Framework for understanding the influences of wildlife water developments in the western United States

RANDY T. LARSEN*, JOHN A. BISSONETTE, JERRAN T. FLINDERS, AND JERICHO C. WHITING

Brigham Young University, Plant and Wildlife Sciences Department and the Monte L. Bean Life Sciences Museum, 407 WIDB, Provo, UT 84602, USA (RTL, JTF)

U.S. Geological Survey, Utah Cooperative Fish and Wildlife Research Unit, Department of Wildland Resources, College of Natural Resources, Utah State University, 5290 Old Main Hill, Logan, UT 84322-5290, USA (JAB)

Gonzales-Stoller Surveillance, 120 Technology Drive, Idaho Falls, ID 83401, USA (JCW)

*Correspondent: randy_larsen@byu.edu

Water both limits and supports life; as such, it is essential for life processes. Free water is a limiting factor for some wildlife species in arid regions of the world. In the western United States, management agencies have installed numerous water developments to benefit wildlife. Despite >50 years as an active management practice, questions have been raised concerning the efficacy and potential negative impacts of wildlife water developments. We propose a conceptual framework for understanding more generally how, when, and where water developments are likely to benefit wildlife that are intended to use such devices. We argue that five elements are fundamental to an integrated understanding of the use of water developments by wildlife: (1) availability of free water in time and space; (2) water state (free, metabolic, or pre-formed) used by wildlife; (3) seasonal temperature and precipitation patterns that influence the physiological need for water by wildlife; (4) behavioral constraints that limit use of otherwise available free water; and (5) proper spacing and placement of water developments for targeted species. These elements are intended to help guide research and management efforts concerning the influences of wildlife water developments.

Key words: conceptual model, desert, guzzler, integration, springs, water sources, wells, wildlife water development

Water both limits and supports life; as such, it is essential for life processes (Ricklefs 2001, Robbins 2001) and may influence population dynamics and distribution of many species (Rosenstock et al. 1999, Simpson et al. 2011). Three general forms of water exist: pre-formed water that is available in food, metabolic water that is created as a byproduct of life processes (e.g., metabolism of fat or breakdown of carbohydrates), and free water (i.e., water available for drinking) (Robbins 2001). Free water is recognized as a fundamental need of wildlife (Leopold 1933) and has been considered limiting for many species in arid regions (Rautenstrauch and Krausman 1989, Bleich et al. 2006, Cain et al. 2006). As a result, close to 7,000 wildlife water developments have been built in the western United States (USA). Water developments are intended to improve performance of wildlife populations (Simpson et al. 2011), influence animal movements and distribution (Leslie and Douglas 1979, Longshore et al. 2009, Simpson et al. 2011), and mitigate loss of naturally occurring sources of free water (Rosenstock et al. 1999, Longshore et al. 2009, Simpson et al. 2011). Wildlife managers have utilized many designs for wildlife water developments including rainwater catchments (Glading 1947) that store water in above- and below-ground tanks, wells (Bleich et al. 1982, Kindschy 1996), modification of existing natural collection areas or tinajas (natural rock catchments) (Halloran and Deming 1958, Bleich and Weaver 1983, Werner 1984), and development of springs (see Bleich et al. 2005 for review).

The construction of water developments for wildlife began in the 1940s to benefit quail (*Callipepla* spp.) in the southwestern USA (Glading 1943, Glading 1947). Soon thereafter, designs were modified and adapted for ungulates in several different habitat types (Halloran 1949, Halloran and Deming 1958, Wright 1959). More recently, mitigation for the loss of naturally occurring sources of free water has encouraged managers to develop water sources for a variety of species (Krausman et al. 2006, O'Brien et al. 2006, Simpson et al. 2011). Construction of wildlife water developments has continued and, in a 1997 survey of state wildlife agencies in the western USA, 10 of 11 states reported ongoing programs with combined annual expenditures in excess of \$1,000,000 (Rosenstock et al. 1999). In 2003, the value of wildlife water developments in Arizona alone was estimated at between 15 and 20 million dollars (Bloom 2003). Ongoing programs currently exist in the western USA, as well as other areas of the world (Borralho et al. 1998, Rosenstock et al. 1999).

Despite >50 years as an active management practice, wildlife water developments are controversial. Authors have questioned both the efficacy of wildlife water developments (Severson and Medina 1983, Deblinger and Alldredge 1991, Burkett and Thompson 1994, Broyles and Cutler 1999) and raised concern over the potential for negative effects of water developments (Broyles 1995). Additional concerns have been raised about the relationship of wildlife water developments to wilderness values (Bleich 2005, Bleich et al. 2005, Krausman et al. 2006). Recent criticism has even targeted the decision processes, civility, and human dignity associated with the controversy surrounding wildlife water developments (Mattson and Chambers 2009). Simpson et al. (2011) provided an excellent review of some concerns associated with wildlife water developments, including water quality, species-specific benefits, mortalities of entrapped animals, competition, and predator-prey relationships. Although Simpson et al. (2011) concluded that most negative effects of wildlife water developments were not supported by available data and were speculative, they emphasized that much remains to be learned.

Despite the controversy surrounding wildlife water developments, fundamental questions concerning the efficacy of these devices remain unresolved (Simpson et al. 2011; Table 1). The importance of wildlife water developments is likely to increase, because

TABLE 1.— Fundamental questions associated with the responses of wildlife populations to water developments that remain unresolved for most species.

Is survival influenced? If so, is this direct¹ or indirect²? Is reproduction influenced? If so, is this direct¹ or indirect²? Are animal movements or distributional patterns influenced? If so, how? Are habitat use patterns influenced? If so, how?

¹ Direct effects are defined as those associated with intake of free water.

² Indirect effects included exploitative or interference competition with other species or conspecifics, altered

wildlife and habitat are influenced by human demands for water and changing weather patterns (Jackson et al. 2001, Dolan 2006, Brown and Thorpe 2008). To address some of these issues, we searched the literature on this topic and produced a conceptual framework for understanding how, when, and where water developments are likely to provide benefits to wildlife. Although elements of our model have been discussed in part by authors over the past several decades, to our knowledge they have not been organized into an integrated framework. As a result, we recommend that the following elements be considered when trying to understand the effectiveness of wildlife water developments: (1) availability of free water in time and space; (2) water state (free, metabolic, or pre-formed) used by wildlife; (3) seasonal temperature and precipitation patterns that influence the physiological need for water by wildlife; (4) behavioral constraints that limit use of otherwise available free water; and, (5) proper spacing and placement of water developments for target species. We anticipate that this framework will be applicable to those managing wildlife in arid landscapes of the western USA.

AVAILABILITY OF FREE WATER IN TIME AND SPACE

The temporal and spatial scales at which availability of free water has varied is rarely considered in the debate regarding wildlife water developments. For example, the Great Basin Desert in the western USA during the late Pleistocene (~12,000 years BP) resembled a lush wetland compared with the current desert it is today (Figure 1). Two large lakes, Bonneville and Lahontan, as well as many other large bodies of water covered much of the western United States with thousands of additional water sources (rivers, streams, and springs) feeding these lakes (Broecker and Kaufman 1965, Currey 1990). More recently, four severe "megadroughts" between 900 and 1300 AD occurred in much of the west (Cook et al. 2004). These dry periods were followed by several hundred years of wet conditions that have begun to change again (Cook et al. 2004). Recent work has strongly linked these patterns to sea surface temperatures of the Pacific Ocean and the southern oscillation cycle of the El Niño (Cook et al. 2007). In coming years, increasing demand for water coupled with changing weather patterns are projected to reduce availability of water for wildlife (Jackson et al. 2001, Brown and Thorpe 2008). Water availability has, and certainly will, continue to vary over long temporal scales and large spatial extents.

The availability of free water also varies over short-temporal scales and smaller spatial extents, and this topic is receiving more interest recently, particularly with advances

vulnerability to predation, habitat changes induced by presence of water developments, and host-parasite and disease interactions facilitated or altered by increased availability of free water and species crowding.

151

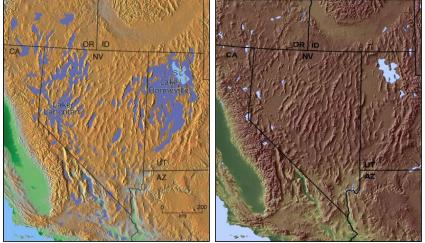


FIGURE 1.—The Great Basin and Mojave deserts and associated water sources during the Late Pleistocene ~12,000 years BP (left) and at present (right). Image at left courtesy of Eric Christiansen, Geological Sciences, Brigham Young University, adapted from Hamblin and Christiansen (2005).

in climate change research (Epps et al. 2004, Westerling et al. 2006, Brown and Thorpe 2008). In Joshua Tree National Park (JTNP), California, the number of natural water sources has declined since the 1950s (Longshore et al. 2009). Between 1948 and 1968, a primary spring for bighorn sheep (Ovis canadensis) decreased from a flow of 222 gallons per day to only an intermittent flow (Longshore et al. 2009). Since 1979, the number of perennial water sources in bighorn sheep habitat in JTNP has declined by 50% from ten to five (Longshore et al. 2009). The effects of this reduction in free water on suitability of bighorn sheep habitat, however, were mitigated by construction of water developments that reduced the loss of potential habitat for bighorn sheep due to drying of springs (Longshore et al. 2009). Although much of the change in water availability within JTNP is presumably due to anthropogenic influences that have lowered water tables, naturally occurring events (e.g., temperature and long-term precipitation patterns) also influence presence and persistence of free water. Loss and degradation of natural sources of free water have, and will, continue to occur in the arid West from continued urban, agricultural, transportation, and industrial development, as well as the effects of climate change (Dolan 2006, Krausman et al. 2006, Simpson et al. 2011).

Water availability can also be linked to the type and structure of vegetation surrounding water sources. Although the water yield hypothesis (i.e., increased free water availability following removal of vegetation with high water demand) is controversial in some habitats (Belsky 1996), others have confirmed increased runoff and spring flow following vegetation change (Ffolliott and Thorud 1977, Hibbert 1983). Deboodt (2008), for example, demonstrated that spring flow increased 225%, and number of days with recordable groundwater increased by an average of 41 days following removal of western juniper (*Juniperus occidentalis*) in a paired watershed study in eastern Oregon. Increased water yield can occur from changes in plant community composition, especially when phreatophytes are removed, but also from alteration of forest stand configuration as it

influences snow deposition and associated runoff (Troendle 1983). Vegetation change at a watershed scale can further be linked to fire histories and broad-scale land-management practices such as forestry and grazing (Milchunas 2006, Stephens et al. 2009). Additionally, animals congregating around water sources can also influence the composition, abundance, and diversity of associated flora in those areas (Weaver 1973, Tolsma et al. 1987, Cole and Landres 1996), further complicating understanding of the variation in availability of free water over time and space.

Among the papers we reviewed, few authors acknowledged inherent variability in available free water over time and space. An evaluation of historical changes in availability of free water across western landscapes — similar to that of Longshore et al. (2009) — would help inform wildlife managers on the value of wildlife water developments as a management and conservation practice (Morgart et al. 2005, Dolan 2006, Simpson et al. 2011). Indeed, wildlife water developments could become increasingly important in the future as mitigation for loss of sources of free water (Dolan 2006, Longshore et al. 2009). More informative, however, would be modeled simulations of future availability of free water based on predicted climatic change. With few exceptions, these predictions indicate that increased aridity and the potential for drought are imminent in the southwestern USA (Seager et al. 2007). We argue that recognition of inherent variability in water availability is central to understanding the long-term responses of wildlife to water developments over extended time periods and across large spatial extents.

WATER STATE (FREE, METABOLIC, OR PRE-FORMED) USED BY WILDLIFE

Native wildlife in arid regions have evolved and adapted to conditions of those environments (Serventy 1971, Randall 1993, Cain et al. 2006). Many animals, particularly those with small body mass, may satisfy water requirements from sources of metabolic or preformed water, rather than from free or drinking water. Some animals can survive indefinitely without the need to drink water given adequate food resources, and have evolved a variety of behavioral, morphological, and physiological adaptations to exist in arid environments and maintain water balance without drinking (Schmidt-Nielsen and Schmidt-Nielsen 1951, Bartholomew 1970, Golightly and Ohmart 1984). Clearly, water developments targeting such species are unlikely to be effective.

Whether or not large mammals can also meet water requirements with metabolic or pre-formed water during all seasons of the year is less clear (Morgart et al. 2005). Large mammals certainly demonstrate adaptations that limit the need for free water, such as evaporative cooling, migration, and timing of activity (Morgart et al. 2005, Cain et al. 2006). Some populations of desert bighorn sheep occupy mountain ranges with no known perennial water sources (Krausman et al. 1985, Alderman et al. 1989, Krausman and Etchberger 1995, Broyles and Cutler 1999). Also, bighorn sheep (Warrick and Krausman 1989) and collared peccaries (*Tayassu tajacu*) (Bissonette 1982) in some areas consume fleshy parts of cacti (*Ferocactus* spp. and *Opuntia* spp.), which likely helps satisfy water needs. Unfortunately, more information is known regarding adaptations of desert ungulates in Africa and the Middle East than for species occupying the western USA (Cain et al. 2006, Simpson et al. 2011). A critically important issue is whether target species can find forage with water content adequate to meet needs during the hottest and driest part of the year. Indeed, in the absence of free water, little is known regarding the level of moisture

content in forage that would be required to maintain water balance for most large mammals in the USA. Additionally, some wildlife may make trade-offs between water content and nutrient content of forage (i.e., eating forage species with high water content but low nutrient content), which may have negative consequences. For most species with a relatively large body mass, however, extreme temperatures coupled with dry forage necessitate the need to

drink free water (Turner 1973, Robbins 2001, Morgart et al. 2005). Differential use of pre-formed and free water may occur for the same species in dissimilar locations. Chukars (*Alectoris chukar*) in the western USA, for example, contend with water shortages in arid and semi-arid environments (Degen et al. 1984, Borralho et al. 1998). Laboratory results indicate that chukars do not require free water during times of cool temperatures (i.e., spring or winter) because metabolic or pre-formed water can satisfy water demands (Alkon et al. 1982, Degen et al. 1983, Alkon et al. 1985). Even during summer, however, chukars in some areas were able to secure water through consumption of succulent food sources such as wild onion bulbs (*Allium* spp.), as reported by Larsen et al. (2010); those authors documented differences in use of free water (some populations used free water, whereas others showed a spatial distribution suggesting no use of this resource) between populations separated by as little as 100 km, and suggested that this dissimilarity occurred because of differential resource availability and behavioral adaptations of those animals (Larsen et al. 2010).

Wildlife water developments installed in areas where target species can meet water requirements with metabolic or pre-formed water are unlikely to achieve desired results. Similarly, research in some of these areas should show no use, or limited use, of water developments by desert-adapted wildlife, but in some areas these animals may still use this resource extensively (Lynn et al. 2008). Managers should not be surprised at different results for the same species in different areas given variation in behavioral adaptations and differential resource availability (e.g., availability of food items high in pre-formed water content). Further work to understand the relative roles of behavioral adaptations and differences in availability of food items high in moisture content in explaining such differences is warranted.

SEASONAL TEMPERATURE AND PRECIPITATION PATTERNS THAT INFLUENCE THE PHYSIOLOGICAL NEED FOR WATER

For species or populations unable to meet all water requirements with metabolic or pre-formed water, individual requirements (i.e., reproductive state and physical condition; Cain et al. 2006, Lynn et al. 2008, Whiting et al. 2011) and animal activity (i.e., whether an animal seeks shade or increased activity during the breeding season; Cain et al. 2008a, Whiting et al. 2010) combined with climatic conditions dictate demand for free water (Turner and Weaver 1980, Robbins 2001, Cain et al. 2006). Despite inherent variability, general patterns of water use exist for populations and should be considered when conducting research on the effectiveness of wildlife water developments. For example, in the Great Basin, chukars used free water most from mid-July to mid-September, which coincided with both high temperatures and dry forage (Larsen et al. 2007). No use of water sources by those birds was documented during November through May (Larsen et al. 2007). Similarly, bighorn sheep used water sources all year, but use was substantially greater in summer (Leslie 1978, Bleich et al. 1997, Whiting et al. 2009). Finally, migrating birds used wildlife

water developments at different times of the year compared with resident species (Lynn et al. 2008). Seasonal use of water sources for other species will vary with temperature and precipitation patterns.

Research documenting use of water sources and population responses of such use should consider that physiological water demands change seasonally and time lags associated with use of this resource may exist. For example, evaluating response of chukars to wildlife water developments would most effectively include measures of over-summer survival, summer movements, and chick survival during that season — all of which happen during the period of increased physiological need for water (Larsen et al. 2007). Contrarily, measures of winter through spring survival or reproductive effort (e.g., nest initiation, nest success, clutch size, etc.) may not be as informative for chukars because these activities occur outside of the summer period of water use. Moreover, male and female bighorn sheep used natural water sources significantly more during rut (October and November) following summer drought conditions than following a summer of normal conditions (Whiting et al. 2010). Thus, certain seasons may experience drought, but the effect of those dry conditions on use of water sources may not be evident until later (Whiting et al. 2009, Whiting et al. 2010, Whiting et al. 2011). Therefore, to detect increases or decreases in use of water sources or to evaluate population-level responses, investigators need to document such use over several seasons and years, especially during and following drought (Whiting et al. 2009, Whiting et al. 2010, Whiting et al. 2011).

The availability of water for wildlife in springs, tinajas, and wildlife water developments changes based on regional temperature and precipitation patterns. In Arizona and New Mexico, where monsoon moisture dominates the late-summer weather pattern, early summer (May to July) can be the most extreme period of water stress (Morgart et al. 2005). Predictably, photographic encounter rates at sources of free water are highest during summer for a variety of species (O'Brien et al. 2006). For mule deer (*Odocoileus hemionus*) this time period also coincides with lactation, which increases water requirements (Short 1981). Conversely, in northern Utah, Rocky Mountain bighorn sheep (*O. c. canadensis*) and chukars used water sources significantly more from July to September (Larsen et al. 2007, Whiting et al. 2009). Regional climate patterns that influence physiological water demand need to be considered during research documenting short-term influences of available free water.

BEHAVIORAL CONSTRAINTS THAT LIMIT USE OF OTHERWISE AVAILABLE FREE WATER

Use of some water sources by prey species may be altered due to a perceived risk of predation at these locations, and species should perceive risks differently depending on their predator-avoidance strategies and habitat surrounding sources of free water (Bleich et al. 1997, Bowyer 2004, Whiting et al. 2011). These behavioral traits have received only limited attention in the literature. Larsen et al. (2007) showed that chukars preferred to use water sources with >11% shrub canopy cover in the immediate (\leq 30 m from water source) area. Delehanty et al. (2004) suggested that mountain quail (*Oreortyx pictus*) preferred wildlife water developments in wooded areas. Recent work with mule deer (Larsen et al. 2011) identified avoidance of wildlife water developments with small-perimeter fencing. These papers attributed observed patterns of differential use of water sources, at least in part, to perceived predation risk. Some of the debate concerning the effectiveness of wildlife water developments has focused on the potential negative implications of increased predation

at these locations (Broyles 1995, DeStefano et al. 2000, Simpson et al. 2011). Simpson et al. (2011) concluded that predation rates most likely do not increase near wildlife water developments; however, they indicated that more research was needed to determine how habitat surrounding water sources influences predators and prey.

Behavioral constraints that limit use of free water could also result from lack of recognition of the presence of water in the catchment. Water available in wildlife water developments is often covered by a collection area or screen. Both strategies help to reduce evaporation, but also make water less visible to raptors and other birds that may not recognize water developments as a source of free water. Additionally, access may be limited for some species because of physical barriers (Larsen et al. 2011), or by design of the development. Bats, for example, prefer to skim open water while flying (Rabe and Rosenstock 2005). Experimental manipulation of existing water sources to increase surface area has resulted in increased use of this resource by bats (Tuttle et al. 2006).

Moreover, males and females of the same species may use free water differently (Bowyer 2004, Whiting et al. 2010). Differential habitat selection between sexes is well documented for many vertebrates (Bleich et al. 1997, Bowyer 2004, Ruckstuhl and Neuhaus 2005). Appreciation of those differences in understanding the use of wildlife water developments, however, often is lacking. Females with young are likely to be more selective in use of free water based on surrounding habitat characteristics than are males, or females without young (Bowyer 1984, Bleich et al. 1997, Bowyer 2004). Whiting et al. (2010) observed that although home ranges overlapped considerably for male and female bighorn sheep, use of different water sources occurred and that consideration should be given to the separate habitat requirements for each sex when evaluating the use of free water. Wildlife water developments constructed in areas used by one sex may not be beneficial for the other (Bleich et al. 1997, Bleich 2009). Further work to understand sex-specific differences in use of wildlife water developments is needed (Whiting et al. 2010, Whiting et al. 2011).

Additionally, native species may use wildlife water developments differently when compared with translocated animals. Native species exhibit impressive adaptations to arid environments (Alderman et al. 1989, Broyles and Cutler 1999), whereas translocated species may be released into areas with much different climate and precipitation patterns compared to their source areas (Whiting et al. 2009, Simpson et al. 2011). For example, many populations of bighorn sheep in Washington, Utah, Oregon, Idaho, and Nevada have come from Kamloops, British Columbia, Canada (Demarchi and Mitchell 1973, Whittaker et al. 2004). Bighorn sheep in British Columbia most likely did not encounter the degree of water stress that is evident in dry regions of the western United States where they were released (Whiting et al. 2009). Translocations are the primary way in which managers and biologists have restored populations of bighorn sheep (Krausman 2000), and much more information is needed regarding the behavior of introduced animals after release (Griffith et al. 1989, Seddon et al. 2007). We recommend considering whether populations are native or introduced when evaluating the effectiveness of wildlife water developments, and we also recommend that managers consider climate of both the source area and release area when selecting animals for translocation.

Some species may compete with, or be displaced by, other animals while accessing free water. For example, surface water may increase competition between bighorn sheep and feral burros (*Equus assinus*), feral horses (*Equus caballus*), or mule deer for succulent vegetation that is associated with that resource (Bleich et al. 1982, Krausman and Leopold

1986, Bleich et al. 2005). Bighorn sheep are poor competitors at water sources, and the presence of feral horses at those locations reduced the use of water by bighorn sheep (Ostermann-Kelm et al. 2008); further, bighorn sheep in that study occupied areas removed from water sources used by feral horses (Ostermann-Kelm et al. 2008). Even feral honey bees (*Apis mellifera*) altered the use and behavior of bighorn sheep at one water source (Boyce et al. 2003). Finally, human use or recreation near water sources can negatively influence use of this resource by wildlife (Campbell and Remington 1979, Leslie and Douglas 1979, Leslie and Douglas 1980). More research is necessary to characterize interactions among species at water sources (Ostermann-Kelm et al. 2008, Simpson et al. 2011, Whiting et al. 2011).

Limited use of free water due to behavioral constraints reduces the effectiveness of management actions and compromises research aimed at evaluating wildlife response to water developments. If, for example, some water sources receive limited use, or even no use, due to behavioral constraints (e.g., increased predation risk or competition) compared with others, but both are treated equally in research design, results could be misleading. Clearly, use of water developments is a prerequisite, and is necessary to properly evaluate the influence of wildlife water developments on population performance. We encourage evaluation of the probability of water source use as part of observational or experimental research. Specifically, use of water sources by target species and sexes should be verified prior to studies involving the removal of water sources.

PROPER SPACING AND PLACEMENT OF WATER DEVELOPMENTS FOR TARGETED SPECIES

Even when all of the framework considerations are met for a given species, there exists a density of water sources at which additional free water will most likely not be beneficial. This relationship is allometric, since home range size and movement patterns generally scale with body mass (Harestad and Bunnell 1979, Sutherland et al. 2000, Kelt and Van Vuren 2001). This relationship with body mass allows for estimation of ecological neighborhoods that can help guide management and research (Bissonette and Adair 2008). Krausman et al. (2006) reviewed information on optimal spacing of water developments for some species; information for a majority of species is, however, lacking. When daily movement data are sparse, but adequate seasonal or annual home range information exists, we suggest using the square root of home range area as a measure of approximate daily movements, as has been proposed for spacing of wildlife road crossings (Bissonette and Adair 2008). This measure serves as a linear metric of home range and provides reasonable estimates of daily movement distances. Managers can then space water resources so that opportunities for visitation are within normal movement patterns for resident species.

The placement of wildlife water developments can also play an important role in facilitating genetic exchange among metapopulations. Wildlife managers need to consider the structure of a metapopulation as they allocate scarce resources (e.g., time and money) related to wildlife water developments (Bleich 2009). Indeed, the persistence of small, isolated populations of bighorn sheep is much more likely to be affected by water shortages than the persistence of populations that are connected to other areas inhabited by that species (Bleich 2009). Although Bleich (2009) discussed decisions regarding where to reprovision wildlife water developments during drought among metapopulations of these ungulates, this same concept can be applied to decisions concerning the construction of wildlife water developments. Units most likely to maximize long-term benefit to target species will be those

placed in areas that support or enhance metapopulation dynamics (sensu Bleich 2009) and, although some wildlife water developments are rarely used, they may play very important roles in facilitating movements of animals within metapopulations (Bleich 2009).

Consideration of optimal spacing is also important in the context of research design. It is conceivable that water sources that are close together function as a single source for relatively mobile organisms. If these sources are treated separately in a research design, but function effectively as one source, then research that measures wildlife response as dependent on the number of available water sources will be compromised. Essentially, this scenario is a scaling problem that needs to be carefully considered before interpretation of data or initiation of management actions. Additional investigation of these issues would be helpful, because we often lack a general understanding of space use and movement patterns in relation to availability of free water for many species.

DISCUSSION

Wildlife water developments remain a viable and important conservation option since wildlife will be managed in increasingly modified habitats in the future (Krausman et al. 2006, O'Brien et al. 2006, Simpson et al. 2011). The importance of this resource will increase, especially if projected water shortages are accurate (Dolan 2006, Pearce 2006, Brown and Thorpe 2008). Successful research concerning the effectiveness of wildlife water developments will likely be achieved when the framework elements we present are taken into consideration. Variation in the availability of free water in time and space is fundamental. The ability of species or populations to meet water needs during part or all of the year with free, metabolic, or pre-formed water is an important consideration. To the extent that metabolic and pre-formed water satisfies needs, benefit from water developments will vary. Annual temperature and precipitation patterns coupled with animal activity create different seasonal water needs. Behavioral constraints of animals may limit water development effectiveness and compromise interpretation of research results. Finally, optimal spacing and placement, based on movement patterns of target species, must be considered.

One reason for the lack of understanding regarding the influence of wildlife water developments is that aggressive construction of these devices was not paired with long-term, multi-year studies during both drought and wet years (Rosenstock et al. 1999, Krausman et al. 2006, Cain et al. 2008b, Simpson et al. 2011). Unpredictability in climatic conditions is part of the reason long-term research spanning multiple wet-dry cycles is needed (Rosenstock et al. 1999, Krausman et al. 2006, Cain et al. 2008b). Meaningful assessment with improved inferential strength — particularly inference to causation — will most likely be achieved with well-designed removal and addition experiments (e.g., BACI designs) replicated in time and space (Simpson et al. 2011). Designing and implementing such studies will help quantify whether wildlife merely use, or also benefit (e.g., increased survival, recruitment, etc; Table 1), from wildlife water developments.

Wildlife water developments will remain a controversial topic, because some view them as manipulations of natural systems (Caughley and Sinclair 1994, Morgart et al. 2005, Krausman et al. 2006). Controversy will likely create additional opportunities for research. We argue that future efforts to evaluate the effects of wildlife water developments, or to benefit wildlife through provisioning of additional free water, can be informed by our framework. If framework elements are integrated into long-term research spanning multiple

wet-dry cycles, as well as the management of wildlife water developments, both research and management will improve. Management actions will be more likely to benefit targeted wildlife species, while research can be more effectively designed to yield robust conclusions.

ACKNOWLEDGMENTS

We thank D. Mitchell, E. Perkins, and other members of the Utah Upland Game Advisory Committee along with S. Espinosa, M. Cox, C. Garrett, and others with the Nevada Department of Wildlife who engaged in meaningful conversations that influenced this manuscript. Initial reviews of an earlier draft were provided by P. Krausman and V. Bleich. The cooperators of the Utah Cooperative Fish and Wildlife Unit are the Utah Division of Wildlife Resources, Utah State University, U.S. Geological Survey, Wildlife Management Institute, and U.S. Fish and Wildlife Service.

LITERATURE CITED

- ALDERMAN, J. A., P. R. KRAUSMAN, AND B. D. LEOPOLD. 1989. Diel activity of female desert bighorn sheep in western Arizona. Journal of Wildlife Management 53:264-271.
- ALKON, P. U., A. A. DEGEN, B. PINSHOW, AND P. J. SHAW. 1985. Phenology, diet, and water turnover rates of Negev Desert chukars. Journal of Arid Environments 9:51-61.
- ALKON, P. U., B. PINSHOW, AND A. A. DEGEN. 1982. Seasonal water turnover rates and body water volumes in desert chukars. Condor 84:332-337.
- BARTHOLOMEW, G. A. 1970. The water economy of seed-eating birds that survive without drinking. Pages 237-254 *in* K. H. Voous, editor. The 25th International Ornithological Congress, The Hague, Netherlands.
- BELSKY, A. J. 1996. Western juniper expansion: is it a threat to arid northwestern ecosystems? Journal of Range Management 49:53-59.
- BISSONETTE, J. A. 1982. Social behavior and ecology of the collared peccary in Big Bend National Park. National Park Service Science Monograph 16:1-95.
- BISSONETTE, J. A., AND W. ADAIR. 2008. Restoring habitat permeability to roaded landscapes with isometrically-scaled wildlife crossings. Biological Conservation 141:482-488.
- BLEICH, V. C. 2005. Politics, promises, and illogical legislation confound wildlife conservation. Wildlife Society Bulletin 33:66-73.
- BLEICH, V. C. 2009. Factors to consider when reprovisioning water developments used by mountain sheep. California Fish and Game 95:153-159.
- BLEICH, V. C., N. G. ANDREW, M. J. MARTIN, G. P. MULCAHY, A. M. PAULI, AND S. S. ROSENSTOCK. 2006. Quality of water available to wildlife in desert environments: comparisons among anthropogenic and natural sources. Wildlife Society Bulletin 34:627-632.
- BLEICH, V. C., AND R. A. WEAVER. 1983. Improved sand dams for wildlife habitat management. Journal of Range Management 36:133.
- BLEICH, V. C., R. T. BOWYER, AND J. D. WEHAUSEN. 1997. Sexual segregation in mountain sheep: resources or predation? Wildlife Monographs 134:1-50.
- BLEICH, V. C., L. J. COOMBES, AND J. H. DAVIS. 1982. Horizontal wells as a wildlife habitat improvement technique. Wildlife Society Bulletin 10:324-328.
- BLEICH, V. C., J. G. KIE, E. R. LOFT, T. R. STEPHENSON, M. W. OEHLER SR., AND A. L. MEDINA. 2005. Managing rangelands for wildlife. Pages 873-897 *in* C. E. Braun, editor.

Techniques for wildlife investigations and management. The Wildlife Society, Bethesda, Maryland, USA.

- BLOOM, F. 2003. Wildlife water development team implementation plan. Arizona Game and Fish Department, Phoenix, USA.
- BORRALHO, R., A. RITO, F. REGO, H. SIMOES, AND P. V. PINTO. 1998. Summer distribution of red-legged partridges *Alectoris rufa* in relation to water availability on Mediterranean farmland. Ibis 140:620-625.
- BOWYER, R. T. 1984. Sexual segregation in southern mule deer. Journal of Mammalogy 65:410-417.
- BOWYER, R. T. 2004. Sexual segregation in ruminants: definitions, hypotheses, and implications for conservation and management. Journal of Mammalogy 85:1039-1052.
- BOYCE, W. M., C. S. O'BRIEN, AND E. S. RUBIN. 2003. Response of bighorn sheep (*Ovis canadensis*) to feral honey bees (*Apis mellifera*) at water. Southwestern Naturalist 48:81-84.
- BROECKER, W. S., AND A. KAUFMAN. 1965. Radiocarbon chronology of Lake Lahontan and Lake Bonneville; part 2, Great Basin. Bulletin of the Geological Society of America 76:537-566.
- BROWN, J. R., AND J. THORPE. 2008. Climate change and rangelands: responding rationally to uncertainty. Rangelands 30:3-6.
- BROYLES, B. 1995. Desert wildlife water developments: questioning use in the southwest. Wildlife Society Bulletin 23:663-675.
- BROYLES, B., AND T. L. CUTLER. 1999. Effect of surface water on desert bighorn sheep in the Cabeza Prieta National Wildlife Refuge, southwestern Arizona. Wildlife Society Bulletin 27:1082-1088.
- BURKETT, D. W., AND B. C. THOMPSON. 1994. Wildlife association with human-altered water sources in semiarid vegetation communities. Conservation Biology 8:682-690.
- CAIN III, J. W., B. D. JANSEN, R. R. WILSON, AND P. R. KRAUSMAN. 2008a. Potential thermoregulatory advantages of shade use by desert bighorn sheep. Journal of Arid Environments 72:1518-1525.
- CAIN III, J. W., P. R. KRAUSMAN, J. R. MORGART, B. D. JANSEN, AND M. P. PEPPER. 2008b Responses of desert bighorn sheep to removal of water sources. Wildlife Monographs 171:1-32.
- CAIN III, J. W., P. R. KRAUSMAN, S. S. ROSENSTOCK, AND J. C. TURNER. 2006. Mechanisms of thermoregulation and water balance in desert ungulates. Wildlife Society Bulletin 34:570-581.
- CAMPBELL, B. H., AND R. REMINGTON. 1979. Bighorn use of artificial water sources in the Buckskin Mountains, Arizona. Desert Bighorn Council Transactions 23:50-56.
- CAUGHLEY, G., AND A. R. E. SINCLAIR. 1994. Wildlife ecology and managment. Blackwell Scientific, Oxford, United Kingdom.
- COLE, D. N., AND P. B. LANDRES. 1996. Threats to wilderness ecosystems: impacts and research needs. Ecological Applications 6:168-184.
- COOK, E. R., R. SEAGER, M. A. CANE, AND D. W. STAHLE. 2007. North American drought: reconstructions, causes, and consequences. Earth-Science Reviews 81:93-134.
- COOK, E. R., C. A. WOODHOUSE, C. M. EAKIN, D. M. MEKO, AND D. W. STAHLE. 2004. Longterm aridity changes in the western United States. Science 306:1015-1018.

- CURREY, D. R. 1990. Quaternary palaeolakes in the evolution of semidesert basins, with special emphasis on Lake Bonneville and the Great Basin, U.S.A. Palaeogeography, Palaeoclimatology, Palaeoecolgy 76:189-214.
- DEBLINGER, R. D., AND A. W. ALLDREDGE. 1991. Influence of free water on pronghorn distribution in a sagebrush/steppe grassland. Wildlife Society Bulletin 19:321-326.
- DEBOODT, T. L. 2008. Watershed response to western juniper control. Oregon State University, Corvallis, USA.
- DEGEN, A. A., B. PINSHOW, AND P. U. ALKON. 1983. Summer water turnover rates in free-living chukars and sand partridges in the Negev Desert. Condor 83:333-337.
- DEGEN, A. A., B. PINSHOW, AND P. J. SHAW. 1984. Must desert chukars (*Alectoris chukar sinaica*) drink water? Water influx and body mass changes in response to dietary water content. Auk 101:47-52.
- DELEHANTY, D. J., S. S. EATON, AND T. G. CAMPBELL. 2004. Mountain quail fidelity to guzzlers in the Mojave Desert. Wildlife Society Bulletin 32:588-593.
- DEMARCHI, D. A., AND H. B. MITCHELL. 1973. The Chilcotin River bighorn population. Canadian Field-Naturalist 87:433-454.
- DESTEFANO, S., S. L. SCHMIDT, AND J. C. DEVOS JR. 2000. Observations of predator activity at wildlife water developments in southern Arizona. Journal of Range Management 53:255-258.
- DOLAN, B. F. 2006. Water developments and desert bighorn sheep: implications for conservation. Wildlife Society Bulletin 34:642-646.
- EPPS, C. W., D. R. MCCULLOUGH, J. D. WEHAUSEN, V. C. BLEICH, AND J. L. RECHEL. 2004. Effects of climate change on population persistence of desert-dwelling mountain sheep in California. Conservation Biology 18:102-113.
- FFOLLIOTT, P. F., AND D. B. THORUD. 1977. Water yield improvement by vegetation management. Journal of the American Water Resources Association 13:563-572.
- GLADING, B. 1943. A self-filling quail watering device. California Fish and Game 29:157-164.
- GLADING, B. 1947. Game watering devices for the arid southwest. Transactions of the North American Wildlife Conference 12:286-292.
- GOLIGHTLY, R. T., AND R. D. OHMART. 1984. Water economy of two desert canids: coyote and kit fox. Journal of Mammalogy 65:51-58.
- GRIFFITH, B., J. M. SCOTT, J. W. CARPENTER, AND C. REED. 1989. Translocation as a species conservation tool: status and strategy. Science 245:477-480.
- HALLORAN, A. F. 1949. Desert bighorn managment. Transactions of the North American Wildlife Conference 14:527-537.
- HALLORAN, A. F., AND O. V. DEMING. 1958. Water development for desert bighorn sheep. Journal of Wildlife Management 22:1-9.
- HAMBLIN, W. K., AND E. H. CHRISTIANSEN. 2005. Earth's dynamic systems. Prentice Hall, Upper Saddle River, New Jersey, USA.
- HARESTAD, A. S., AND F. L. BUNNELL. 1979. Home range and body weight a reevaluation. Ecology 60:389-402.
- HIBBERT, A. R. 1983. Water yield improvement potential by vegetation managment on western rangelands. American Water Resources Association 19:375-381.
- JACKSON, R. B., S. R. CARPENTER, C. N. DAHM, D. M. MCKNIGHT, R. J. NAIMAN, S. L. POSTEL, AND S. W. RUNNING. 2001. Water in a changing world. Ecological Applications 11:1027-1045.

- KELT, D. A., AND D. H. VAN VUREN. 2001. The ecology and macroecology of mammalian home range area. American Naturalist 157:637-645.
- KINDSCHY, R. R. 1996. Fences, waterholes, and other range improvements. Pages 369-381 in P. R. Krausman, editor. Rangeland wildlife. Society for Range Management, Denver, Colorado, USA.
- KRAUSMAN, P. R. 2000. An introduction to the restoration of bighorn sheep. Restoration Ecology 8:3-5.
- KRAUSMAN, P. R., 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.
- KRAUSMAN, P. R., AND R. C. ETCHBERGER. 1995. Response of desert ungulates to a water project in Arizona. Journal of Wildlife Management 59:292-300.
- KRAUSMAN, P. R., S. S. ROSENSTOCK, AND J. W. CAIN III. 2006. Developed waters for wildlife: science, perception, values, and controversy. Wildlife Society Bulletin 34:563-569.
- KRAUSMAN, P. R., S. G. TORRES, L. L. ORDWAY, J. J. HERVERT, AND M. BROWN. 1985. Diel activity of ewes in the Little Harquahala Mountains, Arizona. Desert Bighorn Council Transactions 29:24-26.
- LARSEN, R. T., J. A. BISSONETTE, J. T. FLINDERS, M. B. HOOTEN, AND T. L. WILSON. 2010. Summer spatial patterning of chukars in relation to free water in western Utah. Landscape Ecology 25:135-145.
- LARSEN, R. T., J. A. BISSONETTE, J. T. FLINDERS, AND A. C. ROBINSON. 2011. Does smallperimeter fencing inhibit mule deer or pronghorn use of water developments? Journal of Wildlife Management 75:1417-1425.
- LARSEN, R. T., J. T. FLINDERS, D. L. MITCHELL, E. R. PERKINS, AND D. G. WHITING. 2007. Chukar watering patterns and water site selection. Rangeland Ecology and Management 60:559-565.
- LEOPOLD, A. 1933. Game management. Charles Scribner's Sons, New York, USA.
- LESLIE, Jr., D. M. 1978. Differential utilization of water sources by desert bighorn sheep in the River Mountains, Nevada. Desert Bighorn Council Transactions 22:23-26.
- LESLIE, JR., D. M., AND C. L. DOUGLAS. 1979. Desert bighorn sheep of the River Mountains, Nevada. Wildlife Monographs 66:1-56.
- LESLIE, JR., D. M., AND C. L. DOUGLAS. 1980. Human disturbance at water sources of desert bighorn sheep. Wildlife Society Bulletin 8:284-290.
- LONGSHORE, K. M., C. LOWREY, AND D. B. THOMPSON. 2009. Compensating for diminishing natural water: predicting the impacts of water development on summer habitat of desert bighorn sheep. Journal of Arid Environments 73:280-286.
- LYNN, J. C., S. S. ROSENSTOCK, AND C. L. CHAMBERS. 2008. Avian use of desert wildlife water developments as determined by remote videography. Western North American Naturalist 68:107-112.
- MATTSON, D. J., AND N. CHAMBERS. 2009. Human-provided waters for desert wildlife: what is the problem? Policy Sciences 42:113-135.
- MILCHUNAS, D. G. 2006. Responses of plant communities to grazing in the southwestern United States. USFS Rocky Mountain Research Station General Technical Report 169:1-126.
- MORGART, J. R., J. J. HERVERT, P. R. KRAUSMAN, J. L. BRIGHT, AND R. S. HENRY. 2005. Sonoran pronghorn use of anthropogenic and natural water sources. Wildlife Society Bulletin 33:51-60.

- O'BRIEN, C. S., R. B. WADDELL, S. S. ROSENSTOCK, AND M. J. RABE. 2006. Wildlife use of water catchments in southwestern Arizona. Wildlife Society Bulletin 34:582-591.
- OSTERMANN-KELM, S., E. R. ATWILL, E. S. RUBIN, M. C. JORGENSEN, AND W. M. BOYCE. 2008. Interactions between feral horses and desert bighorn sheep at water. Journal of Mammalogy 89:459-466.
- PEARCE, F. 2006. When the rivers run dry: water the defining crisis of the twenty-first century. Beacon Press, Boston, Massachusetts, USA.
- RABE, M. J., AND S. S. ROSENSTOCK. 2005. Influence of water size and type on bat captures in the lower Sonoran Desert. Western North American Naturalist 65:87-90.
- RANDALL, J. A. 1993. Behavioral adaptations of desert rodents (*Heteromyidae*). Animal Behaviour 45:263-287.
- RAUTENSTRAUCH, K. R. AND P. R. KRAUSMAN. 1989. Influence of water availability and rainfall on movements of desert mule deer. Journal of Mammalogy 70:197-201.
- RICKLEFS, R. E. 2001. The economy of nature. W. H. Freeman and Company, New York, USA.
- ROBBINS, C. T. 2001. Wildlife feeding and nutrition. Academic Press, San Diego, California, USA.
- ROSENSTOCK, S. S., W. B. BALLARD, AND J. C. DEVOS JR. 1999. Viewpoint: benefits and impacts of wildlife water developments. Journal of Range Management 52:302-311.
- RUCKSTUHL, K. E., AND P. NEUHAUS. 2005. Sexual segregation in verebrates: ecology of the two sexes. Cambridge University Press, Cambridge, United Kingdom.
- SCHMIDT-NIELSEN, B., AND K. SCHMIDT-NIELSEN. 1951. A complete account of the water metabolism in kangaroo rats and an experimental verification. Journal of Cellular and Comparative Physiology 38:165-181.
- SEAGER, R., M. F. TING, I. HELD, Y. KUSHNIR, J. LU, G. VECCHI, H. P. HUANG, N. HARNIK, A. LEETMAA, N. C. LAU, C. H. LI, J. VELEZ, AND N. NAIK. 2007. Model projections of an imminent transition to a more arid climate in southwestern North America. Science 316:1181-1184.
- SEDDON, P. J., D. P. ARMSTRONG, AND R. F. MALONEY. 2007. Developing the science of reintroduction biology. Conservation Biology 21:303-312.
- SERVENTY, D. L. 1971. Biology of desert birds. Pages 287-339 *in* D. S. Farner, J. R. King and K. C. Parkes, editors. Avian biology. Academic Press, New York, USA.
- SEVERSON, K. E., AND A. L. MEDINA. 1983. Deer and elk habitat management in the southwest. Journal of Range Management Monograph 2:1-64.
- SHORT, H. L. 1981. Nutrition and metabolism. Pages 99-127 in O.C. Wallmo, editor. Mule and black-tailed deer of North America. University of Nebraska Press, Lincoln, USA.
- SIMPSON, N. O., K. M. STEWART, AND V. C. BLEICH. 2011. What have we learned about water developments for wildlife? Not enough! California Fish and Game 97:190-209.
- STEPHENS, S. L., J. J. MOGHADDAS, C. EDMINSTER, C.E. FIEDLER, S. HAASE, M. HARRINGTON, J. E. KEELEY, E. E. KNAPP, J. D. MCIVER, K. METLEN, C. N. SKINNER, AND A. YOUNGBLOOD. 2009. Fire treatment effects on vegetation structure, fuels, and potential fire severity in western U.S. forests. Ecological Applications 19:305-320.
- SUTHERLAND, G. D., A. S. HARESTAD, K. PRICE, AND K. P. LERTZMAN. 2000. Scaling of natal dispersal distances in terrestrial birds and mammals. *Conservation Ecology* 4:16. Available from: http://www.consecol.org/Journal/vol4/iss1/art16
- TOLSMA, D. J., W. H. O. ERNST, AND R. A. VERWEY. 1987. Nutrients in soil and vegetation around two artificial waterpoints in eastern Botswana. Journal of Applied Ecology 24:991-1000.

- TROENDLE, C. A. 1983. The potential for water yield augmentation from forest management in the Rocky Mountain Region. American Water Resources Association 19:359-373.
- TURNER, J. C. 1973. Water, energy, and electrolyte balance in the desert bighorn sheep, *Ovis* canadensis. Ph.D. Dissertation, University of California, Riverside, USA.
- TURNER, J. C., AND R. A. WEAVER. 1980. Water. Pages 100-112 in G. Monson and L. Sumner, editors. The desert bighorn: its life history, ecology, and management. University of Arizona Press, Tucson, USA.
- TUTTLE, S. R., C. L. CHAMBERS, AND T. L. THEIMER. 2006. Potential effects of livestock watertrough modifications on bats in northern Arizona. Wildlife Society Bulletin 34:602-608.
- WARRICK, G. D., AND P. R. KRAUSMAN. 1989. Barrel cactus consumption by desert bighorn sheep. Southwestern Naturalist 34:483-486.
- WEAVER, R. A. 1973. Burro versus bighorn. Desert Bighorn Council Transactions 17:90-94.
- WERNER, W. E. 1984. Bighorn sheep water development in southwestern Arizona. Transactions of the Desert Bighorn Council 28:12-13.
- WESTERLING, A. L., H. G. HIDALGO, D. R. CAYAN, AND T. W. SWETNAM. 2006. Warming and earlier spring increase western U.S. forest wildfire activity. Science 313:940-943.
- WHITING, J. C., V. C. BLEICH, R. T. BOWYER, AND R. T. LARSEN. 2011. Water availability and bighorn sheep: life-history characteristics and persistence of populations. Pages 131-163 in J. A. Daniels, editor. Advances in Environmental Research. Nova Publishers, Hauppauge, New York, USA.
- WHITING, J. C., R. T. BOWYER, AND J. T. FLINDERS. 2009. Annual use of water sources by reintroduced Rocky Mountain bighorn sheep Ovis canadensis canadensis: effects of season and drought. Acta Theriologica 54:127-136.
- WHITING, J. C., R. T. BOWYER, J. T. FLINDERS, V. C. BLEICH, AND J. G. KIE. 2010. Sexual segregation and use of water by bighorn sheep: implications for conservation. Animal Conservation 13:541-548.
- WHITTAKER, D. G., S. D. OSTERMANN, AND W. M. BOYCE. 2004. Genetic variability of reintroduced California bighorn sheep in Oregon. Journal of Wildlife Management 68:850-859.
- WRIGHT, J. T. 1959. Desert wildlife. Arizona Game and Fish Department, Phoenix, USA.

Received 10 May 2012 Accepted 10 July 2012 Associate Editor was V. Bleich