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Recovery of Rare Species: Case Study of the Masked Bobwhite

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Abstract

*Recovery of threatened and endangered species under the Endangered Species Act (ESA) is accomplished via federally mandated recovery plans. Unfortunately, many recovery plans are limited in effectiveness because they suffer from various limitations; one of which is the lack of scientific data. Because recovery plans for endangered species are inherently plagued by lack of biological data of focal species, new approaches are warranted in recovery-plan development to use what little data are available more effectively. The use of academic-agency partnerships has been suggested as a means to accomplish this objective; academics contribute scientific knowledge, and agency personnel contribute federal regulation expertise. We used the masked bobwhite (*Colinus virginianus ridgwayi*), the only endangered quail in North America, as a case study to illustrate how such partnerships can be employed to incorporate the latest scientific knowledge into recovery planning. Because the case study of the masked bobwhite embodies many of the difficulties associated with endangered species recovery (e.g., lack of biological data, limited personnel, limited resources), our approach to linking biology, ecology, and management can serve as a general model for recovery planning of other endangered species. We began with a comprehensive review and synthesis of masked bobwhite literature. Based on this information, we then interpreted existing masked bobwhite knowledge within the context of current ecological understanding of quail demography. This integrated knowledge provided the foundation to discuss demographic, habitat, and genetic challenges facing masked bobwhites from the perspective of general population phenomena. Our synthesis led to the conclusions that masked bobwhite populations probably 1) experience chronic low reproduction resulting from living in a desert environment, 2) have not been negatively impacted by the historic conversion of grasslands to brushlands, and 3) have not been as detrimentally impacted as other avian species by the establishment of nonnative grasses within their range because these plants possess functional value for masked bobwhites. We also identified 4 immediate conservation needs: recognition of the significant role México possesses in masked bobwhite conservation and proactive involvement in international collaboration, the need for a reconnaissance of masked bobwhite habitat and populations in México, and the implementation and recognition of the critical role habitat management plays in masked bobwhite recovery efforts. These objectives must be accomplished if recovery is to succeed. Currently, the future of masked bobwhite is precarious. Masked bobwhite recovery inevitably will involve international collaboration as well as partnerships between agency biologists, private landowners, and research scientists. (JOURNAL OF WILDLIFE MANAGEMENT 70(3):617–631; 2006)*

Key words

*Arizona, *Colinus virginianus ridgwayi*, endangered species, masked bobwhite, Sonora, México.*

The Endangered Species Act (ESA) is considered to be one of the most important legislative acts for biological conservation in the United States (Tear et al. 1995, Clark et al. 2002, Taylor et al. 2005). Recovery of threatened and endangered species under the ESA is addressed through federally mandated recovery plans that are required to contain 1) site-specific management actions necessary for species persistence; 2) objective, measurable criteria to assess attainment of recovery objectives; and 3) projected time schedules and costs associated with recovery. Because most recovery plans also provide information on species' biology, recovery plans represent a central repository for information on listed species and become focal documents guiding the recovery process (Clark et al. 2002). However, recovery plans often do not achieve their full utility because they suffer from various limitations (Tear et al. 1993, Tear et al. 1995, Foin et al. 1998); one of which is an overall lack of detailed, scientific data (Boersma et al. 2001, Clark et al. 2002).

Ineffective recovery plans arise partly because of the lack of biological data associated with rare species (Tear et al. 1995, Foin

et al. 1998). Ineffective recovery plans also arise from failure of plans to explicitly incorporate available scientific knowledge (Boersma et al. 2001, Clark et al. 2002). Recovery plans generally have failed to effectively link biology, ecology, and management (Clark et al. 2002). As a result, biological information contained within recovery plans often focuses on species distribution and population size but neglects important population processes (Tear et al. 1995). This skewed pattern in information distribution produces recovery plans primarily composed of descriptive biological and historical accounts but which lack current scientific knowledge. Recovery plans that merely invoke general platitudes of ecology or conservation biology are not likely to succeed (Boersma et al. 2001:648).

Because conservationists likely will never have complete biological knowledge, new approaches are warranted in recovery-plan development to use what little data are available more effectively (Foin et al. 1998). However, effectively linking basic biology, ecological theory, and management is a difficult task (Floyd 2001). Boersma and DeWeerd (2001) suggested that integration of available knowledge could be enhanced if academic-agency partnerships were employed. Academics contribute detailed

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Figure 1. Wild masked bobwhite male in Sonora, México, exhibiting dark-colored head characteristic of the species. Masked bobwhite, a subspecies of northern bobwhite, is the only endangered quail in North America. The last known native masked bobwhite in United States was believed to be collected in 1897. (Photograph by R. E. Tomlinson.)

knowledge of species biology and recent research, and agency personnel contribute first-hand knowledge of federal regulations (Boersma and DeWeerd 2001).

We used the endangered masked bobwhite as a case study to illustrate how such a partnership could be used to effectively integrate available scientific knowledge into recovery planning. Our objectives were to link basic biology, ecological theory, and management for masked bobwhites in a manner that illustrated 1) effective use of available data, 2) explicit incorporation of scientific data into recovery planning, and 3) collaboration between academic and agency personnel. To accomplish this, we began with a review of masked bobwhite discovery, population status and distribution, recovery history, and life history. Based on this knowledge, we then discussed processes influencing the population dynamics of masked bobwhites by comparing their ecology with current understanding of quail population dynamics. We highlighted the risks that masked bobwhites faced by existing as a fragmented population in a stressful environment and altered landscape. We also discussed the conservation issues and needs emerging from such risks and concluded with an epilogue on the future of the species.

The case study of the masked bobwhite embodies many of the difficulties facing recovery of endangered species (e.g., lack of biological data, limited personnel, and limited resources); there-

fore, our approach to linking biology, ecology, and management can serve as a general model for recovery planning of other endangered species.

Case Study Overview

Masked bobwhite, a subspecies of the northern bobwhite (*Colinus virginianus*), is the only endangered quail in North America (Fig. 1). It was listed as endangered by the U.S. government in 1968 with the passage of the Endangered Species Conservation Act. Masked bobwhites maintained their endangered status when the original legislation was modified with the passage of the Endangered Species Act of 1973 (U.S. Fish and Wildlife Service 1995). The total number of free-ranging masked bobwhites is restricted to one reintroduced population on the Buenos Aires National Wildlife Refuge (BANWR) in southern Arizona and 2 known native populations on private ranches in north-central Sonora, México (Kuvlesky et al. 2000). Although reliable censuses have not been conducted, it is estimated that the entire population of masked bobwhites consists of 1,000–2,000 individuals (Carroll et al. 1994, Engel-Wilson and Kuvlesky 2002). However, recent surveys (2005) estimate the population at 500–800 individuals (S. Gall, U.S. Fish and Wildlife Service, Sasabe, Ariz., USA, personal communication). The current status of masked bobwhite populations in México and the United States is precarious at best.

Limited information exists regarding the life history, ecology, and management of masked bobwhites. Most of what is known represents anecdotal information from early studies (Ligon 1952) or observations from field biologists (Tomlinson 1972a). In fact, relatively few quantitative studies have been conducted on masked bobwhites, and most of those were conducted during the latter part of the 20th century (Goodwin and Hungerford 1977, Simms 1989, White 1995, King 1998, Guthery et al. 2000, 2001a,b). Although the knowledge base for masked bobwhites can be characterized as isolated, incomplete, and often obscure, an extensive database exists for eastern races of the species (Brennan 1999, Hernández et al. 2002) from which valuable information can be gleaned.

Several reviews have been conducted for masked bobwhite in an attempt to summarize the rather disjunct literature (Tomlinson 1972b, Stromberg et al. 1984, Kuvlesky et al. 2000, Engel-Wilson and Kuvlesky 2002). However, these reviews are limited because they focus on a worthy but often specific view of masked bobwhite research, such as the historical account of population status and distribution or past recovery efforts. An integrative synthesis that interprets masked bobwhite research within the context of current ecological knowledge of quail demography does not exist. This is a critical point, given that the development and implementation of effective recovery planning for the subspecies depends on such knowledge.

Historical Background

Discovery and Taxonomy

Three species of *Colinus* are recognized; of which, the northern bobwhite is by far the most widely distributed and most varied group, represented by 22 named subspecies (Brennan 1999). Taxonomic classifications within the genus *Colinus* are based largely on geographic location and morphology, the latter of

which is highly variable within and among populations, such that the taxonomic relationships are somewhat uncertain (Johnsgard 1988). In fact, the main difference among several subspecies is plumage coloration of males, whereas females are virtually indistinguishable (Brennan 1999). It is not surprising then that much confusion existed regarding the taxonomic classification of masked bobwhite upon their discovery during the late 1800s.

The type specimen of masked bobwhite was collected in August 1884 about 29 km southwest of Sasabe, Sonora, México, and was identified as *C. ridgwayi* (Brewster 1885). Masked bobwhites, however, had been reported previously as a bird of Arizona in March 1884 but had been identified as *Ortyx* (now *Colinus*) *virginianus* (Brown 1884). The reported occurrence of *O. virginianus* in Arizona was questioned by Ridgway (1884), who argued that specimens identified by Brown (1884) were likely Massena quail (*Cyrtonix massena*; now Montezuma quail [*Cyrtonyx montezumae*]) or one of the Mexican bobwhites (*O. graysoni* [now *C. virginianus graysoni*]). Subsequent examination of incomplete specimens led Ridgway to conclude that the species was in fact *O. graysoni* (Grinnell 1884). Apparently unaware of these happenings (Allen 1886a), Brewster (1885) identified the species as *C. ridgwayi* in his description, which became the identification used in subsequent publications (Brown 1885). Ridgway (1886), however, continued the taxonomic debate insisting his identification of *O. graysoni* was correct. An examination of all the specimens present at that time ($n = 19$) finally led Allen (1886a) to conclude that the species was *C. ridgwayi*. This designation as a species remained until 1944, when masked bobwhites were reduced to subspecies standing and named *C. virginianus ridgwayi* (Brown and Ellis 1977). More information on the taxonomic history of masked bobwhites can be found in Allen (1886b,c, 1887), Scott (1886), Brown (1904), and Aldrich (1946).

The exact taxonomic relationship of masked bobwhites with other members of *Colinus* is unknown. Early morphological comparisons suggested that masked bobwhite were closely related to either *C. virginianus graysoni* or *texanus* (Brewster 1887, Allen 1887, 1889), with females of masked bobwhites being virtually indistinguishable from females of *C. virginianus texanus* (Allen 1886b, 1887). Morphological comparisons are limited, however, because masked bobwhites exhibit considerable variation in plumage (Allen 1886b, 1887, Banks 1975). Unfortunately, few genetic studies have been conducted at the population or subspecies level within the genus *Colinus*. Nedbal et al. (1997) observed genetic differentiation (2.8% mtDNA sequence divergence) between 2 subspecies of northern bobwhites in Texas (*C. virginianus texanus* and *C. virginianus mexicanus*). An analysis of mtDNA control region sequences at a broader geographic scale also indicated genetic structuring among northern bobwhites in the southeastern United States (White et al. 2000). The analysis indicated that captive masked bobwhites were more similar to *C. virginianus texanus* from south Texas than *C. virginianus texanus* were to subspecies of northern bobwhite in the southeastern United States. Only 2 nucleotide substitutions separated masked bobwhite and *C. virginianus texanus*, whereas 5 substitutions separated the masked and south Texas group from all other samples (White et al. 2000). Given the available research, masked bobwhites appear to be a valid subspecies, exhibiting the closest

taxonomic relationship with Texas bobwhites based on morphological and genetic evidence.

Distribution and Population Size

Early accounts characterize masked bobwhites as a Mexican species whose historic distribution extended northward (48–80 km) just beyond the Sonora–Arizona border (Fig. 2; Allen 1886a, Brown 1904). Masked bobwhites never had an extensive distribution in Arizona, being confined to the area east of the Baboquivari Mountains and west to the Santa Cruz River Valley, a distance of about 110 km (Brown and Ellis 1977). In Sonora, the ancestral distribution extended into México, possibly nearing the coast of the Gulf of California (Brown and Ellis 1977) but, more likely, only to southern Sonora (R. E. Tomlinson, U.S. Fish & Wildlife Service [retired], personal communication). Decreased precipitation limited the western and northwestern boundaries of the masked bobwhite distribution, whereas the replacement of grassland savannahs by dense thornscrub limited the eastern and southern boundaries (Brown and Ellis 1977).

Brown (1904:209) mentioned that masked bobwhites were plentiful in Arizona during the “early days” and common during the 1860s. However, excessive grazing pressure coupled with extended drought during the early 1890s deteriorated the grasslands of southern Arizona such that masked bobwhites drastically declined and became extirpated from the state (Brown 1900). By the beginning of the 20th century, Brown (1904:209) considered masked bobwhites to be “one of the rare, if not rarest, native birds in Arizona.” Phillips et al. (1964) noted that the last known specimens were taken in 1897. Gallizioli et al. (1967) speculated that masked bobwhites had disappeared from Arizona by 1912.

The population in Sonora also declined due to circumstances similar to those responsible for masked bobwhite in Arizona; however, the decline occurred about 50 years later (Tomlinson 1972a,b). The livestock industry did not become pervasive in Sonora until the 1940s and 1950s (Ligon 1952, Tomlinson 1972a). Ligon (1952) reported that masked bobwhites were present in considerable numbers in central and southern Sonora during the late 1930s, especially in areas lacking livestock. An upsurge in the livestock industry during the 1940s resulted in the development of ranches in areas previously not used for grazing (Ligon 1952). Subsequent visits by Ligon during the 1950s indicated that areas where masked bobwhites had once been abundant now were devoid of them (Ligon 1952). As in Arizona, excessive grazing and extended drought conditions had converted former suitable habitat in Sonora into unsuitable landscapes.

The current distribution and population size of masked bobwhites is unknown. The last intensive and extensive search for masked bobwhites was conducted in Sonora during the late 1960s by Tomlinson (1972a). He used various methods (e.g., interviews with hundreds of Mexican ranchmen, field searches both with and without bird dogs, and auditory surveys) to investigate leads of past occurrences. He concluded that masked bobwhites persisted in only 2 known areas in México, a population estimated at 1,000 birds near the town of Benjamin Hill and a very small population near Mazatán, which disappeared during his study (R. E. Tomlinson, U.S. Fish & Wildlife Service [retired], personal communication), with no populations anywhere in the United States. The wild population near Benjamin Hill currently

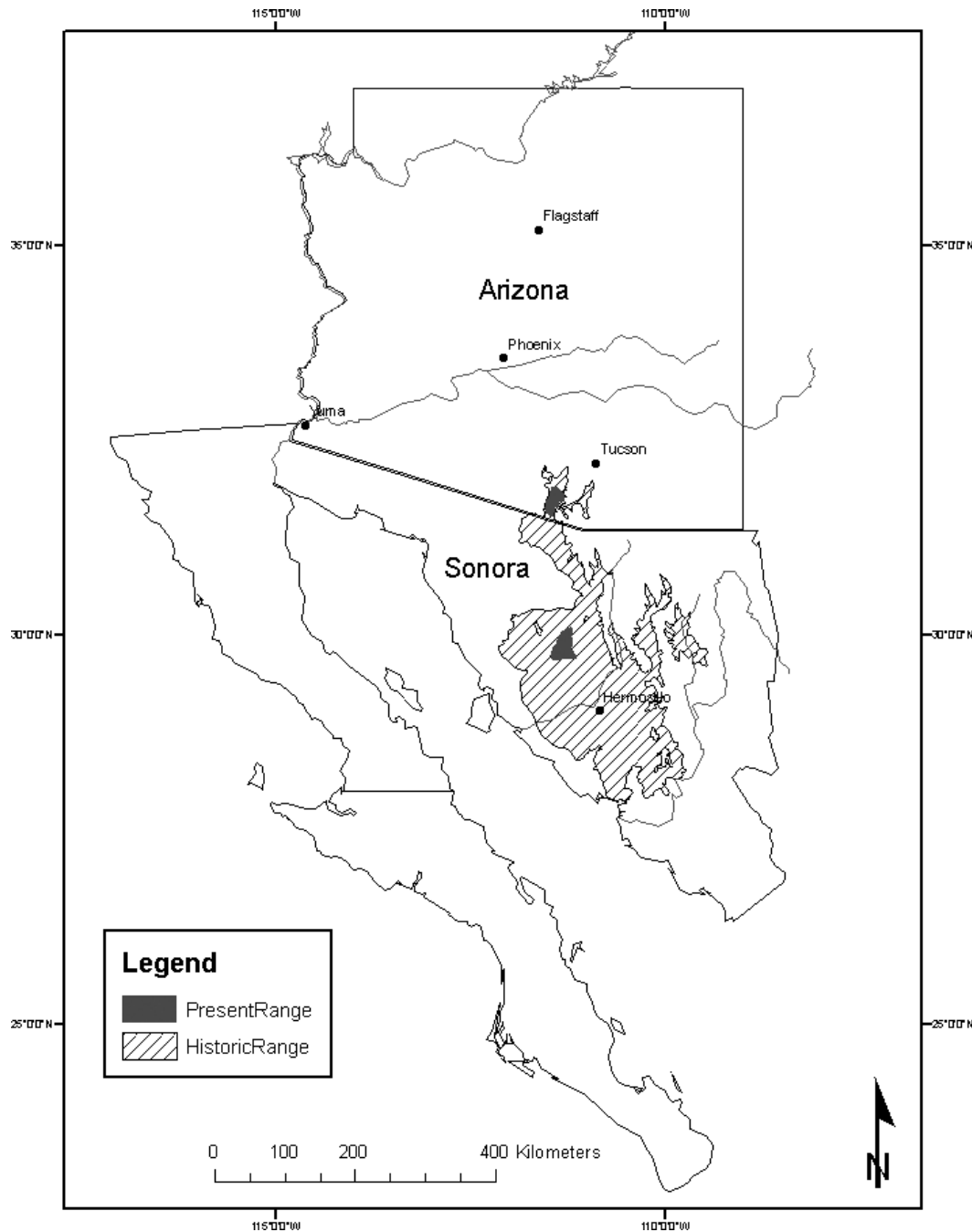


Figure 2. Historic and current distribution of masked bobwhites in North America. Distribution map modified from Brown and Ellis (1977).

persists in Sonora, but there is no information available regarding the Mazatán population. Carroll et al. (1994) estimated the population near Benjamin Hill ranged between 1,200–1,500 individuals. In the United States, masked bobwhites are restricted to BANWR, where releases of wild and pen-reared masked bobwhites have occurred. Periodic sightings of masked bobwhites have occurred outside of the refuge.

Previous Recovery Efforts

Most recovery efforts for masked bobwhites have been focused in Arizona. These efforts have involved translocation of wild bobwhites from Sonora, release of captive-reared masked bobwhites, and release of captive-reared broods imprinted to

vasectomized Texas bobwhite males. Despite a recovery history spanning more than 70 years, the recovery effort for masked bobwhites has met with little success.

Translocation of wild masked bobwhites.—The first translocation attempt of masked bobwhites into the United States occurred in 1937 when 132 masked bobwhites were captured in Sonora and were released in Arizona and New Mexico. That same year, an additional 25 Sonoran birds were translocated to southern Arizona (Lawson 1951, Ligon 1952). Unfortunately, the grasslands in the Altar Valley of Arizona, the historic range of masked bobwhites in the United States, were in such poor condition that releases had to be conducted outside of their historic range

(Arrington 1942). These translocation efforts proved unsuccessful. Numerous other translocation attempts occurred during the next 50 years with no apparent success (Brown and Ellis 1977). The last translocation was conducted in 1999, when 37 masked bobwhites were captured in Sonora and released on the central portion of BANWR. Verified sightings of masked bobwhites have occurred annually in the vicinity of the release site since 1999. Moreover, unbanded masked bobwhites have been observed and live-trapped on BANWR, suggesting that natural reproduction has occurred.

Release of captive-reared masked bobwhites.—The passage of the Endangered Species Conservation Act in 1968 provided the U.S. Fish & Wildlife Service (USFWS) with a legal mandate to begin recovery efforts for masked bobwhites. During the late 1960s, a captive population was established at the Patuxent Wildlife Research Center (Laurel, Md., USA) with almost 60 masked bobwhites trapped in Sonora (R. E. Tomlinson, U.S. Fish & Wildlife Service [retired], personal communication). The captive population was established, in part, as an insurance measure against extinction should the wild populations in Sonora become extirpated and to provide a source of masked bobwhites for future releases. Between 1971 and 1978, more than 7,000 captive-reared masked bobwhites were released in various locations throughout their historic range on private, state, and federal land leased by USFWS (U.S. Fish & Wildlife Service 1995). However, released birds were in poor physical condition and not bred for wild environments. In an effort to better-prepare captive-reared birds for life in the wild, a screening program and 2 soft-release techniques were implemented to produce hardier birds. Release attempts included modifications of the call-box conditioning program (Hardy and McConnell 1967) and the foster-parent adoption method (Stoddard 1931, Hart 1933). In addition, USFWS began to compensate ranchers for removing livestock from pastures that had been leased for masked bobwhite restoration. Modifications of release protocol and improved habitat conditions on release pastures succeeded temporarily in establishing a population on the Buenos Aires Ranch. A pair of masked bobwhites was observed with a brood in 1977, and several dozen masked bobwhites survived successive winters between 1977 and 1979 (Goodwin 1982). Unfortunately, masked bobwhite numbers on the release areas declined substantially during the early 1980s, presumably because habitat conditions deteriorated due to drought and resumption of grazing. By 1984, only 9 masked bobwhites were observed on the Buenos Aires Ranch (Ough and deVos 1984). It was this initial success on state and private lands with limited grazing that provided the impetus to purchase property for a National Wildlife Refuge.

When BANWR was established in 1985, refuge management determined that masked bobwhite recovery could best be accomplished by continuing the foster-parent adoption method that led to establishing the short-lived masked bobwhite population in the late 1970s. Consequently, almost 20,000 captive-reared masked bobwhite chicks were released with several hundred sterilized Texas bobwhite males between 1986 and 1994 (Gall et al. 2000). Despite these massive releases, annual surveys indicated poor survival. Refuge management initiated habitat improvements as a means of improving postrelease survival. An

intensive, prescribed burning program was implemented in 1988. For several years thereafter, masked bobwhites were observed on the refuge and, on multiple occasions, unbanded masked bobwhites were live-trapped, indicating that natural reproduction was occurring. However, despite the aggressive, prescribed burning program, annual surveys revealed that masked bobwhites still were not established on BANWR (Kuvlesky et al. 2000).

Because of limited success, refuge biologists continued revisions of release protocol in an adaptive manner beginning in 1995 (Gall et al. 2000). These revisions called for more intensive and prolonged prerelease conditioning methods and, eventually, for the suspension of the foster-parent program. The use of Texas bobwhite males as foster parents was no longer recommended because of its high cost, the potential for disease transmission, and the threat of hybridization (Kuvlesky et al. 2000). Further, on several occasions, Texas males were observed paired with masked bobwhite hens during the breeding season. Even if progeny were not produced from these pairings, masked bobwhite hens were being removed from the breeding population (Kuvlesky et al. 2000).

As of 2005, BANWR suspended the release of captive-reared masked bobwhites in an attempt to critically evaluate the efficiency and effectiveness of the program. It is not clear whether, when, or how the propagation-and-release program will be reinstated.

Ecology and Life History

General Life History

To our knowledge, there is only one published study that documents general life history of wild masked bobwhites (Tomlinson 1972a). The available information suggests that masked bobwhites exhibit a life history very similar to that of eastern races, only somewhat modified to reflect the conditions of their more arid environment (Grinnell 1884, Brewster 1887, Tomlinson 1972a). Average annual rainfall within the geographic distribution of masked bobwhites ranges between 26 cm (Sonora) and 42 cm (Altar Valley, Ariz., USA), with about 75% occurring during the summer (Jul–Sep; Tomlinson 1984, Camou et al. 1998). Thus, masked bobwhites have evolved to inhabit a semiarid environment, with a pronounced seasonal peak in precipitation, and their life history reflects such evolution (Brown 1989).

The actual beginning of the breeding season appears to differ between native populations in Sonora and reintroduced populations in Arizona. Tomlinson (1972a) reported that masked bobwhites remained in coveys in Sonora until late June, whereas pairs have been observed at BANWR in March–May (Simms 1989, M. Hunnicutt, U.S. Fish and Wildlife Service, Sasabe, Ariz., USA, personal communication). This discrepancy in timing of pairing might be due to differences in behavior (native vs. reintroduced), precipitation amount (26 cm vs. 42 cm), year (1972 vs. 1989), or other factors. In Sonora, Tomlinson (1972a) noted that masked bobwhites did not begin their breeding season until July, coincident with summer precipitation. He documented that calling activity by breeding males began only after minimum daily temperatures and relative humidity reached 13°C and 25%, respectively. Thus, calling generally began during 25 June–15 July and terminated during 14–20 September. Camou et al. (1998)

subsequently analyzed the data reported by Tomlinson (1972a) and determined that calling activity by males peaked on 19 August, with >90% of peak calling occurring during 9–28 August.

Tomlinson (1972a) estimated that initial nest incubation began during mid-August, based on the fact that peak hatching occurred during the middle of September. However, when using the backdating technique of juvenile molts as described by Petrides and Nestler (1943), he concluded that hatching began in late July, peaked during 5–20 September, and terminated during late October or early November (Tomlinson 1972a). His field observations of first broods during late September supported this general timeline. These observations suggest the breeding season of masked bobwhites is short, with calling and nesting activity lasting only about 70 and 90 days, respectively (Tomlinson 1972a).

Simms (1989) provides the only published study regarding home-range size and the movements of masked bobwhites (reintroduced). Home ranges for reintroduced masked bobwhites in Arizona averaged 10.9 ha, with a mean size of 10.0 ha during breeding season (mid-May to early Oct) and 11.4 ha during the nonbreeding season (mid-Oct to early May). Straight-line distances between release locations and sites of first trapping averaged 3.1 km (range: 64 m–23.7 km). Masked bobwhites ($n = 32$) generally exhibited short-distance movements: 72% moved <1 km between their release site and the center of their home range, 33% moved between 1.5 and 4.0 km, and 6% moved >10 km. Simms (1989) hypothesized that long-distance movements could result from either inadequate habitat conditions at certain release locations or social behavior. She did not have data to evaluate her habitat hypothesis; however, she did document that masked bobwhites visited captive-bobwhite facilities that were up to 24 km away on several occasions. Simms (1989) speculated that long-distance movements of masked bobwhites were related to the low population density on her study site.

Habitat Ecology

Information regarding the habitat ecology of masked bobwhites can be grouped into 2 broad categories that are temporally separated by more than 50 years: numerous descriptive accounts during the early 1900s, followed by a limited number of quantitative studies toward the end of the 20th century. As a result, there is still a dearth of information regarding the specific habitat needs of masked bobwhites (e.g., important food plants, nesting and loafing substrates). However, as noted above in the Life History section, the available information suggests that the general habitat requirements of masked bobwhites are similar to that of the well-studied *C. virginianus*, a point noted by Brewster (1887) and Guthery et al. (2001b).

Descriptive accounts.—The early literature abounds with anecdotal and descriptive accounts of masked bobwhite habitat based on observations at collection sites or field encounters. From these early descriptions, several habitat components emerge as common features of masked bobwhite habitat: level terrain, moderate elevation, abundant grass cover, interspersed woody cover, and abundant seed-producing plants.

Masked bobwhites generally have been associated with grassy river bottoms and broad level plains (Brown and Ellis 1977). Herbert Brown described the masked bobwhite as a bird inhabiting mesas, valleys, and foothills of mountains (Grinnell

1884) but not brushy canyons (Brown 1885). Van Rossem (1945) supported this observation, stating that masked bobwhites favored grass plains, river valleys, and foothills in the lower Sonoran zone. Based on these early descriptions, Tomlinson (1972a,b) surmised that optimum habitat for masked bobwhites consisted of desert grasslands found at moderate elevations (240–760 m).

Regarding specific habitat components, early descriptions noted the importance of robust herbaceous cover, woody cover, and food plants (forbs) for masked bobwhites. Stephens (1885:227) stated that masked bobwhites in the Altar Valley were found, “in the best grass we saw on the route.” Ligon (1952:48) added, “This quail is definitely a dweller of deep-grass-weed habitat, a type of cover incompatible with heavy use by livestock.” Subsequent observations further emphasized the importance of dense stands of grasses as a key component of masked bobwhite habitat (Phillips et al. 1964, Gallizioli et al. 1967). Tomlinson (1972b) observed that robust grasses like sacaton (*Sporobolus* sp.) were used for protective cover, whereas areas with sparser grasses such as gramas (*Bouteloua* spp.) were preferred for foraging. Sacaton generally was found in the sandy bottomlands, whereas grama grasses dominated the surrounding plains where bobwhite densities were highest (Tomlinson 1972b).

Brush cover was also noted as an important component of masked bobwhite habitat by early biologists. Tomlinson (1972b:10) stated, “There is a tacit understanding . . . that open grasslands with adjoining brushy areas were preferred by masked bobwhites.” Tomlinson (1984) observed that use of woody cover by masked bobwhites varied by season. Grasslands were used often by breeding masked bobwhites during the summer, but shrublands received greater use during winter. In Sonora, masked bobwhites were most abundant along areas where brush cover and grasslands abutted (Tomlinson 1972a). Thus, Tomlinson (1984) concluded that grasslands had to be surrounded and intersected by brushlands to represent suitable habitat for masked bobwhites.

The remaining component of masked bobwhite habitat that emerges from early habitat descriptions is the abundance of forbs. Brewster (1887:160) noted that birds collected in northeastern Sonora, “were haunting patches of weeds in gardens and barren sand wastes, where they fed on the seeds . . .” Tomlinson (1972a) noticed that masked bobwhites preferred areas with weedy growths contained within stands of moderately dense grasses such as gramas and three-awns (*Aristida* spp.). Early diet studies provided more specific information regarding important food plants. An analysis of the stomach contents of 3 masked bobwhites collected in Arizona indicated a diet of seeds, mast, insects, and green vegetation (Bendire 1892). Cottam and Knappen (1939) reported a diet consisting of 79.1% and 20.1% plant and animal material, respectively, based on the stomach contents of 10 masked bobwhites collected in Sonora. They reported seeds from a variety of plants including acacia (*Acacia angustissima*), ground cherry (*Physalis* spp.), panic grasses (*Panicum* spp.), day flower (*Commelina elegans*), and partridge pea (*Cassia leptadenia*). Animal material consisted primarily of grasshoppers (Orthoptera). Tomlinson (1984) concluded that an abundance of seed-producing plants such as legumes and panic grasses, in conjunction with an abundance of insects, was an important habitat component for masked bobwhites.

Quantitative studies.—The Goodwin and Hungerford (1977) report represents one of the first studies to quantify habitat for masked bobwhites. Their study evaluated habitat for reintroduced masked bobwhites that occurred sympatrically with Gambel's (*Callipepla gambelii*) and scaled quail (*C. squamata*) in the Altar Valley. Unfortunately, they reported few quantitative data for masked bobwhites and broadly characterized habitat as consisting of dense vegetation (75–100% ground cover), excellent plant diversity, and abundant insects. Reichenbacher and Mills (1984) provided more specific attributes of suitable habitat for masked bobwhites based on discussions with Goodwin. They described suitable habitat as 10–15% woody cover, 12–15% grass cover, and 10–12% forb cover, with at least 450 kg/ha of grass standing crop, 300 kg/ha of forb standing crop, and 20 grass and forb species. Similar requirements were reported by Simms (1989) for radio-marked masked bobwhites that had been reintroduced into Arizona. She characterized habitat for masked bobwhites as consisting of 10% canopy cover of woody plants, 50% canopy cover of grass, and 15% canopy cover of forbs. Adequate diversity of grasses and forbs consisted of at least 10 species each.

Despite these initial studies, much remained unknown regarding habitat ecology of masked bobwhite until the latter part of the 20th century, when a series of studies were initiated to address this void (Guthery et al. 2000, Guthery et al. 2001a,b). Guthery et al. (2000) compared the habitat ecology of Texas bobwhites and masked bobwhites in Arizona and Sonora. Their results indicated a high degree of commonality for screening cover, operative temperature (measure of temperature experienced by an organism; Goldstein 1984, Bakken 1992), and exposure to aerial predators across all sites, suggesting these habitat features were important in habitat-use decisions by bobwhites. Bobwhites in all areas used patches with higher canopy coverage of woody plants than was randomly available; however, the domain of selection was broader in Texas and Arizona (20–100% coverage) than in Sonora (9–46% coverage). Similarly, mean operative temperature was lower at used points than at random points for all sites. Bobwhites selected points that were <39°C in Texas (Forrester et al. 1998), <32°C in Sonora, and <29°C in Arizona. However, masked bobwhites selected for higher canopy coverage of herbaceous vegetation in Sonora (34–100%) and Arizona (17–100%) than bobwhites in Texas (0–30%). Guthery et al. (2000) concluded, therefore, that general aspects of the habitat ecology of Texas bobwhites transferred to masked bobwhites given the habitat commonalities observed between all sites. Habitat management for masked bobwhites, however, needed to focus more on herbaceous cover.

The study of Guthery et al. (2000) evaluated masked bobwhite from a univariate perspective that did not address how habitat features could interact to influence habitat-use decisions. In a follow-up study, Guthery et al. (2001b) conducted a multivariate analysis using the previously collected data to understand the multidimensionality of habitat space. They used neural-network models with 5 input variables (percentage of woody cover, percentage of bare ground, exposure to ground predators, exposure to aerial predators, and operative temperature) to discriminate between used and random patches. Their findings suggested that native masked bobwhites from Sonora were adapted to a broader

range of conditions than reintroduced bobwhites in Arizona. Guthery et al. (2001b) also documented that an acceptable range for a particular habitat feature was influenced by other habitat features (i.e., existence of a multidimensional habitat-space interaction). For example, in Sonora, the acceptable range for canopy coverage of woody vegetation was broad (0–60%) when all other habitat features were at acceptable values. However, as other habitat values trended away from optima, the acceptable range for canopy coverage of woody vegetation constricted (15–40%). Guthery et al. (2001b) hypothesized that masked bobwhites were less sensitive to any particular habitat feature when other habitat features were closer to their acceptable values. Thus, management conceivably could address a deficiency in one habitat feature by managing other variables, without addressing the deficiency per se (Guthery et al. 2001b).

Interspecific competition.—A habitat-ecology concern that existed for masked bobwhite recovery was the possibility of interspecific competition between sympatric masked bobwhite, Gambel's quail, and scaled quail. Goodwin and Hungerford (1977) reported that there was no indication of interspecific competition between the 3 species from either a habitat or social perspective. The 3 species preferred rather distinct vegetation types. Gambel's quail were closely associated with dense stands of tall (>2 m) woody plants found along sandy washes and did not appear sensitive to a lack of dense understory cover. In contrast, scaled quail were associated with areas containing sparse grass-forb cover and scattered, low-growing (<2 m) shrubs. Scaled quail, therefore, avoided the tall, dense growth favored by Gambel's quail and the lovegrass-grama grass flats used by masked bobwhites.

Subsequent research by Guthery et al. (2001b) supported this general finding of species-specific habitat partitioning. Even though all 3 quail used habitat patches that reduced their risk to predation and hyperthermia, thereby creating potential for interference competition, each species used different structural properties of the habitat to meet their risk-avoidance needs. Masked bobwhites reduced risks by using patches with relatively high canopy coverage of woody and herbaceous vegetation. Gambel's quail minimized risks also by using patches with high canopy coverage of woody vegetation but used lower amounts of herbaceous cover than the 2 other species. Scaled quail used habitat patches with low cover consisting of herbaceous vegetation and half-shrubs. This partitioning in habitat structure led to an important management implication: addition of woody cover to scaled quail habitat created Gambel's quail habitat, whereas addition of herbaceous cover to Gambel's quail habitat created bobwhite habitat (Guthery et al. 2001b).

Regarding social interactions, Goodwin and Hungerford (1977) never documented any interspecific aggression between the 3 quails. In fact, on one occasion, all 3 species were observed underneath a loafing shrub with no apparent social aggression.

Population and Landscape Challenges Facing Masked Bobwhite Recovery

The evolution of masked bobwhites in a semiarid environment and the alteration of their natural habitat hamper species recovery. Masked bobwhites are adapted to hot, semiarid grasslands

characterized by pronounced precipitation peaks that occur during late summer. As a result, they typically initiate breeding much later in the year (Jun) and experience a much shorter breeding season (90 days) compared with their eastern counterparts (Mar and 150 days, respectively), life history modifications that can result in serious demographic consequences for the subspecies. Further, landscapes have changed since the time when masked bobwhites prospered. Lehmann lovegrass (*Eragrostis lehmanniana*), a nonnative grass, dominates large expanses of the landscape within the historic distribution of masked bobwhites in Arizona (Anable et al. 1992). In Sonora, expansion of woody plants and establishment of nonnative buffel grass (*Cenchrus ciliaris*) have altered the former habitat. In addition, the apparent isolation of existing populations may pose challenges to the genetic welfare of the species. We elaborate below on the implications of these challenges on masked bobwhite recovery efforts.

Population Challenges

Reproduction.—It has been recognized for many years that quail species inhabiting southwestern rangelands are strongly influenced by precipitation, increasing during relatively wet periods and decreasing during drought (Swank and Gallizioli 1954, Kiel 1976, Brown et al. 1978). More recently, heat stress has also been proposed as a potential factor influencing quail population dynamics (Heffelfinger et al. 1999, Guthery et al. 2001c). Understanding how low precipitation and high temperatures may influence the population dynamics of masked bobwhites is critical for recovery of the species.

The relationship between quail abundance and timing and the amount of precipitation has been documented in 5 of the 6 quail species that occur in the United States: California quail (*Callipepla californica*; Francis 1970), Gambel's quail (Heffelfinger et al. 1999), scaled quail (Campbell et al. 1973), Montezuma quail (*Cyrtonyx montezumae*; Brown 1989), and northern bobwhites (Kiel 1976). Thus, it is reasonable to expect that timing and amount of precipitation also influence masked bobwhite populations, but how and to what extent remains unknown.

Hernández et al. (2005) reported that Texas bobwhites experienced lower survival and reproductive effort during drought (<51 cm precipitation). They documented a lower proportion of nesting hens (53%), lower nesting rates (1.2 nests/hen), and lower productivity (69% juvenile in fall harvest) during drought compared with a wet period (100%, 2.3 nests/hen, and 78%, respectively). The desert grasslands inhabited by masked bobwhites generally receive low amounts (<35 cm) of annual precipitation (Tomlinson 1972a, Camou et al. 1998). Camou et al. (1998) documented that masked bobwhite populations increased in 11 of 13 years when mean summer precipitation was >20 cm, but populations declined in 13 of 14 years when mean summer precipitation was <20 cm. Tomlinson (1972a) and Goodwin and Hungerford 1977) also noted that masked bobwhites did not initiate breeding until relative humidity was high (>25%), a condition that correlated with summer precipitation. Thus, if masked bobwhites respond to arid conditions in a manner similar to that reported by Hernández et al. (2005), then the desert climate could be limiting masked bobwhite reproduction and represents a serious challenge to

recovery from a demographic standpoint (Guthery and Kuvlesky 1998).

Heat can also detrimentally impact quail populations. Extremely hot temperatures can limit bobwhite reproduction by reducing egg fertility or production (Lehmann 1946:115–116, Roseberry and Klimstra 1984:76), shortening the length of the nesting season (Klimstra and Roseberry 1975, Guthery et al. 1988), and reducing the amount of thermally suitable habitat (Guthery et al. 2001c). Guthery et al. (1988) reported evidence that heat reduced the proportion of bobwhite hens that were laying and males that were producing sperm. They also documented a shorter breeding period for bobwhites in southwestern Texas compared with the more mesic southeastern region (3 vs. 5 months, respectively). They attributed these findings to the higher temperatures and evaporation rates in southwestern Texas. Summer temperatures in Sonora commonly reached 38–42°C and did not fall below 38°C until summer rains (Tomlinson 1972a). In that region, masked bobwhites exhibited a shorter nesting season compared with the eastern races, an adaptation possibly resulting from the arid environment inhabited by the subspecies. This shortened nesting season can limit masked bobwhites' capacity for reneating and increase their susceptibility to reproductive failure, demographic consequences that could result in chronic low productivity.

The negative impacts of drought on bobwhite reproduction may increase the limiting influence of other population processes (e.g., predation) as well. Generally speaking, galliformes experience low success (<30%) of individual nests (Wadsworth and McCabe 1996). However, populations are able to sustain such high nest-depredation rates because reneating results in a higher overall hen success (Guthery 1996). Masked bobwhite populations may not be able to mediate a high incidence of nest depredation if their short nesting season limits their capacity for reneating. Rosene (1969) reported that bobwhites required about 47–55 days to lay and incubate their first clutch. Moreover, Burger et al. (1995) documented that bobwhites required 20–34 days between nesting attempts. Thus, a complete nesting cycle (i.e., from first nest to start of second) would require about 65–89 days, thereby making the completion of a second nest difficult for masked bobwhites given their 90-day nesting season. Adding to that, the possibility that a prolonged drought or heat wave could further restrict the already short breeding period, it is not difficult to comprehend the severity of the demographic consequences associated with living in a hot, arid environment.

It is unknown to what degree the desert climate of Arizona and Sonora negatively impacts masked bobwhite populations. Perhaps masked bobwhites never were as abundant or as extensive (Ligon 1952) as cited in early accounts, or perhaps the habitat conditions that existed when masked bobwhites prospered mediated the impacts of a desert climate. In any case, recognizing that climate (i.e., aridity and heat) influences masked bobwhite populations will help to align recovery goals with realistic demographic expectations. Further, such an acknowledgment emphasizes the crucial role that habitat management plays in recovery of the species via creation or maintenance of usable space (Guthery 1997).

Population genetics.—Because of the lack of genetic studies in bobwhites, we only present broad unifying patterns of existing

data, and we develop general predictions regarding the effects habitat continuity and census size on the genetic diversity and viability of masked bobwhite populations.

Population genetics theory indicates that drastic fluctuations in census size, coupled with low individual dispersal rates, should result in a loss of population genetic variation due to genetic drift (Nei et al. 1975, Vucetich and Waite 1999). Given the population dynamics of the northern bobwhite, it is intuitive to expect that populations would be characterized by low within-population genetic diversity and a high degree of genetic structure among populations. The few available data do not support these face-value predictions. Although New World quails appear to be genetically structured on a regional geographic scale (Gutierrez et al. 1983, Nedbal et al. 1997, White et al. 2000), populations within regions are relatively unstructured (Zink et al. 1987, Ellsworth et al. 1989). Populations in these studies were genetically similar and had few private alleles indicating high gene flow (Zink et al. 1987, Ellsworth et al. 1989). The apparent lack of genetic structuring and the persistence of populations in the face of local extirpations suggest northern bobwhites possibly exist as some type of high-dispersal metapopulation. High-dispersal rates are necessary for species with high-turnover rates to ensure persistence of viable populations (Hastings and Harrison 1994). Such high dispersal among populations results in broad genetic similarity among subpopulations (Hastings and Harrison 1994, Harrison and Hastings 1996). As noted above, existing genetic data support this type of population structure, as do recent field data. Townsend et al. (2003) reported that 41% of radio-marked northern bobwhite in Oklahoma dispersed distances >2 km.

Given this hypothesized population structure, the spatial distribution of the estimated 1,000–2,000 masked bobwhites in Sonora becomes especially critical because the degree to which subpopulations of masked bobwhites are subject to the rescuing effects of dispersal (Martin et al. 2000) hinges upon their spatial distribution. In the absence of immigration, the severe annual fluctuations in census size of masked bobwhites will inevitably result in a low long-term average effective population size (Frankham 1995) and loss of genetic variation (Nei et al. 1975, Vucetich and Waite 1999). Reduction in genetic diversity has been documented for Texas bobwhites existing as fragmented populations (Nedbal et al. 1997). The loss of any population genetic diversity could be perilous for masked bobwhites because genetic variability, demography, individual fitness, and population viability are closely linked, although often in complex ways (Allendorf and Leary 1986, Hedrick and Miller 1992, Hedrick 2001, Spielman et al. 2004). One tangible symptom of reduced genetic diversity in avian species is decreased hatchability of eggs, which affects both population viability and rate of population recovery (Briskie and Mackintosh 2004). Naturally, this result would be disastrous for masked bobwhites.

We recognize the speculative nature of this section; however, by organizing the available information into a conceptual model of bobwhite population genetics, we were able to identify research topics warranting immediate attention for effective recovery planning (see below).

Landscape Challenges

The landscapes inhabited today by masked bobwhites are drastically different than those that occurred during the 19th century. Rangelands have been transformed from grasslands to shrublands (Archer 1994) and from native-plant ecosystems to nonnative-plant communities (Anable et al. 1992). The effect of these landscape alterations on masked bobwhite habitat has not been researched. We use available data to discuss the potential impacts that such landscape changes may have on masked bobwhite habitat.

Expansion of woody plants.—Many semiarid rangelands in North America that existed as grasslands during European settlement have been replaced by shrublands (Archer 1994). Research indicates that rates and patterns of this transition have been rapid (occurring over 100- to 200-year time spans), accentuated by periodic drought, influenced by topographic factors, and nonreversible over time frames relevant to management (Archer 1994). Many of the grasslands where masked bobwhites historically existed have experienced this increase in woody plant establishment. The net effect of this woody-plant establishment on masked bobwhite habitat depends on whether the resulting coverage lies within the bounds of habitat suitability for masked bobwhites.

Masked bobwhites use habitat patches with a higher canopy coverage of woody plants than is randomly available, selecting for about 10–45% brush coverage in Sonora and 20–100% in Arizona (Guthery et al. 2000). Given these suitability bounds, masked bobwhites in Arizona would be expected to be less sensitive to increases in brush canopy coverage than bobwhites in Sonora because they exhibit a broader domain of selection. The findings of Guthery et al. (2000) provide some support for this generalization.

Guthery et al. (2000) reported that the most severe habitat deficiency in Sonora was canopy coverage of woody vegetation, with about 48% of the habitat being lost because of a lack of woody plants. In Arizona, the greatest habitat deficiency was quantity of herbaceous cover, followed by operative temperature at 15 cm aboveground and canopy coverage of woody vegetation. Thus, the primary habitat deficiency of masked bobwhites, in general, was a condition resulting from increased exposure to aerial predators and unacceptably high operative temperatures at ground level, a condition that could be addressed by increasing the density of brush (within limits) and increasing the height and density of herbaceous cover (Guthery et al. 2000). Increases in canopy coverage of brush or a functional equivalent (e.g., tall, robust herbaceous cover), therefore, would increase the quantity of usable space (Guthery 1997) in Sonora and Arizona and, accordingly, increase populations of masked bobwhites (Guthery et al. 2000).

We surmise that the expansion of woody plants that has occurred over the past 100 years has not detrimentally impacted, generally speaking, habitat for masked bobwhites.

Nonnative plant establishment.—Nonnative grasses currently dominate millions of hectares of southwestern rangelands in the United States (Cable 1971, Holt 1985, Ibarra-F et al. 1995). Nonnative grasses have been documented to negatively impact grassland birds because they reduce species diversity of native-

plant communities and negatively impact insect populations (Cable 1971, Bock et al. 1986, Cox et al. 1988). Two nonnative grasses, buffelgrass and Lehmann lovegrass, have become established over wide areas within the historic range of masked bobwhites. In Sonora, buffelgrass was introduced to increase forage for cattle. In Arizona, Lehmann lovegrass was introduced to mitigate soil erosion as well as to provide forage for livestock. Both grasses now have become naturalized and occupy thousands of hectares within historic masked bobwhite habitat. The effect of nonnative grass establishment on habitat suitability of masked bobwhites is unknown.

Only one study has quantified the impact of nonnative grasses on northern bobwhites (Flanders et al. 2006). He documented that ground-foraging bird species in southern Texas were less abundant on study sites dominated by Lehmann lovegrass and buffelgrass compared with study sites dominated by native grasses. Bobwhite breeding densities were almost twice as high on sites dominated by native grasses (2.7 bobwhites/ha) compared with sites dominated by nonnative grasses (1.4 bobwhites/ha). Flanders et al. (2006) believed that ground-foraging birds were less abundant on nonnative study sites because food was limited due to the lower insect abundance and lower grass and forb diversity than was apparent on nonnative study sites.

Given this background, areas dominated by nonnative grasses generally are not considered suitable bobwhite habitat because they are associated with lower plant diversity and insect abundance (Bock et al. 1986), as well as lower seed-germination rates of important seed-producing plants for bobwhites (Nurdin and Fulbright 1990). In addition, movement of masked bobwhites is restricted in dense vegetation, a condition associated with monocultures of buffelgrass. If this phenomenon is indeed occurring within the range of masked bobwhites, then non-native-grass establishment could be impeding masked bobwhite recovery because fewer masked bobwhites are being supported on such areas. However, suitability of landscapes containing non-native grass species could depend on the nonnative species, the habitat attribute being considered, and the degree of dominance. For example, King (1998) reported that the number of masked bobwhite observations were similar between areas dominated by native vegetation and those containing Lehmann lovegrass. She noted that native vegetation was always nearby the patches of Lehmann lovegrass where masked bobwhites were found, thereby indicating a low degree of dominance. Kuvlesky et al. (2002) noted that masked bobwhites in Sonora commonly were found in pastures containing buffelgrass, particularly during drought, presumably because buffelgrass provided suitable escape and nesting cover. Guthery and Koerth (1992) also reported that bobwhite densities approached 5 birds/ha on pastures containing buffelgrass in southern Texas. In addition, both scaled quail and northern bobwhites have been observed in high abundance on Texas rangelands characterized by moderate stands of buffelgrass interspersed with native grasses, forbs, and open ground (F. Hernández, Caesar Kleberg Wildlife Research Institute, Kingsville, Tex., USA, personal observation).

We surmise that the impacts of nonnative grasses on masked bobwhite habitat range from detrimental under high-to-complete

dominance of nonnative grasses to suitable under low-to-moderate establishment.

Conservation Issues and Needs

The conservation history of masked bobwhite may be characterized as one with much conservation interest but with relatively little conservation progress. Tomlinson (1972b:1) wrote, "Although there has been considerable concern that the masked bobwhite would become extinct, little work (other than collecting) has been done on these birds. Therefore, few facts are known concerning the life history and natural ecology of the subspecies." It is surprising that >30 years since the publication of that statement, the quote still largely characterizes our knowledge of masked bobwhite and its conservation effort.

Our collective review of the literature identified 4 key conservation priorities that are necessary for restoring wild populations of masked bobwhites: international collaboration, population monitoring, habitat restoration, and genetic assessment.

International Collaboration

The extirpation of masked bobwhites in Arizona and the persistence of native populations in Sonora, the core range of the species, dictate that the future of masked bobwhites lies in conservation of the native populations in México. The intricacies associated with international collaboration, however, have clouded this realization. As a result, arguments both for and against the conservation of masked bobwhites in México have been postulated.

Russell (1984) argued that the greatest chances of recovery for a diminishing masked bobwhite population existed in the geographical areas where remnants of the population still persisted and not in reintroduction of masked bobwhites into areas where the species had not existed naturally for nearly 100 years. His disdain toward reintroduction of masked bobwhites into Arizona as the primary recovery focus centered on current habitat conditions not reflecting historic habitat conditions when masked bobwhites prospered during the 1800s. Further, Russell (1984) noted that general biological phenomena precluded the sole reliance on reintroduction. He argued that populations at the center of a species range generally represented contiguous populations of higher density and greater genetic variation compared with periphery populations, which were subject to substantial fluctuations in numbers (Mayr 1963). He posited that the biology of the species dictated that masked bobwhite recovery needed to focus on Sonora and that any success in reestablishing masked bobwhites in Arizona only represented short-term success.

Murrieta (1984) countered the arguments presented by Russell (1984). Murrieta (1984) noted that responsibility of endangered species in Sonora had transferred from the Ministry of Agriculture and Water Resources to the Ministry of Urban Development and Ecology. This transfer of agency responsibility had resulted in a mission shift from one of biological conservation to one of resource utilization, respectively. Although endangered species still fell within the responsibility of the new ministry, conservation priority was given to economically important fauna, such as desert bighorn (*Ovis canadensis*) and not masked bobwhite, for which there were no budgeted funds (Murrieta 1984). He further stated

that the Russell (1984) recommendation for the establishment of refuges in Sonora was not feasible because of insufficient land in Sonora to establish new sanctuaries. Moreover, previous refuges had been established on degraded habitat and were in need of restoration. Murrieta (1984:44) concluded, "There is little hope to offer in the foreseeable future for progress in conservation of the masked bobwhite in Mexico. If the masked bobwhite is to be saved, it is to be saved in the United States."

There is no doubt that masked bobwhite conservation involves complex international collaborations. Fortunately, there has been continued ecological interest in masked bobwhite conservation from Sonoran landowners where native populations of masked bobwhites persist. Further, recent discussions within a consortium of United States and Mexican biologists, agency personnel, and researchers have renewed and garnered interest for masked bobwhites. The Russell (1984:18–19) comment on masked bobwhite conservation captures the importance of international collaboration, "To admit defeat in negotiating with Mexico, to give up and flatly say that nothing can be done there, may well seal the fate of the masked bobwhite."

Population Monitoring

Call counts of breeding males (Bennitt 1951) have been conducted in Sonora since 1968 by various agency personnel (Tomlinson 1972a, Camou et al. 1998). However, these call counts have been restricted to the only site known to contain a wild population of masked bobwhites, a relatively small area (several thousand hectares) on a private ranch near Benjamin Hill, Sonora. There are 2 main limitations associated with the existing monitoring approach.

Restricting call counts to Benjamin Hill will not allow for detection of other potential populations. Numerous unsubstantiated reports exist of masked bobwhite sightings in other parts of Sonora. The need exists to initiate a coarse-scale reconnaissance throughout the historic range of masked bobwhites in Sonora to potentially locate other populations. A reconnaissance similar to that of Tomlinson (1972a) would aid in verification of these reports. Knowing of the existence, or lack thereof, of other wild populations in Sonora will have significant implications for prioritizing and implementing recovery efforts for masked bobwhites.

A second limitation with the existing monitoring approach is that call counts of breeding males only provide an index of the population (i.e., number of calling males/listening point). Because factors such as variability in observer hearing, habitat, and weather can affect detectability of calling birds, indices may not provide an accurate assessment of abundance (Anderson 2001, Hansen and Guthery 2001, Thompson 2002). Although information on a population's trend is valuable, an estimate of population size would provide a more accurate perspective of the actual status of masked bobwhites. We acknowledge that the low density of masked bobwhites complicates the application of certain density estimators such as mark-recapture (Seber 1982) or distance sampling (Buckland et al. 2001). Kuvlesky et al. (1989) reported that distance sampling yielded imprecise estimates (coefficient of variation >50%) of bobwhite density for low populations because few coveys were detected. At low densities, a greater total distance of transects was required to obtain sufficient observations for a

precise density estimation, an effort that rendered the technique impractical, given the required effort.

The use of helicopters to transverse transects for distance sampling may provide an effective alternative. Shupe et al. (1987) reported that helicopter transects yielded similar density estimates of northern bobwhite as those obtained via walking transects and mark-recapture methods. However, the reluctance-to-flush behavior exhibited by some masked bobwhites in response to approaching humans (B. Kuvlesky, Caesar Kleberg Wildlife Research Institute, Kingsville, Tex., USA, personal communication) and the expense of helicopter surveys may limit the effectiveness and feasibility of this technique.

Morning covey-call counts (Rosene 1969) represent another alternative. This technique has been used to estimate the density of northern bobwhite (Wellendorf et al. 2004). However, we are cautious about recommending this method because its underlying assumptions have been questioned (DeMaso et al. 1992).

Habitat Restoration

Guthery et al. (2000) documented that the primary habitat deficiency for masked bobwhites was inadequate herbaceous cover. Restoring habitat for masked bobwhites, however, will require more than mere management of livestock grazing pressure. Succession in semiarid landscapes may not follow a traditional Clementsian trajectory but rather a state-and-transition process (Westoby et al. 1989, Friedel 1991, Laycock 1991). Succession in a state-and-transition model is characterized by stable states of vegetation that persist over a range of environmental conditions and transitions between states that are triggered by disturbance. Prolonged and excessive grazing has been documented to cause semiarid rangelands to enter stable states in which simple removal of grazing may not result in habitat change or movement toward a climax community (Laycock 1991). Thus, sole management of livestock grazing pressure may not necessarily increase herbaceous cover for masked bobwhites. We believe actual habitat management will be required to restore masked bobwhite habitat. Guthery et al. (2000) recommended the use of mechanical treatments that fractured the soil surface and permitted water infiltration as a means of promoting herbaceous cover. They observed that discing and aeration improved the quantity and diversity of herbaceous cover in Sonora. Proper application of prescribed fire may also be an effective practice for creating vegetative conditions suitable for masked bobwhites (D. E. Brown, Arizona State University, personal communication). In any case, restoring wild populations of masked bobwhites will inevitably entail management of former habitat beyond mere management of grazing.

Genetic Conservation

The genetic conservation status of masked bobwhites cannot be answered at present. It is certain that masked bobwhites have experienced a severe range contraction and decline in census size during the past century. Therefore, serious concerns are warranted in terms of both short-term and long-term population viability. Genetic research is sorely needed.

Genetic studies of the current Sonoran population would aid in determining the level of fragmentation and gene flow among demes of the current wild population. Comparison with viable

populations of similar taxa, such as northern bobwhites, may be useful in understanding the importance of dispersal in bobwhite population dynamics and how the geographic size and distance among habitats influence rates of dispersal and gene flow. Genetic analysis of historic (museum) specimens throughout the range of masked bobwhite would aid in our understanding of historical levels of genetic variation so that the genetic data from current populations can be interpreted within the appropriate context, similar to the Bouzat et al. (1998) approach with prairie chickens. Finally, and perhaps most important, is the discovery or establishment of additional wild populations of masked bobwhite. The discovery or establishment of additional populations would not only buffer against loss of the sole known wild population, but it also might offer the possibility of genetic rescue (e.g., to alleviate the effects of inbreeding depression) through reciprocal transfers of birds among populations (Tallmon et al. 2004).

Future of Masked Bobwhites

What Needs to Be Done

We recommend 2 primary objectives if masked bobwhites are to be restored on both sides of the United States–México border and ultimately be removed from the Endangered Species list. First, we recommend a comprehensive assessment of the status of masked bobwhite populations and habitat. Information from a molecular genetics analysis of effective population size and minimum habitat area will be fundamental for understanding the viability of the Sonoran population. The same information needs to be obtained for the wild masked bobwhites that are apparently persisting at BANWR. In addition, we recommend that all potential masked bobwhite habitat be identified using landscape technology such as Geographic Information Systems (GIS). This exercise will highlight new areas where masked bobwhites could be present, thereby guiding reconnaissance efforts and providing an indication of the degree of habitat connectivity and, therefore, population isolation. Second, we recommend that active management (e.g., aerating, discing, and prescribed burning) of masked bobwhite habitat must occur, and those management actions must be implemented on as much area as possible. Although helpful, passive approaches to management (e.g., simple removal of grazing) will not restore, create, or maintain masked bobwhite habitat.

In addition to these immediate needs, other important issues must be addressed, namely, the future of the captive breeding program, the role of BANWR in recovery, and the use of conservation agreements and incentives.

Captive breeding program.—Efforts at using a captive breeding strategy to restore masked bobwhite populations have not been successful. The captive population at BANWR is plagued by disease, deformities, inbreeding, and numerous other maladies. Furthermore, efforts to release captive birds in the wild have drawn resources away from what could be more productive restoration efforts, by focusing on habitat, and working cooperatively with Arizona and Sonora ranchers to promote masked bobwhite conservation. Despite these sound arguments against the existence of a captive propagation program, we recognize the program cannot be dissolved because of legal mandates emanating from the Endangered Species Act. Therefore, we recommend that

captive propagation of masked bobwhites be outsourced to outside entities better suited for such activities, such as zoos. In this manner, BANWR personnel would be able to realign management and conservation priorities to focus on reestablishing a viable wild population and not raising and releasing captive-reared masked bobwhites.

BANWR.—Few endangered species have an entire refuge devoted to their conservation. The acquisition and establishment of BANWR was a significant first step toward the conservation of this species. The designation of BANWR for masked bobwhite recovery not only ensured a conservation focus but also made resources and land available for recovery. We note that a potential factor limiting the role of BANWR in masked bobwhite recovery is its location. The refuge is located on the northern fringe of the species' geographic range. Being located on the edge of a species' range can be somewhat problematic because populations in such locations can expand and contract in relation to weather and habitat conditions resulting in drastic population fluctuations. Northern bobwhites exhibit this phenomenon along the western fringe of their range in places such as Texas. However, bobwhite populations are able to persist and thrive in Texas because a critical mass of habitat remains available and because private landowners, not a national wildlife refuge, spearheaded conservation of northern bobwhite. Masked bobwhites at BANWR do not have these luxuries. Therefore, we propose the role of BANWR is to preserve and manage one of the largest expanses of habitat and sole population of masked bobwhites that exist in the United States and to actively coordinate conservation efforts between agency personnel, researchers, and landowners on behalf of the species.

Conservation agreements and incentives.—We contend that masked bobwhite recovery hinges upon involvement of private landowners and not acquisition of more land per se. The formation of BANWR was, and in some cases remains, unpopular with many ranchers in southern Arizona. As such, there is probably insufficient political will or capital to either expand BANWR or form another refuge for masked bobwhites in the United States or México. We propose that a more productive strategy would be to forge conservation agreements with private landowners and perhaps offer incentives for those who demonstrate viable masked bobwhite conservation efforts. This approach has been followed to a limited extent in Sonora but with much success. There is no doubt that private landowners have played a significant role in masked bobwhite recovery in México. We recommend such a model be expanded in México and be pursued as a means of garnering private landowner interest and support for masked bobwhite recovery in United States.

Dealing with Uncertainty

The future of the masked bobwhite is, like most endangered species, uncertain. It is unknown whether a viable population can be established at BANWR. The status of habitat and populations in the core area of their geographic range in Sonora also is uncertain.

Despite this uncertainty, there are several factors operating in favor of the masked bobwhite. As a galliform, it enjoys the status of a charismatic species that attracts the attention of birders and

game bird enthusiasts, even though it is unlikely to ever be hunted. In Sonora, there are landowners who have a deep appreciation for the *mascarita*, as it is affectionately called. These landowners manage grazing and other land uses with an eye on conserving masked bobwhite habitat. They do this based on their own motivation and priorities, not because of any law, regulation, or policy. Such a conservation ethic by the landowners in Sonora has probably saved the masked bobwhite from extinction. Such a conservation ethic by more landowners and ranchers in Arizona and México is essential for the restoration and conservation of masked bobwhites. Masked bobwhites do not recognize political boundaries; it is the people who are responsible for conserving the species who must ultimately overcome such barriers.

Literature Cited

- Aldrich, J. W. 1946. The United States races of bob-white. *Auk* 63:493–508.
- Allen, J. A. 1886a. The masked bob-white (*Colinus ridgwayi*) of Arizona, and its allies. *Bulletin of the American Museum of Natural History* 7:273–291.
- Allen, J. A. 1886b. The masked bob-white (*Colinus ridgwayi*) in Arizona. *Auk* 3: 275–276.
- Allen, J. A. 1886c. The type specimen of *Colinus ridgwayi*. *Auk* 3:483.
- Allen, J. A. 1887. A further note on *Colinus ridgwayi*. *Auk* 4:74–75.
- Allen, J. A. 1889. Note on the first plumage of *Colinus ridgwayi*. *Auk* 6:189.
- Allendorf, F. W., and R. F. Leary. 1986. Heterozygosity and fitness in natural populations of animals. Pages 57–76 in M. E. Soule, editor. *Conservation biology: the science of scarcity and diversity*. Sinauer, Sunderland, Massachusetts, USA.
- Anable, M. E., M. P. McClaran, and G. B. Ruyle. 1992. Spread of introduced Lehmann lovegrass (*Eragrostis lehmanniana* Nees) in southern Arizona. *Biological Conservation* 61:181–188.
- Anderson, D. R. 2001. The need to get the basics right in wildlife field studies. *Wildlife Society Bulletin* 29:1294–1297.
- Archer, S. 1994. Woody plant encroachment into southwestern grasslands and savannas: rates, patterns, and proximate causes. Pages 13–68 in M. Vavra, W. A. Laycock, and R. D. Pieper, editors. *Ecological implications of livestock herbivory in the west*. Society for Range Management, Denver, Colorado, USA.
- Arrington, O. N. 1942. A survey of possible refuge areas for masked bobwhite in the Arivaca and Altar Valleys. Arizona Game and Fish Commission Special Report Project 11D, Phoenix, USA.
- Bakken, G. S. 1992. Measurements and application of operative and standard operative temperatures in biology. *American Zoologist* 32:194–216.
- Banks, R. C. 1975. Plumage variation in the masked bobwhite. *Condor* 77: 486–487.
- Bendire, C. 1892. Life histories of North American birds. *Special Bulletin, U.S. National Museum* 3.
- Bennitt, R. 1951. Some aspects of Missouri quail and quail hunting 1938–1948. Missouri Conservation Commission, Technical Bulletin 2, Jefferson City, USA.
- Bock, C. E., J. H. Bock, K. L. Jepson, and J. C. Ortega. 1986. Ecological effects of planting African lovegrasses in Arizona. *National Geographic Research* 2:456–463.
- Boersma, P. D., and S. DeWeerd. 2001. Tapping the ivory tower: how academic–agency partnerships can advance conservation. *Conservation Biology in Practice* 2:28–32.
- Boersma, P. D., P. Kareiva, W. F. Fagan, J. A. Clark, and J. M. Hoekstra. 2001. How good are endangered species recovery plans? *BioScience* 51: 643–649.
- Bouzat, J. L., J. A. Lewin, and K. N. Paige. 1998. The ghost of genetic diversity past: historical DNA analysis of the greater prairie-chicken. *American Naturalist* 152:1–6.
- Brennan, L. A. 1999. Northern bobwhite (*Colinus virginianus*). Account 397 in A. Poole and F. Gill, editors. *The birds of North America*. Academy of Natural Sciences, Philadelphia, Pennsylvania, and American Ornithologists' Union, Washington, D.C., USA.
- Brewster, W. 1885. Additional notes on some birds collected in Arizona and the adjoining province of Sonora, Mexico, by Mr. F. Stephens in 1884; with a description of a new species of *Ortyx*. *Auk* 2:196–200.
- Brewster, W. 1887. Further notes on the masked bob-white (*Colinus ridgwayi*). *Auk* 4:159–160.
- Briskie, J. V., and M. Mackintosh. 2004. Hatching failure increases with severity of population bottlenecks in birds. *Proceedings of the National Academy of Sciences* 101:558–561.
- Brown, D. E. 1989. Arizona game birds. University of Arizona Press, Tucson, USA.
- Brown, D. E., and D. H. Ellis. 1977. Status summary and recovery plan for the masked bobwhite. U.S. Fish and Wildlife Service, Albuquerque, New Mexico, USA.
- Brown, D. E., C. L. Cochran, and T. E. Waddell. 1978. Using call-counts to predict hunting success for scaled quail. *Journal of Wildlife Management* 42: 281–287.
- Brown, H. 1884. *Ortyx virginianus* in Arizona. *Forest and Stream* 22:104.
- Brown, H. 1885. Arizona Quail notes. *Forest and Stream* 25:445.
- Brown, H. 1900. Conditions governing bird life in Arizona. *Auk* 17:31–34.
- Brown, H. 1904. Masked bob-white (*Colinus ridgwayi*). *Auk* 21:210–213.
- Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas. 2001. Introduction to distance sampling: estimating abundance of biological populations. Oxford University Press, New York, New York, USA.
- Burger, L. W., Jr., M. R. Ryan, T. V. Dailey, and E. W. Kurzejeski. 1995. Reproductive strategies, success, and mating systems of northern bobwhite in Missouri. *Journal of Wildlife Management* 59:417–426.
- Cable, D. R. 1971. Lehmann lovegrass on the Santa Rita Experimental Range, 1937–1968. *Journal of Range Management* 24:17–21.
- Camou, L. G., W. P. Kuvlesky, Jr., and F. S. Guthery. 1998. Rainfall and masked bobwhites in Sonora, Mexico. *USDA Forest Service Proceedings RMRS-R-5:253–260*.
- Campbell, H., D. K. Martin, P. E. Ferkovich, and B. K. Harris. 1973. Effects of hunting and some other environmental factors on scaled quail in New Mexico. *Wildlife Monographs* 34.
- Carroll, J. P., W. P. Kuvlesky, Jr., S. A. Gall, and F. G. Salazar. 1994. Status of Mexican quail. *Transactions of the North American Wildlife and Natural Resource Conference* 59:457–465.
- Clark, J. A., J. M. Hoekstra, P. D. Boersma, and P. Kareiva. 2002. Improving U.S. Endangered Species Act recovery plans: key findings and recommendations of the SCB recovery plan project. *Conservation Biology* 16: 1510–1519.
- Cottam, C., and P. Knappen. 1939. Foods of some uncommon North American birds. *Auk* 56:138–169.
- Cox, M. H., Martin-R, F. A. Ibarra-F, J. H. Fourie, N. F. G. Rethman, and D. G. Wilcox. 1988. The influence of climate and soils on the distribution of four African grasses. *Journal of Range Management* 41:127–139.
- DeMaso, S. J., F. S. Guthery, G. S. Spears, and S. M. Rice. 1992. Morning covey calls as an index of northern bobwhite density. *Wildlife Society Bulletin* 20:94–101.
- Ellsworth, D. L., J. L. Roseberry, and W. D. Klimstra. 1989. Genetic structure and gene flow in northern bobwhite. *Auk* 106:492–495.

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- Engel-Wilson, R., and W. P. Kuvlesky, Jr. 2002. Arizona quail: species in jeopardy? *Proceedings of the National Quail Symposium* 5:1–7.
- Flanders, A. A., W. P. Kuvlesky, Jr., D. C. Ruthven III, R. E. Zaiglin, R. L. Bingham, T. E. Fulbright, F. Hernández, and L. A. Brennan. 2006. Effects of invasive exotic grasses on south Texas rangeland breeding birds. *Auk* 123:171–182.
- Floyd, T. 2001. Complexity simplified (but who's paying attention?). *Ecology* 82:904–905.
- Foin, T. C., S. P. D. Riley, A. L. Pawley, D. R. Ayres, T. M. Carlsen, P. J. Hodum, and P. V. Switzer. 1998. Improving recovery planning for threatened and endangered species. *BioScience* 48:177–184.
- Forrester, N. D., F. S. Guthery, S. D. Kopp, and W. E. Cohen. 1998. Operative temperature reduces habitat space for northern bobwhites. *Journal of Wildlife Management* 62:1505–1510.
- Francis, W. J. 1970. The influence of weather on population fluctuations in California quail. *Journal of Wildlife Management* 34:249–266.
- Frankham, R. 1995. Conservation genetics. *Annual Review of Genetics* 29:305–327.
- Friedel, M. H. 1991. Range condition assessment and the concept of thresholds: a viewpoint. *Journal of Range Management* 44:422–426.
- Gall, S. A., W. P. Kuvlesky, Jr., G. Gee, J. C. Lewis, and D. Steinbach. 2000. Releasing captive-reared masked bobwhites: a new strategy. *National Quail Symposium* 4:147–152.
- Gallizioli, S., S. Levy, and J. Levy. 1967. Can the masked bobwhite be saved from extinction? *Audubon Field Notes* 2:571–575.
- Goldstein, D. L. 1984. The thermal environment and its constraint on activity of desert quail in summer. *Auk* 101:542–550.
- Goodwin, J. G. 1982. Habitat needs of masked bobwhite in Arizona. University of Arizona, contract report to U.S. Fish and Wildlife Service, Albuquerque, New Mexico, USA.
- Goodwin, J. G., Jr., and C. R. Hungerford. 1977. Habitat use by native Gambel's and scaled quail and released masked bobwhite quail in southern Arizona. USDA Forest Service Report, Research Paper RM-197, Fort Collins, Colorado, USA.
- Grinnell, G. B. 1884. A quail new to the United States fauna. *Forest and Stream* 12:243.
- Guthery, F. S. 1996. Coyotes and upland gamebirds. Pages 104–107 in D. Rollins, C. Richardson, T. Blankenship, K. Canon, and S. E. Henke, editors. *Coyotes in the southwest: a compendium of knowledge*. Texas Parks and Wildlife Department, San Angelo, USA.
- Guthery, F. S. 1997. A philosophy of habitat management for northern bobwhites. *Journal of Wildlife Management* 61:291–301.
- Guthery, F. S., and N. E. Koerth. 1992. Substandard water intake and inhibition of bobwhite reproduction during drought. *Journal of Wildlife Management* 56:760–768.
- Guthery, F. S., and W. P. Kuvlesky. 1998. The effect of multiple-brooding on age ratios of quail. *Journal of Wildlife Management* 62:540–549.
- Guthery, F. S., N. M. King, W. P. Kuvlesky, Jr., S. DeStefano, S. A. Gall, and N. J. Silvy. 2001a. Comparative habitat use by three quails in desert grassland. *Journal of Wildlife Management* 65:850–860.
- Guthery, F. S., N. M. King, K. R. Nolte, W. P. Kuvlesky, Jr., S. A. DeStefano, S. A. Gall, and N. J. Silvy. 2000. Comparative habitat ecology of Texas and masked bobwhites. *Journal of Wildlife Management* 64:407–420.
- Guthery, F. S., N. M. King, K. R. Nolte, W. P. Kuvlesky, Jr., S. A. DeStefano, S. A. GallNova, and J. Silvy. 2001b. Multivariate perspectives on patch use by masked bobwhites. *Journal of Wildlife Management* 65:118–124.
- Guthery, F. S., N. E. Koerth, and D. S. Smith. 1988. Reproduction of northern bobwhites in semiarid environments. *Journal of Wildlife Management* 52:144–149.
- Guthery, F. S., C. L. Land, and B. W. Hall. 2001c. Heat loads on reproducing bobwhites in the semiarid subtropics. *Journal of Wildlife Management* 65:111–117.
- Gutierrez, R. J., R. M. Zink, and S. Y. Yang. 1983. Genic variation, systematic, and biogeographic relationships of some galliform birds. *Auk* 100:33–47.
- Hansen, H. M., and F. S. Guthery. 2001. Calling behavior of bobwhite males and the call-count index. *Wildlife Society Bulletin* 29:145–152.
- Hardy, J. W., and C. A. McConnell. 1967. Bobwhite quail: propagation, conditioning, and habitat management. Tennessee Game and Fish Commission, Nashville, USA.
- Harrison, S., and A. Hastings. 1996. Genetic and evolutionary consequences of metapopulation structure. *Trends in Ecology and Evolution* 11:180–183.
- Hart, D. 1933. Stocking with day-old quail. *Game Breeder and Sportsman* 37:271–275.
- Hastings, A., and S. Harrison. 1994. Metapopulation dynamics and genetics. *Annual Review of Ecology and Systematics* 25:167–188.
- Hedrick, P. W. 2001. Conservation genetics: where are we now? *Trends in Ecology and Evolution* 16:629–636.
- Hedrick, P. W., and P. S. Miller. 1992. Conservation genetics: techniques and fundamentals. *Ecological Applications* 2:30–46.
- Heffelfinger, J. R., F. S. Guthery, R. J. Olding, C. L. Cochran, Jr., and C. M. McMullen. 1999. Influence of precipitation timing and summer temperatures on reproduction of Gambel's quail. *Journal of Wildlife Management* 63:154–161.
- Hernández, F., F. S. Guthery, and W. P. Kuvlesky, Jr. 2002. The legacy of bobwhite research in south Texas. *Journal of Wildlife Management* 66:1–18.
- Hernández, F., F. Hernández, J. A. Arredondo, F. C. Bryant, R. L. Bingham, and L. A. Brennan. 2005. Influence of precipitation on demographics of northern bobwhites in southern Texas. *Wildlife Society Bulletin* 33:1071–1079.
- Holt, E. C. 1985. Buffelgrass a brief history. Pages 1–3 in E. C. A. Runge and J. L. Schuster, editors. *Buffelgrass: adaptation, management, and forage quality symposium*. Texas Agriculture Experiment Station Report MP-1575, College Station, USA.
- Ibarra, F., A. Fernando, J. R. Cox, M. H. Martin-R., T. A. Crowl, and C. A. Call. 1995. Predicting Buffelgrass survival across a geographic and environmental gradient. *Journal of Range Management* 48:53–57.
- Johnsgard, P. A. 1988. The quails, partridges, and francolins of the world. Oxford University Press, New York, New York, USA.
- Kiel, W. H. 1976. Bobwhite quail population characteristics and management implications in south Texas. *Transactions of the North American Wildlife Conference* 41:407–420.
- King, N. M. 1998. Habitat use by endangered masked bobwhites and other quail on the Buenos Aires National Wildlife Refuge, Arizona. Thesis, University of Arizona, Tucson, USA.
- Klimstra, W. D., and J. L. Roseberry. 1975. Nesting ecology of the bobwhite in southern Illinois. *Wildlife Monograph* 41:1–37.
- Kuvlesky, W. P., Jr., T. E. Fulbright, and R. Engel-Wilson. 2002. The impact of invasive exotic grasses on quail in the southwestern United States. *Proceedings of the 5th National Quail Symposium* 5:118–128.
- Kuvlesky, W. P., Jr., S. A. Gall, S. J. Dobrott, S. Tolley, F. S. Guthery, S. A. DeStefano, N. King, K. R. Nolte, N. J. Silvy, J. C. Lewis, G. Gee, G. Camou Luders, and R. Engel-Wilson. 2000. The status of endangered masked bobwhite recovery in the United States and Mexico. *Proceedings of the National Quail Symposium* 4:42–57.
- Kuvlesky, W. P., B. H. Koerth, and N. J. Silvy. 1989. Problems of estimating northern bobwhite populations at low density. *Proceedings of the Annual Conference Southeast Association of Fish and Wildlife Agencies* 43:260–267.
- Lawson, L. L. 1951. Masked bobwhite and Benson quail trapping in Sonora, Mexico. Arizona Game and Fish Department Federal Aid Project W-40-R-2, Work Plan 2, Job 2, Completion Report, Phoenix, USA.
- Laycock, W. A. 1991. Stable states and thresholds of range condition on North American rangelands: a viewpoint. *Journal of Range Management* 44:247–432.
- Lehmann, V. W. 1946. Bobwhite quail reproduction in southwestern Texas. *Journal of Wildlife Management* 10:124–136.
- Ligon, J. S. 1952. The vanishing masked bobwhite. *Condor* 54:48–50.
- Martin, K., P. B. Stacey, and C. E. Braun. 2000. Recruitment, dispersal, and demographic rescue in spatially-structured white-tailed ptarmigan populations. *Condor* 102:503–516.
- Mayr, E. 1963. *Animal species and evolution*. Harvard University, Cambridge, Massachusetts, USA.
- Murrieta, X. 1984. Role of the Mexican government in protection and management of masked bobwhite in Sonora. Page 4 in Stromberg, M. R., T. B. Johnson, and S. W. Hoffman, editors. *Masked bobwhite biology and conservation: proceedings of a Symposium*. Arizona Game and Fish Department, Tucson, USA.
- Nedbal, M. A., R. L. Honeycutt, S. G. Evans, R. M. Whiting, Jr., and D. R. Dietz. 1997. Northern bobwhite restocking in east Texas: a genetic assessment. *Journal of Wildlife Management* 61:854–863.
- Nei, M., T. Maruyama, and R. Chakraborty. 1975. The bottleneck effect and genetic variability in populations. *Evolution* 29:1–10.

- Nurdin, and T. E. Fulbright. 1990. Germination of two legumes in leachate from introduced grasses. *Journal of Range Management* 43:466–467.
- Ough, W. D., and J. C. deVos, Jr. 1984. Masked bobwhite investigations on the Buenos Aires Ranch in 1982. Report to the U.S. Fish and Wildlife Service, Albuquerque, New Mexico, USA.
- Petrides, G. A., and R. B. Nestler. 1943. Age determination in juvenile bobwhite quail. *American Midland Naturalist* 30:774–782.
- Phillips, A., J. Marshall, and G. Monson. 1964. *The birds of Arizona*. University of Arizona Press, Tucson, USA.
- Reichenbacher, F. W., and G. S. Mills. 1984. Techniques for evaluating potential masked bobwhite habitat. Pages 29–31 in M. R. Stromberg, T. B. Johnson, and S. W. Hoffman, editors. *Masked bobwhite biology and conservation: Proceedings of a Symposium*. Arizona Game and Fish Department, Tucson, USA.
- Ridgway, R. 1884. *Ortyx virginianus* not in Arizona. *Forest and Stream* 22:124.
- Ridgway, R. 1886. Arizona quail. *Forest and Stream* 25:484.
- Roseberry, J. L., and W. D. Klimstra. 1984. Population ecology of the bobwhite. Southern Illinois University, Carbondale, USA.
- Rosene, W. 1969. The bobwhite quail—its life and management. Rutgers University, News Brunswick, New Jersey, USA.
- Russell, S. M. 1984. What price preservation? Pages 18–21 in M. R. Stromberg, T. B. Johnson, and S. W. Hoffman, editors. *Masked bobwhite biology and conservation: proceedings of a symposium*. Arizona Game and Fish Department, Tucson, USA.
- Scott, W. E. D. 1886. On the avi-fauna of Pinal County, with remarks on some birds of Pima and Gila counties, Arizona. *Auk* 3:383–389.
- Seber, G. A. F. 1982. *The estimation of animal abundance and related parameters*. Second edition. Blackburn, Griffin, London, United Kingdom.
- Shupe, T. E., F. S. Guthery, and S. L. Beasom. 1987. Use of helicopters to survey northern bobwhite populations on rangeland. *Wildlife Society Bulletin* 15:458–462.
- Simms, K. M. 1989. Home range, habitat use, and movements of reintroduced masked bobwhite. Thesis, University of Arizona, Tucson, USA.
- Spielman, D., B. W. Brook, and R. Frankham. 2004. Most species are not driven to extinction before genetic factors impact them. *Proceedings of the National Academy of Sciences* 101:15261–15264.
- Stephens, F. 1885. Notes of an ornithological trip in Arizona and Sonora. *Auk* 2:225–231.
- Stoddard, H. L. 1931. The bobwhite quail: its habits, preservation and increase. Charles Scribner's Sons, New York, New York, USA.
- Stromberg, M. R., T. B. Johnson, and S. W. Hoffman. 1984. Masked bobwhite biology and conservation: proceedings of a symposium. Arizona Game and Fish Department, Tucson, USA.
- Swank, W. G., and S. Gallizioli. 1954. The influence of hunting and of rainfall upon Gambel's quail populations. *Transactions of the North American Wildlife Conference* 19:283–297.
- Tallmon, D. A., G. Luikart, and R. S. Waples. 2004. The alluring simplicity and complex reality of genetic rescue. *Trends in Ecology and Evolution* 19:489–496.
- Taylor, M. F. J., K. F. Suckling, and J. J. Rachlinski. 2005. The effectiveness of the Endangered Species Act: a quantitative analysis. *BioScience* 55:360–367.
- Tear, T. H., J. M. Scott, P. H. Hayward, and B. Griffith. 1993. Status and prospects for success of the endangered Species Act: a look at recovery plans. *Science* 262:976–977.
- Tear, T. H., J. M. Scott, P. H. Hayward, and B. Griffith. 1995. Recovery plans and the Endangered Species Act: are criticisms supported by data? *Conservation Biology* 9:182–195.
- Thompson, W. L. 2002. Towards reliable bird surveys: accounting for individuals present but not detected. *Auk* 119:18–25.
- Tomlinson, R. E. 1972a. Current status of the endangered masked bobwhite quail. *Transactions of the North American Wildlife Conference* 37:294–311.
- Tomlinson, R. E. 1972b. Review of literature on the endangered masked bobwhite. U.S. Fish and Wildlife Service Resource Publication 108, Washington, D.C., USA.
- Tomlinson, R. E. 1984. Habitat needs of the masked bobwhite in Mexico. Pages 12–14 in M. R. Stromberg, T. B. Johnson, and S. W. Hoffman, editors. *Masked bobwhite biology and conservation: proceedings of a symposium*. Arizona Game and Fish Department, Tucson, USA.
- Townsend, D. E., D. M. Leslie, Jr., R. L. Lochmiller, S. J. DeMaso, S. A. Cox, and A. D. Peoples. 2003. Fitness costs and benefits associated with dispersal in northern bobwhites (*Colinus virginianus*). *American Midland Naturalist* 150:73–82.
- U.S. Fish and Wildlife Service. 1995. Masked bobwhite recovery plan. Second revision. Albuquerque, New Mexico, USA.
- Van Rossem, A. J. 1945. A distributional survey of the birds of Sonora, Mexico. *Occ. Papers Mus. Zool. Louisiana State University* 21:379.
- Vucetich, J. A., and T. A. Waite. 1999. Erosion of heterozygosity in fluctuating populations. *Conservation Biology* 13:860–868.
- Wadsworth, K. G., and R. E. McCabe. 1996. Issues and problems in predation management to enhance avian recruitment. Wildlife Management Institute, Washington, D.C., USA.
- Wellendorf, S. D., W. E. Palmer, and P. T. Bromley. 2004. Estimating calling rates of northern bobwhite coveys and measuring abundance. *Journal of Wildlife Management* 68:672–682.
- Westoby, M., B. Walker, and I. Noy-Meir. 1989. Opportunistic management for rangelands not at equilibrium. *Journal of Range Management* 42:266–274.
- White, S. L. 1995. Comparative anatomy of Texas and masked bobwhites. Thesis, Texas A&M University-Kingsville, Kingsville, USA.
- White, S. L., K. R. Nolte, W. P. Kuvlesky, Jr., and F. S. Guthery. 2000. Comparative morphology and phylogenetic relatedness among bobwhites in the southern United States and Mexico. *National Quail Symposium Proceedings* 4:111–114.
- Zink, R. M., D. F. Lott, and D. W. Anderson. 1987. Genetic variation, population structure, and evolution of California quail. *Condor* 89:395–405.

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