the Texas experimental ranch. *Journal of Range Management* 40:502–506.
- Grings, E. E., M. R. Haferkamp, R. K. Heitschmidt, and M. G. Karl. 1996. Mineral dynamics in forages of the northern Great Plains. *Journal of Range Management* 49:234–240.
- Halloran, A. F., and H. B. Crandell. 1953. Notes on bighorn food in the Sonoran zone. *Journal of Wildlife Management* 17:318–320.
- Halvorson, W. L., and D. T. Patten. 1974. Seasonal water potential changes in Sonoran Desert shrubs in relation to topography. *Ecology* 55:173–177.
- Hanley, T. A. 1978. A comparison of the line-interception and quadrat estimation methods of determining shrub canopy coverage. *Journal of Range Management* 31:60–62.
- . 1997. A nutritional view of understanding and complexity in the problem of diet selection by deer (*Cervidae*). *Oikos* 79:209–218.
- , C. T. Robbins, A. E. Hagerman, and C. McArthur. 1992. Predicting digestible protein and digestible dry matter in tannin-containing forages consumed by ruminants. *Ecology* 73:537–541.
- Harveson, L. A., B. Route, F. Armstrong, N. J. Silvy, and M. E. Tewes. 1999. Trends in populations of mountain lion in Carlsbad Caverns and Guadalupe Mountains National Parks. *Southwestern Naturalist* 44:490–494.
- Hass, C. C. 1989. Bighorn lamb mortality: predation, inbreeding, and population effects. *Canadian Journal of Zoology* 67:699–705.
- Hayes, C. L., E. S. Rubin, M. C. Jorgensen, R. A. Botta, and W. M. Boyce. 2000. Mountain lion predation of bighorn sheep in the Peninsular Ranges, California. *Journal of Wildlife Management* 64:954–959.
- Heady, H. F., R. P. Gibbens, and R. W. Powell. 1959. A comparison of the charting, line intercept, and line point methods of sampling shrub types of vegetation. *Journal of Range Management* 12:180–188.
- Hebert, D., and I. M. Cowan. 1971. Natural salt licks as a part of the ecology of the mountain goat. *Canadian Journal of Zoology* 49:605–610.
- Hemker, T. P., F. G. Lindzey, and B. B. Ackerman. 1984. Population characteristics and movement patterns of cougars in southern Utah. *Journal of Wildlife Management* 48:1275–1284.
- Herbel, C. H., F. N. Ares, and R. A. Wright. 1972. Drought effects of a semidesert grassland range. *Ecology* 53:1084–1093.
- Hervet, J. J., R. S. Henry, M. T. Brown, and R. L. Kearns. 1998. Sighting rates of bighorn sheep during helicopter surveys on the Kofa National Wildlife Refuge, Arizona. *Desert Bighorn Council Transactions* 42:11–26.
- Hoban, P. A. 1990. A review of desert bighorn sheep in the San Andres Mountains, New Mexico. *Desert Bighorn Council Transactions* 34:14–22.
- Hobbs, N. T., D. L. Baker, and R. B. Gill. 1983. Comparative nutritional ecology of montane ungulates during winter. *Journal of Wildlife Management* 47:1–16.
- , and R. A. Spowart. 1984. Effects of prescribed fire on nutrition of mountain sheep and mule deer during winter and spring. *Journal of Wildlife Management* 48:551–560.
- , and D. M. Swift. 1985. Estimates of habitat carrying capacity incorporating explicit nutritional constraints. *Journal of Wildlife Management* 49:814–822.
- Hodgman, T. P., B. B. Davitt, and J. R. Nelson. 1996. Monitoring mule deer diet quality and intake with fecal nitrogen. *Journal of Range Management* 49:215–222.
- Holl, S. A., V. C. Bleich, and S. G. Torres. 2004. Population dynamics of bighorn sheep in the San Gabriel Mountains, California, 1967–2002. *Wildlife Society Bulletin* 32:412–426.
- Holt, B. S., W. H. Miller, and B. F. Wakeling. 1992. Composition and quality of mountain sheep diets in the Superstition Mountains, Arizona. *Desert Bighorn Council Transactions* 36:36–40.
- Howery, L. D., and J. A. Pfister. 1990. Dietary and fecal concentrations of nitrogen and phosphorus in penned white-tailed deer does. *Journal of Wildlife Management* 54:383–389.
- Hudson, R. J., and J. Z. Adamczewski. 1990. Effect of supplementing summer ranges on lactation and growth of wapiti (*Cervus elaphus*). *Canadian Journal of Animal Science* 70:551–560.
- Iriarte, J. A., W. L. Franklin, W. E. Johnson, and K. H. Redford. 1990. Biogeographic variation of food habits and body size of the American puma. *Oecologia* 85:185–190.
- Irvine, C. A. 1969. Factors affecting the desert bighorn sheep in southeastern Utah. *Desert Bighorn Council Transactions* 13:6–13.
- Irwin, L. L., J. G. Cook, D. E. McWhirter, S. G. Smith, and E. B. Arnett. 1993. Assessing winter dietary quality in bighorn sheep via fecal nitrogen. *Journal of Wildlife Management* 57:41–421.
- Jessup, D. A. 1985. Diseases of domestic livestock which threaten bighorn sheep populations. *Desert Bighorn Council Transactions* 29:29–33.

- Johnson, D. H. 1999. The insignificance of statistical significance testing. *Journal of Wildlife Management* 63:763–772.
- Johnson, M. K., R. C. Belden, and D. R. Aldred. 1984. Differentiating mountain lion and bobcat scats. *Journal of Wildlife Management* 48:239–244.
- Jones, D. I. H., D. G. Miles, and K. B. Sinclair. 1967. Some effects of feeding sheep on low-sodium hay with and without sodium supplement. *British Journal of Nutrition* 21:391–397.
- Jones, J. H., and N. S. Smith. 1979. Bobcat density and prey selection in central Arizona. *Journal of Wildlife Management* 43:666–672.
- Jones, R. L., and H. P. Weeks. 1985. Ca, Mg, and P in the annual diet of deer in south-central Indiana. *Journal of Wildlife Management* 49:129–133.
- Jorgenson, J. T., M. Festa-Bianchet, J.-M. Gaillard, and W. D. Wishart. 1997. Effects of age, sex, disease, and density on survival of bighorn sheep. *Ecology* 78:1019–1032.
- Kamler, J. F., R. M. Lee, J. C. deVos Jr., W. B. Ballard, and H. A. Whitlaw. 2002. Survival and cougar predation of translocated bighorn sheep in Arizona. *Journal of Wildlife Management* 66:1267–1272.
- Kearney, T. H., and R. H. Peebles. 1973. *Arizona flora*. University of California Press, Berkeley, USA.
- Kemp, P. R. 1983. Phenological patterns of Chihuahuan Desert plants in relation to timing of water availability. *Journal of Ecology* 71:427–436.
- Koehler, G. M., and M. G. Hornocker. 1991. Seasonal resource use among mountain lions, bobcats, and coyotes. *Journal of Mammalogy* 72:391–396.
- Krausman, P. R., B. F. Bobek, F. M. Whiting, and W. H. Brown. 1988. Dry matter and energy intake in relation to digestibility in desert bighorn sheep. *Acta Theriologica* 33:121–130.
- , A. J. Kuenzi, R. C. Etchberger, K. R. Rautenstrauch, L. L. Ordway, and J. J. Hervert. 1997. Diets of desert mule deer. *Journal of Range Management* 50:513–522.
- , and B. D. Leopold. 1986. The importance of small populations of desert bighorn sheep. *Transactions of the North American Wildlife and Natural Resources Conference* 51:52–61.
- , ———, R. F. Seegmiller, and S. G. Torres. 1989. Relationships between desert bighorn sheep and habitat in western Arizona. *Wildlife Monographs* 102:1–66.
- , L. L. Ordway, F. M. Whiting, and W. H. Brown. 1990. Nutritional composition of desert mule deer forage in the Picacho Mountains, Arizona. *Desert Plants* 10:32–34.
- , A. V. Sandoval, and R. C. Etchberger. 1999. Natural history of desert bighorn sheep. Pages 139–191 in R. Valdez, and P. R. Krausman, editors. *Mountain sheep of North America*. University of Arizona Press, Tucson, USA.
- Kucera, T. E. 1997. Fecal indicators, diet, and population parameters in mule deer. *Journal of Wildlife Management* 61:550–560.
- Kunkel, K. E., T. K. Ruth, D. H. Pletscher, and M. G. Hornocker. 1999. Winter prey selection by wolves and cougars in and near Glacier National Park, Montana. *Journal of Wildlife Management* 63:901–910.
- Laing, S. P., and F. G. Lindzey. 1993. Patterns of replacement of resident cougars in southern Utah. *Journal of Mammalogy* 74:1056–1058.
- Laundré, J. W. 2005. Puma energetics: a recalculation. *Journal of Wildlife Management* 69:723–732.
- Lenarz, M. S. 1979. Social structure and reproductive strategy in desert bighorn sheep (*Ovis canadensis mexicana*). *Journal of Mammalogy* 60:671–678.
- Leopold, B. D., and P. R. Krausman. 1986. Diets of 3 predators in Big Bend National Park, Texas. *Journal of Wildlife Management* 50:290–295.
- , and ———. 1991. Factors influencing desert mule deer distribution and productivity in southwestern Texas. *Southwestern Naturalist* 36:67–74.
- Leslie, D. M. Jr., and C. L. Douglas. 1979. Desert bighorn sheep of the River Mountains, Nevada. *Wildlife Monographs* 66:1–56.
- , and ———. 1982. Simulated demography of the River Mountain herd. *Desert Bighorn Council Transactions* 26:97–99.
- , J. A. Jenks, M. Chilleli, and G. R. Lavigne. 1989. Nitrogen and diaminopimelic acid in deer and moose feces. *Journal of Wildlife Management* 53:216–218.
- , and E. E. Starkey. 1985. Fecal indices to diet quality of cervids in old-growth forests. *Journal of Wildlife Management* 49:142–146.
- , and ———. 1987. Fecal indices to dietary quality: a reply. *Journal of Wildlife Management* 51:321–325.
- Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* 68:619–640.
- Lindzey, F. G., W. D. VanSickle, B. B. Ackerman, D. Barnhurst, T. P. Hemker, and S. P. Laing. 1994. Cougar population dynamics in southern Utah. *Journal of Wildlife Management* 58:619–624.
- , ———, S. P. Laing, and C. S. Mecham. 1992. Cougar population response to manipulation in southern Utah. *Wildlife Society Bulletin* 20:224–227.
- Link, W. A., and J. D. Nichols. 1994. On the importance of sampling variance to investigations of temporal variation in animal population size. *Oikos* 69:539–544.
- Litvaitis, J. A., and D. J. Harrison. 1989. Bobcat-coyote niche relationships during a period of coyote population increase. *Canadian Journal of Zoology* 67:1180–1188.
- Logan, K. A., and L. L. Irwin. 1985. Mountain lion habitats in the Big Horn Mountains, Wyoming. *Wildlife Society Bulletin* 13:257–262.
- , and L. L. Swenor. 2001. *Desert puma*. Island Press, Washington, D. C., USA.
- Major, J. T., and J. A. Sherburne. 1987. Interspecific relationships of coyotes, bobcats, and red foxes in western Maine. *Journal of Wildlife Management* 51:606–616.
- Marshal, J. P., P. R. Krausman, and V. C. Bleich. 2005. Dynamics of mule deer forage in the Sonoran Desert. *Journal of Arid Environments* 60:593–609.
- , ———, ———, W. B. Ballard, and J. S. McKeever. 2002. Rainfall, El Niño, and dynamics of mule deer in the Sonoran Desert, California. *Journal of Wildlife Management* 66:1283–1289.
- Massey, B. N., F. W. Weckerly, C. E. Vaughn, and D. R. McCullough. 1994. Correlations between fecal nitrogen and diet composition in free-ranging black-tailed deer. *Southwestern Naturalist* 39:165–170.
- Mayland, H. F., and G. E. Shewmaker. 2001. Animal health problems caused by silicon and other mineral imbalances. *Journal of Range Management* 54:441–446.
- Mazaika, R., P. R. Krausman, and R. C. Etchberger. 1992. Forage availability for mountain sheep in Pusch Ridge Wilderness, Arizona. *Southwestern Naturalist* 37:372–378.
- McBride, G. B., J. C. Loftis, and N. C. Adkins. 1993. What do significance tests really tell us about the environment? *Environmental Management* 17:423–432.
- McCutchen, H. E. 1988. Desert bighorn sheep nursing behavior in relation to population quality and lamb survival. *Desert Bighorn Council Transactions* 32:7–10.
- McKinney, T., S. R. Boe, and J. C. deVos Jr. 2003. GIS-based evaluation of escape terrain and desert bighorn sheep populations in Arizona. *Wildlife Society Bulletin* 31:1229–1236.
- , J. C. deVos Jr., and R. D. Broscheid. 2000. Public intervention in wildlife research—a case history. *Desert Bighorn Council Transactions* 44:14–21.
- , and T. H. Noon. 2002. Mineral concentrations of desert bighorn sheep forages in the Mazatzal Mountains, Arizona. *Desert Bighorn Council Transactions* 46:25–38.
- , T. W. Smith, and J. D. Hanna. 2001. Precipitation and desert bighorn sheep in the Mazatzal Mountains, Arizona. *Southwestern Naturalist* 46:345–353.
- McNamara, J. M., and A. I. Houston. 1987. Starvation and predation as factors limiting population size. *Ecology* 68:1515–1519.
- Messier, F. 1991. The significance of limiting and regulating factors in the demography of moose and white-tailed deer. *Journal of Animal Ecology* 60:377–393.
- Meyer, M. W., R. D. Brown, and M. W. Graham. 1984. Protein and energy content of white-tailed deer diets in the Texas Coastal Bend. *Journal of Wildlife Management* 48:527–534.
- Miller, G. D., and W. S. Gaud. 1989. Composition and variability of desert bighorn sheep diets. *Journal of Wildlife Management* 53:597–606.
- Miller, M. W. 2001. Pasteurellosis. Pages 330–339 in E. S. Williams, and I. K. Barker, editors. *Infectious diseases of wild mammals*. 3rd edition. Iowa State University Press, Ames, USA.
- Monello, R. J., D. L. Murray, and E. F. Cassirer. 2001. Ecological correlates of pneumonia epizootics in bighorn sheep herds. *Canadian Journal of Zoology* 79:1423–1432.
- Moore, T. D., L. E. Spence, C. E. Dugnolle, and W. G. Hepworth. 1974. Identification of the dorsal guard hairs of some mammals in Wyoming. *Wyoming Game and Fish Department, Bulletin* 14:1–177.
- Mooring, M. S., T. A. Fitzpatrick, T. T. Nishihira, and D. C. Reisig. 2004. Vigilance, predation risk, and the Allee effect in desert bighorn sheep. *Journal of Wildlife Management* 68:519–532.
- Morgart, J. R., P. R. Krausman, W. H. Brown, and F. M. Whiting. 1986. Chem-

- ical analysis of mountain sheep forage in the Virgin Mountains, Arizona. University of Arizona College of Agriculture Technical Bulletin 257:1-11.
- Morrison, M. L., W. M. Block, M. D. Strickland, and W. L. Kendall. 2001. Wildlife study design. Springer-Verlag, New York, New York, USA.
- Mouton, R. J., R. M. Lee, and R. J. Olding. 1991. A desert bighorn sheep decline in Aravaipa Canyon, Arizona. Desert Bighorn Council Transactions 35:18-19.
- Mubanga, G., J. L. Holocheck, R. Valdez, and S. D. Schemnitz. 1985. Relationship between diet and fecal nutritive quality in mule deer. Southwestern Naturalist 30:573-578.
- Mueller, C. C., and R. M. F. S. Sadlier. 1977. Changes in the nutrient composition of milk of black-tailed deer during lactation. Journal of Mammalogy 58:421-423.
- Murie, O. J. 1954. A field guide to animal tracks. Houghton-Mifflin, Boston, Massachusetts, USA.
- Murphy, D. A., and J. A. Coates. 1966. Effects of dietary protein on deer. Transactions of the North American Wildlife and Natural Resources Conference 31:129-139.
- National Research Council. 1996. Nutrient requirements of cattle. Seventh edition. National Academy Press, Washington, D.C., USA.
- Noon, T. H., S. L. Wesche, D. Cagle, D. G. Mead, E. J. Bicknell, G. A. Bradley, S. Riplog-Peterson, D. Edsall, and C. Reggiardo. 2002. Hemorrhagic disease in bighorn sheep in Arizona. Journal of Wildlife Diseases 38:172-176.
- Núñez, R., B. Miller, and F. Lindzey. 2000. Food habits of jaguars and pumas in Jalisco, Mexico. Journal of Zoology (London) 252:373-379.
- Oehler, M. W., R. T. Bowyer, and V. C. Bleich. 2003. Home ranges of female mountain sheep, *Ovis canadensis nelsoni*: effects of precipitation in a desert ecosystem. Mammalia 67:385-401.
- O'Hara, T. M., G. Carroll, P. Barboza, K. Mueller, J. Blake, V. Woshner, and C. Willetto. 2001. Mineral and heavy metal status as related to a mortality event and poor recruitment in a moose population in Alaska. Journal of Wildlife Diseases 37:509-522.
- Osborn, R. G., and T. F. Ginnett. 2001. Fecal nitrogen and 2,6-diaminopimelic acid as indices to dietary nitrogen in white-tailed deer. Wildlife Society Bulletin 29:1131-1139.
- , and J. A. Jenks. 1998. Assessing dietary quality of white-tailed deer using fecal indices: effects of supplemental feeding and area. Journal of Mammalogy 79:437-447.
- Patton, D. R., and J. M. Hall. 1966. Evaluating key areas by browse age and form class. Journal of Wildlife Management 30:476-480.
- Pierce, B. M., V. C. Bleich, and R. T. Bowyer. 2000. Social organization of mountain lions: does a land-tenure system regulate population size? Ecology 81:1533-1543.
- Prestwood, A. K., T. P. Kistner, F. E. Kellogg, and F. A. Hayes. 1974. The 1971 outbreak of hemorrhagic disease among white-tailed deer of the southeastern United States. Journal of Wildlife Diseases 10:217-224.
- Provenza, F. D. 1995. Postingestive feedback as an elementary determinant of food preference and intake in ruminants. Journal of Range Management 48: 2-17.
- Puls, R. 1994. Mineral levels in animal health: diagnostic data. Second edition. Sherpa International, Clearbrook, British Columbia, Canada.
- Putman, R. J., and G. J. Hemmings. 1986. Can dietary quality of free-ranging ungulates be simply determined from faecal chemistry? Acta Theriologica 31:257-270.
- Rabe, M. J., S. S. Rosenstock, and J. C. deVos Jr. 2002. Review of big-game survey methods used by wildlife agencies of the western United States. Wildlife Society Bulletin 30:46-52.
- Ratti, J. T., and E. O. Garton. 1994. Research and experimental design. Pages 1-23 in T. A. Bookhout, editor. Research and management techniques for wildlife habitats. Wildlife Society, Bethesda, Maryland, USA.
- Reed, J. D., R. J. Baker, W. B. Ballard, and B. T. Kelley. 2004. Differentiating Mexican gray wolf and coyote scats using DNA analysis. Wildlife Society Bulletin 32:685-692.
- Reed, J. M., and A. R. Blaustein. 1997. Biologically significant population declines and statistical power. Conservation Biology 11:281-282.
- Reichman, O. J., and K. M. Van De Graaff. 1975. Associations between ingestion of green vegetation and desert rodent populations. Journal of Mammalogy 56:503-506.
- Remington, R. 1989. Population characteristics. Pages 82-108 in R. M. Lee, editor. The desert bighorn sheep in Arizona. Arizona Game and Fish Department, Phoenix, USA.
- Riley, S. J., and R. A. Malecki. 2001. A landscape analysis of cougar distribution and abundance in Montana, USA. Environmental Management 28:317-323.
- Robbins, C. T. 1992. Wildlife feeding and nutrition. Second edition. Academic Press, New York, New York, USA.
- , T. A. Hanley, A. E. Hagerman, O. Hjeljord, O. Baker, D. L. Schwartz, and W. W. Mautz. 1987. Role of tannins in defending plants against ruminants: reduction in protein availability. Ecology 68:98-107.
- , S. M. Parish, and B. L. Robbins. 1985. Selenium and glutathione peroxidase in mountain goats. Canadian Journal of Zoology 63:1544-1547.
- Robinette, W. L., C. H. Baer, R. E. Pillmore, and C. E. Knittle. 1973. Effects of nutritional change on captive mule deer. Journal of Wildlife Management 37: 312-326.
- , J. S. Gashwiler, and O. W. Morris. 1959. Food habits of the cougar in Utah and Nevada. Journal of Wildlife Management 23:261-273.
- Robinson, J. J., and T. J. Forbes. 1968. The effect of protein intake during gestation on ewe and lamb performance. Animal Production 10:297-309.
- Romesburg, H. C. 1981. Wildlife science: gaining reliable knowledge. Journal of Wildlife Management 45:293-313.
- Rominger, E. M., and M. E. Weisenberger. 1999. Biological extinction and a test of the "conspicuous individual hypothesis" in the San Andres Mountains, New Mexico. North American Wild Sheep Conference 2:293-309.
- , H. A. Whitlaw, D. L. Weybright, W. C. Dunn, and W. B. Ballard. 2004. The influence of mountain lion predation on bighorn sheep translocations. Journal of Wildlife Management 68:993-999.
- Rosas-Rosas, O. C., R. Valdez, L. C. Bender, and D. Daniel. 2003. Food habits of pumas in northwestern Sonora, Mexico. Wildlife Society Bulletin 31: 528-535.
- Ross, P. I., M. G. Jalkotzy, and M. Festa-Bianchet. 1997. Cougar predation on bighorn sheep in southwestern Alberta during winter. Canadian Journal of Zoology 74:771-775.
- Rubin, E. S., W. M. Boyce, and V. C. Bleich. 2000. Reproductive strategies of desert bighorn sheep. Journal of Mammalogy 81:769-786.
- , ———, and E. P. Caswell-Chen. 2002a. Modeling demographic processes in an endangered population of bighorn sheep. Journal of Wildlife Management 66:796-810.
- , ———, M. C. Jorgensen, S. G. Torres, C. L. Hayes, C. S. O'Brien, and D. A. Jessup. 1998. Distribution and abundance of bighorn sheep in the Peninsular Ranges, California. Wildlife Society Bulletin 26:539-551.
- , ———, C. J. Stermer, and S. G. Torres. 2002b. Bighorn sheep habitat use and selection near an urban environment. Biological Conservation 104: 251-263.
- Russo, J. P. 1956. The desert bighorn sheep in Arizona. Arizona Game and Fish Department Wildlife Bulletin 1:1-153.
- Ruth, T. K., K. A. Logan, L. L. Sweanor, M. G. Hornocker, and L. J. Temple. 1998. Evaluating cougar translocation in New Mexico. Journal of Wildlife Management 62:1264-1275.
- Saether, B-E. 1997. Environmental stochasticity and population dynamics of large herbivores: a search for mechanisms. Trends in Ecology and Evolution 12:143-149.
- , S. Engen, F. Filli, R. Aanes, W. Schroder, and R. Andersen. 2002. Stochastic population dynamics of an introduced Swiss population of the ibex. Ecology 83:3457-3465.
- Salve, R., and B. Allen-Diaz. 2001. Variations in soil moisture content in a rangeland catchment. Journal of Range Management 54:44-51.
- Sams, M. G., R. L. Lochmiller, C. W. Qualls Jr., and D. M. Leslie Jr. 1998. Sensitivity of condition indices to changing density in a white-tailed deer population. Journal of Wildlife Diseases 34:110-125.
- Samson, J., J. T. Jorgenson, and W. D. Wishart. 1989. Glutathione peroxidase activity and selenium levels in Rocky Mountain bighorn sheep and mountain goats. Canadian Journal of Zoology 67:2493-2496.
- Sandoval, A. V. 1980. Management of a psoroptic scabies epizootic in bighorn sheep (*Ovis canadensis mexicana*) in New Mexico. Desert Bighorn Council Transactions 24:21-28.
- , A. S. Elenowitz, and J. R. DeForge. 1987. Pneumonia in a transplanted population of bighorn sheep. Desert Bighorn Council Transactions 31:18-22.
- Sawyer, H., and F. Lindzey. 2002. A review of predation on bighorn sheep (*Ovis canadensis*). Wyoming Cooperative Fish and Wildlife Research Unit, Laramie, USA.
- Schaefer, R. I., S. G. Torres, and V. C. Bleich. 2000. Survivorship and cause-

- specific mortality in sympatric populations of mountain sheep and mule deer. *California Fish and Game* 86:127–135.
- Schwartz, C. C., J. G. Nagy, and R. W. Rice. 1977. Pronghorn dietary quality relative to forage availability and other ruminants in Colorado. *Journal of Wildlife Management* 41:161–168.
- Schwartz, O. A., V. C. Bleich, and S. A. Holl. 1986. Genetics and the conservation of mountain sheep *Ovis canadensis nelsoni*. *Biological Conservation* 37:179–190.
- Scrivner, J. H., C. E. Vaughn, and M. B. Jones. 1988. Mineral concentrations of black-tailed deer diets in California chaparral. *Journal of Wildlife Management* 52:37–41.
- Seegmiller, R. F., P. R. Krausman, W. H. Brown, and F. M. Whiting. 1990. Nutritional composition of desert bighorn sheep forage in the Harquahala Mountains, Arizona. *Desert Plants* 10:87–90.
- , and R. D. Ohmart. 1982. Desert bighorn lamb and adult-yearling diets from western Arizona. *Desert Bighorn Council Transactions* 26:34–38.
- Short, H. L., D. R. Dietz, and E. E. Remmenga. 1966. Selected nutrients in mule deer browse plants. *Ecology* 47:222–229.
- Siegel, S., and N. J. Castellan Jr. 1988. Nonparametric statistics for the behavioral sciences. McGraw-Hill, New York, New York, USA.
- Sinclair, A. R. E. 1991. Science and the practice of wildlife management. *Journal of Wildlife Management* 55:767–773.
- Skalski, G. T., and J. F. Gilliam. 2001. Functional responses with predator interference: viable alternatives to the Holling Type II model. *Ecology* 82:3083–3092.
- Skogland, T. 1991. What are the effects of predators on large ungulate populations? *Oikos* 61:401–411.
- Smallwood, K. S. 1994. Trends in California mountain lion populations. *Southwestern Naturalist* 39:67–72.
- , and E. L. Fitzhugh. 1995. A track count for estimating mountain lion *Felis concolor californica* population trend. *Biological Conservation* 71:251–259.
- Smith, N. S. 1984. Reproduction in Coues white-tailed deer in the Southwest relative to drought and cattle stocking rates. Pages 13–20 in P. R. Krausman, and N. S. Smith, editors. *Deer in the Southwest: a workshop*. Arizona Cooperative Wildlife Research Unit and University of Arizona, Tucson, USA.
- Smith, R. H., and A. LeCount. 1979. Some factors affecting survival of desert mule deer fawns. *Journal of Wildlife Management* 43:657–665.
- Spaulding, R., P. R. Krausman, and W. B. Ballard. 2000. Observer bias and analysis of gray wolf diets from scats. *Wildlife Society Bulletin* 28:947–950.
- Sprinkle, J. E., E. J. Bicknell, T. H. Noon, C. Reggiardo, D. F. Perry, and H. M. Frederick. 2000. Variation of trace minerals in forage by season and species and the effects of mineral supplementation upon beef cattle production. *Proceedings of the Western Section, American Society of Animal Science* 51:276–280.
- Stauber, E. H., C. H. Nellis, R. A. Magonigle, and H. W. Vaughn. 1977. Prevalence of reactors to selected livestock pathogens in Idaho mule deer. *Journal of Wildlife Management* 41:515–519.
- Stephenson, T. E., J. L. Holocheck, and C. B. Kuykendall. 1985. Drought effect on pronghorn and other ungulate diets. *Journal of Wildlife Management* 49:146–151.
- Stewart-Oaten, A., W. W. Murdoch, and S. J. Walde. 1995. Estimation of temporal variability in populations. *American Naturalist* 146:519–535.
- Thomas, L. 1996. Monitoring long-term population change: why are there so many analysis methods? *Ecology* 77:49–58.
- Thomson, W., and A. M. Thomson. 1953. Effect of diet on milk yield of the ewe and growth of her lamb. *British Journal of Nutrition* 7:263–274.
- Thornton, D. H., M. E. Sunquist, and M. B. Main. 2004. Ecological separation within newly sympatric populations of coyotes and bobcats in south-central Florida. *Journal of Mammalogy* 85:973–982.
- Thurow, T. L., and C. A. Taylor Jr. 1999. Viewpoint: the role of drought in range management. *Journal of Range Management* 52:413–419.
- Treves, A., and K. U. Karanth. 2003. Human-carnivore conflict and perspectives on carnivore management worldwide. *Conservation Biology* 17:1491–1499.
- Turner, J. C., and C. G. Hansen. 1980. Reproduction. Pages 145–151 in G. Monson, and L. Sumner, editors. *The desert bighorn: its life history, ecology, and management*. University of Arizona Press, Tucson, USA.
- , and J. B. Payson. 1982. The occurrence of selected infectious diseases in the desert bighorn sheep, *Ovis canadensis cremnobates*, herds of the Santa Rosa Mountains, California. *California Fish and Game* 68:235–243.
- Turner, J. W., and M. L. Morrison. 2001. Influence of predation by mountain lions on numbers and survivorship of a feral horse population. *Southwestern Naturalist* 46:183–190.
- Ullrey, D. E., W. G. Youatt, H. E. Johnson, A. B. Cowan, L. D. Fay, R. L. Covert, W. T. Magee, and K. K. Keahey. 1975. Phosphorus requirements of weaned white-tailed deer fawns. *Journal of Wildlife Management* 39:590–595.
- Urness, P. J. 1973. Chemical analyses and in vitro digestibility of seasonal deer forages. Pages 39–52 in *Deer nutrition in Arizona chaparral and desert habitats*. United States Forest Service, Rocky Mountain Forest and Range Experimental Station, and Arizona Game and Fish Department. Special Report 3. Tempe and Phoenix, Arizona, USA.
- , W. Green, and R. K. Watkins. 1971. Nutrient intake of deer in Arizona chaparral and desert habitats. *Journal of Wildlife Management* 35:469–475.
- Van Ballenberghe, V., and W. B. Ballard. 1994. Limitation and regulation of moose populations: the role of predation. *Canadian Journal of Zoology* 72:2071–2077.
- VandenBerge, R. J., C. S. Caldes, and M. K. Haderlie. 1984. A management update, Kofa National Wildlife Refuge. *Desert Bighorn Council Transactions* 28:30–31.
- Van Sickle, W. D., and F. G. Lindzey. 1992. Evaluation of road track surveys for cougars (*Felis concolor*). *Great Basin Naturalist* 52:232–236.
- Verme, L. J. 1965. Reproduction studies on penned white-tailed deer. *Journal of Wildlife Management* 29:74–79.
- Vucetich, J. A., R. O. Peterson, and C. L. Schaefer. 2002. The effect of prey and predator densities on wolf predation. *Ecology* 83:3003–3013.
- Wakeling, B. F., and W. H. Miller. 1989. Bedsite characteristics of desert bighorn sheep in the Superstition Mountains, Arizona. *Desert Bighorn Council Transactions* 33:6–8.
- Wallmo, O. C., L. H. Carpenter, W. L. Regelin, R. B. Gill, and D. L. Baker. 1977. Evaluation of deer habitat on a nutritional basis. *Journal of Range Management* 30:122–127.
- Ward, A. C. S., D. L. Hunter, M. D. Jaworski, P. J. Benolkin, M. P. Dobel, J. B. Jeffress, and G. A. Turner. 1997. *Pasteurella* spp. in sympatric bighorn and domestic sheep. *Journal of Wildlife Diseases* 33:544–557.
- Warrick, G. D., and P. R. Krausman. 1989. Barrel cacti consumption by desert bighorn sheep. *Southwestern Naturalist* 34:483–486.
- Walters, C. J., and R. Green. 1997. Valuation of experimental management options for ecological systems. *Journal of Wildlife Management* 61:987–1006.
- Weaver, J. L., and S. H. Fritz. 1979. Comparison of coyote and wolf scat diameters. *Journal of Wildlife Management* 43:786–788.
- Weeks, H. P., and C. M. Kirkpatrick. 1976. Adaptations of white-tailed deer to naturally occurring sodium deficiencies. *Journal of Wildlife Management* 40:610–625.
- Wehausen, J. D. 1987. Some probabilities associated with sampling for diseases in bighorn sheep. *Desert Bighorn Council Transactions* 31:8–10.
- . 1995. Fecal measures of diet quality in wild and domestic ruminants. *Journal of Wildlife Management* 59:816–823.
- . 1996. Effects of mountain lion predation on bighorn sheep in the Sierra Nevada and Granite Mountains of California. *Wildlife Society Bulletin* 24:471–479.
- , V. C. Bleich, B. Blong, and T. L. Russi. 1987. Recruitment dynamics in a southern California mountain sheep population. *Journal of Wildlife Management* 51:86–98.
- White, T. C. R. 1978. The importance of a relative shortage of food in animal ecology. *Oecologia* 33:71–86.
- Wikeem, B. M., and M. D. Pitt. 1987. Evaluation of methods to determine use of browse by California mountain sheep. *Wildlife Society Bulletin* 15:430–433.
- Witham, J. H., and E. L. Smith. 1979. Desert bighorn movements in a southwestern Arizona mountain complex. *Desert Bighorn Council Transactions* 23:20–24.
- Wofford, H., J. L. Holechek, M. L. Galvean, J. D. Wallace, and M. Cardenas. 1985. Evaluation of fecal indices to predict cattle diet quality. *Journal of Range Management* 38:450–454.
- Yáñez, J. L., J. C. Cadenas, P. Gezelle, and F. M. Jaksic. 1986. Food habits of the southernmost mountain lions (*Felis concolor*) in South America: natural versus livestocked ranges. *Journal of Mammalogy* 67:604–606.

Yoccoz, N. G. 1991. Use, overuse, and misuse of significance tests in evolutionary biology and ecology. *Bulletin of the Ecological Society of America* 72:106–111.

Zar, J. H. 1996. *Biostatistical analysis*. Prentice Hall, Upper Saddle River, New Jersey, USA.

Zuercher, G. L., P. S. Gipson, and G. C. Stewart. 2003. Identification of

carnivore feces by local peoples and molecular analyses. *Wildlife Society Bulletin* 31:961–970.

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Desert bighorn sheep (left to right: 2 adult females, lamb, mature male) on the Mazatzal Mountains study area (photo by Ted McKinney).