

FACTORS AFFECTING SURVIVAL AND RECRUITMENT IN FEMALE MERRIAM'S TURKEYS

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ABSTRACT

Merriam's turkeys (*Meleagris gallopavo merriami*) historically occurred in ponderosa pine (*Pinus ponderosa*) and Gambel's oak (*Quercus gambelli*) forests in the southwestern U.S. They have been successfully transplanted into a wide array of habitats outside their original range. Some introduced populations are more robust than those within the original range. Annual survival fluctuates widely, ranging from 30 to 76 percent for adults. Survival of subadult hens is typically lower than adults. Predation is the primary mortality factor and coyotes are the most common predator. Percent of females attempting to nest (nesting rates) ranges from ~30 to >90 percent for adults. Yearling females nest at lower rates, and within the historical range of Merriam's turkeys, nesting by yearling hens may be almost nonexistent. Management that would increase nesting by yearlings probably has the greatest potential to influence populations given the existing biological limitations to Merriam's turkeys. Nesting rates of adult and yearling hens is likely related to habitat quality or productivity, possibly nutrition-related. Since survival of poults is low, maintaining high-quality meadows with an abundant component of herbaceous vegetation and invertebrates might increase poult survival.

Key words: Merriam's turkeys, *Meleagris gallopavo merriami*, nesting, population characteristics, survival.

INTRODUCTION

Merriam's turkey (*Meleagris gallopavo merriami*) populations historically have experienced dramatic declines (Ligon 1946) and increases (Mosby 1975). Initial declines resulted from unregulated harvest, habitat degradation from timber and range management practices, and predation (Ligon 1946, MacDonald and Janzen 1967). Populations continue to fluctuate even in the presence of regulated timber harvest and improved land management practices. An understanding of the natural variation of vital rates among Merriam's turkey populations can provide resource managers with insight to a range of fluctuation expected, based on climate, harvest, and land management practices.

Historically, Merriam's turkeys were found in Colorado, New Mexico, Arizona,

and west Texas (Schorger 1966). Their distribution was generally concurrent with ponderosa pine (*Pinus ponderosa*) and oak (*Quercus* spp.) forests of the southwest (Ligon 1946, McDonald and Janzen 1967). The current range of Merriam's turkeys extends beyond the historical range (Bailey 1980, Kennamer and Kennamer 1996), and some transplants outside the historical range of Merriam's turkeys have been highly successful, e.g., particularly the release of Merriam's turkeys in the Black Hills of South Dakota. Between 1948 and 1951, 29 Merriam's turkeys (sex ratios unknown) from Colorado and New Mexico were released in the Black Hills (Petersen and Richardson 1975). By fall 1952, the wild turkey population in the Black Hills was estimated at 1000 birds, and by 1960 the population was estimated at 5000 to 7000

birds. Merriam's turkeys were not native to the North Kaibab Plateau, Arizona, and subsequent introductions resulted in robust populations (Wakeling and Goodwin 1999). Success of the Merriam's turkey in the Black Hills led to subsequent transplants throughout the region including the ponderosa pine hills and buttes and deciduous woodlands of northeastern Wyoming, southeastern Montana (Jonas 1966), and western South Dakota. Substantial populations now occur in plains cottonwood (*Populus deltoides*), bur oak (*Q. macrocarpa*), and green ash (*Fraxinus pennsylvanica*) prairie-woodlands, and the ponderosa pine-covered buttes throughout the northern Great Plains. Deciduous woodlands in prairie and high desert regions are usually associated with streams and mesic north to northeast slopes in steep topography such as river breaks or foothills. Currently, distribution of Merriam's turkeys includes all of the contiguous U.S. north and west of the historical range (Stangel et al. 1992).

Given the broad array of habitats that Merriam's turkeys occupy, a similarly broad array of vital rates are expected. Parameters affecting populations of Merriam's turkey vary spatially and temporally. We summarize the available literature on nesting and survival of Merriam's turkeys. Despite many studies of Merriam's turkey populations and habitat, comparable data on population parameters is lacking among many of these studies. We obtained sufficient data from Arizona ($n=201$, 1987-1991, Wakeling 1991), Montana ($n=74$, 1988-1992, Thompson 1993), and South Dakota ($n=119$, 1986-1992, unpubl. data, Rocky Mountain Research Station) to calculate Kaplan-Meier survival (Parmar and Machin 1995) estimates for these areas.

Terminology and methods for estimates of nest parameters are not consistent among papers. For example, some papers calculate nesting rates as

$$\frac{\text{nests found}}{\text{\# of hens}}$$

whereas others used localization of movements by hens as evidence for

initiation of a nest (e.g., Rumble and Hodorff 1993). Some papers calculate nest success as

$$\frac{\text{nests hatched}}{\text{nests found}}$$

although others calculate Mayfield (1975) nest survival rates. We refer readers to the original papers if methods for estimates are a concern. Here, we use nest success since it provides a slightly biased estimate of nest survival. The literature also does not clearly define terminology describing age of turkeys. We use "poults" for birds from hatching to fall, "subadults" for birds from fall up to the first nest season, and "yearlings" for birds in their first breeding season. At ~15 months of age, birds cannot be aged using plumage (Leopold 1943), and we refer to those birds as "adults." Hen success is defined as the proportion of hens that successfully hatch ≥ 1 egg during a nesting season (Cowardin et al. 1985). Where practical, we applied these terms when interpreting findings from other studies. For ease of comparison, we provide a summary of values used in our paper in Table 1.

Survival and Mortality

Merriam's turkeys are physiologically capable of being long-lived. The oldest marked female in Arizona survived for >8 years (B. F. Wakeling, pers. obs.). However, annual survival of female Merriam's turkeys varied spatially and temporally. Kaplan-Meier survival rates for all radio-marked birds adjusted from 1 January to 30 December were 68 percent in South Dakota, 57 percent in Arizona, and 45 percent in Montana. In South Dakota annual survival of female Merriam's turkeys ranged from 33 to 76 percent. Annual survival of subadult females in Arizona ranged from 20 percent to 65 percent, whereas that of adult females ranged from 84 to 100 percent (Wakeling 1991). We did not calculate survival rates for each year of the study in Montana because sufficient data were not available. Survival of subadult females varied more than other vital rates measured and

Table 1. List of population metrics referenced in the text and for Merriam’s turkeys that occur in the literature or in our data files.

Population metric	State ^{1,2}	Value ³
Annual survival		
♀ all ages	MT	45%
♀ all ages	SD	33-76% ($\bar{x}$ = 68%)
♀ all ages	AZ	57%
♀ subadult	AZ	20-65%
♀ adult survival	AZ	84-100%
Relative mortality accountable to predation		
	AZ, MT	80%
Coyotes	AZ	65%
Bobcat	AZ	13%
Avian	AZ	22%
Hunting	AZ	<10%
Fall harvest composition		
Adult ♀	AZ	30-40%
Hen mortality during nesting		
	SD (BH)	20%
	SD (C)	11%
Winter survival		
Subadult ♀	AZ	79%
Adult ♀	AZ	82%
Mortality during severe winter weather		
Subadult ♀ (Jan. – early Apr.)	AZ	90%
Subadult ♀ (<2 weeks after severe storm)	SD (BH)	100%
Adult ♀ (Jan. – early Apr.)	AZ	38%
Nesting rates		
Adult	SD (BH)	97%
Adult	SD (C)	77%
Adult	AZ	45%
Adult	CO (WC)	100%
Adult	CO (SC)	62%
Adult	NM (SE)	75%
Adult	NM (SC)	76%
Adult	OR	100%
Yearling	SD (BH)	73%
Yearling	SD (C)	17%
Yearling	AZ	0%
Yearling	CO (WC)	96%
Yearling	CO (SC)	8%
Yearling	NM (SC)	11%
Yearling	NM (SE)	8%
Yearling	OR	25%
Nest survival		
Adult	SD (BH)	36%
Adult ($n = 16$) and yearling ($n = 1$)	SD (C)	44%
Adult and yearling averaged	NM (SC)	31%
Adult and yearling averaged	NM (SE)	40%
Yearling	SD (BH)	23%
Renesting rate		
Adult	SD (C)	13%
Adult	AZ	18%
Adult	NM (SE)	35%
Adult	NM (SC)	27%

Table 1 (continued)

	Population metric	State ^{1,2}	Value ³
Renest survival	Adult (attempts/bird)	SD (BH)	1.18%
	Yearling (attempts/bird)	SD (BH)	0.57%
	Yearling	AZ	0%
	Yearling	NM (SE)	0%
	Second nest	SD (BH)	35%
	Third nest	SD (BH)	67%
	All renests	AZ	50%
	Adult	NM	35%
Hen success (% of hens that ultimately hatch ≥1 egg)			
	Yearling	SD (BH)	24%
	Yearling	MT	25%
	Yearling	NM (SE)	4%
	Adult	SD (BH)	48%
	Adult	MT	50%
	Adult	NM (SE)	37%
Relative cause of nest loss			
	Birds	SD (BH)	35%
	Mammals	SD (BH)	26%
	Mammals	SD (C)	86%
Poult mortality			
	2 weeks	MO	50-75%
	8 weeks	WY	64%
	Hen:poult ratio	SD (BH)	>40%
	Hen:poult ratio	AZ	41-65%
	8 weeks	SD (C)	57%
	Complete brood mortality	SD(C)	35%

¹ (C) = south central South Dakota, (BH) = Black Hills South Dakota, (SE) = southeast New Mexico, (SC) = south central New Mexico.

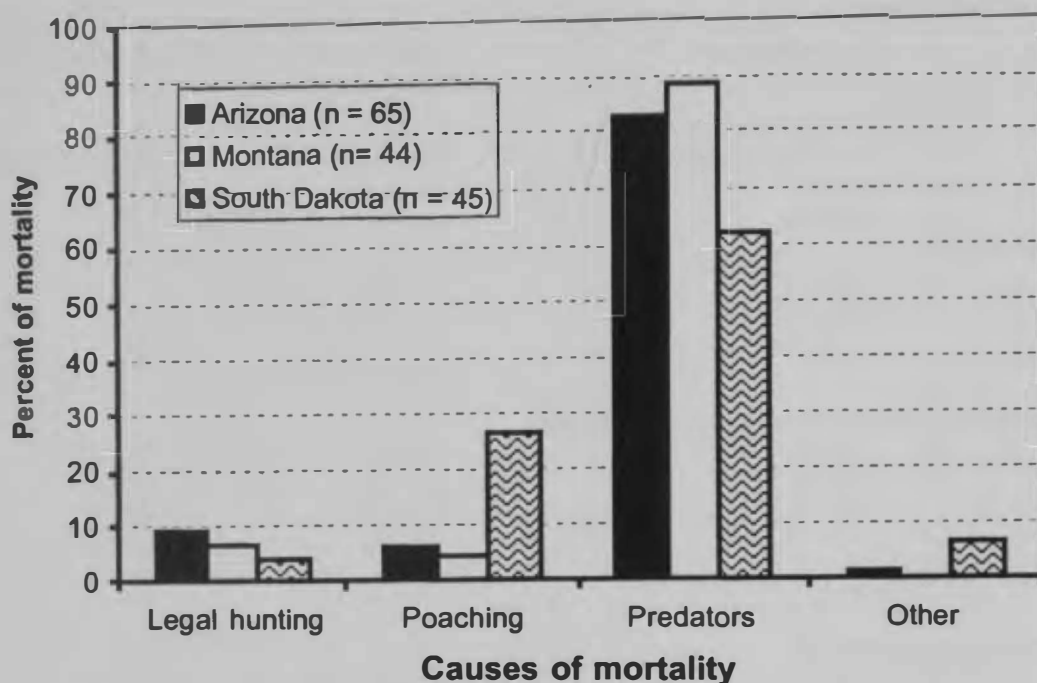
² Merriam's turkey populations from Montana, Oregon, South Dakota, and Wyoming were all introduced.

³ Expressed at percentage except as noted.

consequently had the greatest influence on populations in Arizona in which only adults nested (Wakeling 1991).

Predators accounted for the majority of mortality events for female Merriam's turkeys throughout their range (Fig. 1). However, the magnitude of predation as a mortality factor differed among populations (Wakeling 1991, Rumble and Hodorff 1993, Thompson 1993, Wakeling and Rogers 1998). Predation accounted for >80 percent of identifiable causes of mortality to female turkeys in Montana and Arizona. In Arizona, coyotes (*Canis latrans*) accounted for 65 percent of the predation events, bobcats (*Lynx rufus*) accounted for 13 percent, and avian predators accounted for 22 percent. Legal hunting accounted for

<10 percent of mortality events among female turkeys. Hunter harvest appears directly related to population size (Wakeling 1991). Hunters harvested <3 percent of adult females during a week-long fall hunt, and modeling suggested that hunter harvest had no significant effect on subsequent populations. Fall turkey hunters in Arizona appeared to harvest the larger birds in fall flocks. The fall harvest comprised 30-40 percent subadult males, and 30-40 percent adult females. The proportion of adult females in the fall harvest increased when nesting occurred later, probably because they presented a larger and more preferred target for hunters than smaller subadults (R. W. Engel-Wilson, Ariz. Game and Fish. Dept., unpubl. data). We believe that



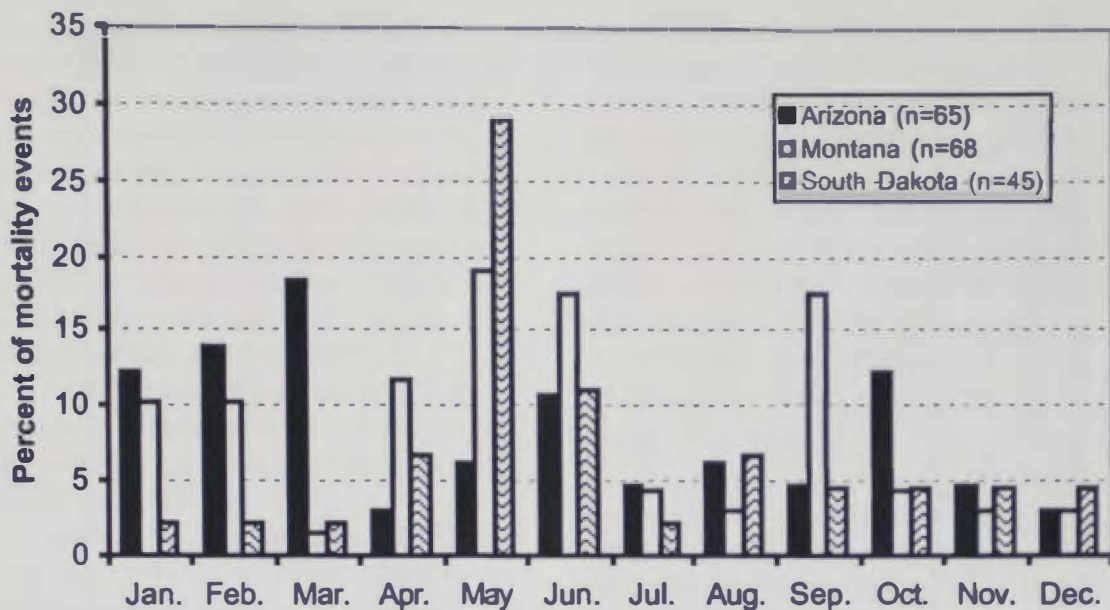
¹Includes only identifiable causes of mortality. Other category includes disease and vehicles.

Figure 1. Causes of mortality to female Merriam's turkeys from Arizona (adapted from Wakeling 1991), Montana (adapted from Thompson 1993), and South Dakota¹.

limited fall turkey harvest has little overall effect on populations of Merriam's turkeys. Because winter survival among populations of Merriam's turkeys tends to be high and because adult females contribute more to the reproductive performance of some populations (Rumble and Hodorff 1993), recovery from population declines or growth of new populations might increase slightly in the absence of fall hunting.

Timing of mortality varied among areas, but there appeared to be regional similarities. The monthly frequency of mortality events in Montana and South Dakota were correlated ($r = 0.6$, $P = 0.04$). Correlations of monthly mortality events between Arizona and the former states showed nonsignificant negative correlations ($r \leq -0.12$, $P \geq 0.5$). Mortality events in Arizona increased from winter through early spring (Fig. 2), but declined during the nesting season. In Arizona, survival of yearling females was greater than adult females from nest initiation through fall (Wakeling 1991). These yearling females had low nesting rates and Wakeling (1991)

attributed their greater survival to their not being encumbered with broods. Lutz and Crawford (1987) suggested that yearling females experienced comparatively high rates of predation and nest loss because they maintained higher levels of activity through the second week of incubation and displayed lower attentiveness to the nest. Increased mortality of female turkeys during late winter to spring is also the result of the cumulative effects of winter on the physiological condition of birds (Rumble and Anderson 1996a, Wakeling and Rogers 1995, 1996). Vulnerability to mortality of birds during nesting and brood rearing was evident in Montana and South Dakota. The onset of nesting corresponded with the period of greatest mortality in South Dakota. Predation during nest initiation or incubation was primarily by coyotes, red fox (*Vulpes fulva*), or raptors and may approach 20 percent of females (Rumble and Hodorff 1993). In south central South Dakota, female turkeys incurred 11 percent mortality from mammalian predators during nesting (Day 1988).



¹ Includes unidentified causes of mortality.

Figure 2. Monthly distribution of mortality events to female Merriam's turkeys in Arizona (Arizona adapted from Wakeling 1991), Montana (adapted from Thompson 1993), and South Dakota¹.

Weather conditions from previous summers can interact with predation, affecting survival of Merriam's turkeys the following spring. During summer 1988, drought reduced the production of ponderosa pine seeds, the preferred winter food of turkeys in the Black Hills (Rumble and Anderson 1996a,b). Consequently, winter diets comprised mostly grass seeds and kinnikinnick (*Arctostaphylos uva-ursi*) seeds (Rumble and Anderson 1996a). During a mild winter, Rumble and Anderson (1996c) documented 25 percent mortality of radio-marked females (all subadults) by predators within 2 weeks of a winter storm in March. Despite the small sample ($n = 4$), this resulted in 100 percent mortality of the radio-marked subadult females in the Black Hills that year. In another instance, anecdotal observations on the North Kaibab during fall 1996 indicated that acorns, the favored mast, were limited (Wakeling and Rogers 1995, 1996). Following several substantial winter snowfalls, mortality rates of female turkeys were high. Over-winter survival of subadult female survival was 10 percent compared to

62 percent among adult females (Wakeling and Goodwin 1999). During typical winters in Arizona, average survival of the respective age groups was 79 and 82 percent (Wakeling 1991). Ultimate factors affecting survival of Merriam's turkeys probably varies across their range and may often be unique. Available data did not allow us to identify the integrated effects of weather, habitat, and age of birds affecting survival of Merriam's turkeys.

Reproductive Parameters

Nesting rates of adult females vary markedly across the range of Merriam's turkeys (Lockwood and Sutcliffe 1985, Schemnitz et al. 1985, Lutz and Crawford 1987, Wakeling 1991, Rumble and Hodorff 1993, Flake and Day 1995). Nesting rates in some introduced populations exceed those from populations within the historical range. For example, in the Black Hills, nesting rates of adults averaged 97 percent (Rumble and Hodorff 1993), but in Arizona adult female nesting rates averaged 45 percent (Wakeling 1991). Nesting by yearling females within the historical range of Merriam's turkeys is normally

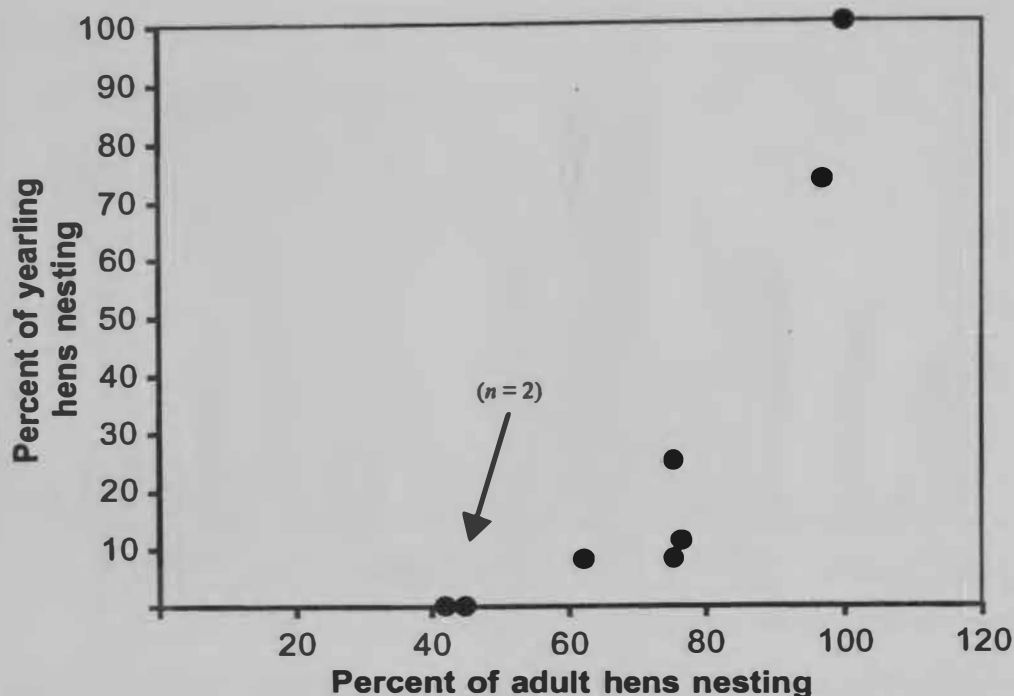


Figure 3. Scatterplot of adult and yearling Merriam's turkey nesting rates from nine studies.

nonexistent or limited (Schemnitz et al. 1985, Lockwood and Sutcliffe 1985, Hoffman 1990, Wakeling 1991, but see Hoffman et al. 1996). Nesting by yearling hens is also uncommon in some introduced populations (Lutz and Crawford 1987, Wertz and Flake 1988, Flake and Day 1995), while other introduced populations have substantial nesting ($\leq 73\%$) by yearling females (Hengel 1990, Rumble and Hodorff 1993, Thompson 1993).

In a generic sense, quality of habitat or some component apparently affects nesting by yearling females and the likelihood for females to renest (Rumble and Hodorff 1993). Hoffman et al. (1996) summarized data from several studies that suggested a link between propensity for subadult females to nest and winter nutrition; populations in which subadult females weighed more than 3.9 kg demonstrated greater nesting effort than those that weighed less than 3.6 kg. In Arizona, some females lost up to 20 percent of their body weight during a relatively snow-free, but mast-limited winter, and there was a weak correlation between nesting rate and mast

production (Wakeling 1991). Nesting rates of females are high in the central Black Hills (Rumble and Hodorff 1993) where ponderosa pine seed, the primary mast source (Rumble and Anderson 1996a), is usually dependable (Boldt and Van Duesen 1974). Wakeling and Rogers (1995) noted that nutritional deficiency of copper and selenium, which can affect nesting (Puls 1988), was evident in a turkey population with a low propensity for nesting.

There appears to be a relation between adult and yearling nesting rates for Merriam's turkeys. Data suggest that yearling nesting is low or nonexistent until adult nesting rate exceeds about 60 percent (Fig. 3).

Although survival of yearling nests (0.23) did not differ ($P = 0.18$) from that of adults (0.36) in the Black Hills, adults contributed more to annual recruitment of Merriam's turkeys in the Black Hills than yearlings (Rumble and Hodorff 1993). Adult females renested more (1.18 attempts/bird) often than yearlings (0.57 attempts/bird) and had greater (48%) hen success than yearlings (24%). Nest outcomes in

southeastern Montana were strikingly similar to the Black Hills in which success of adult and yearling hens was 50 and 25 percent, respectively (Thompson 1993). In the Black Hills, renesting was correlated ($r=0.96$) with spring-summer precipitation (Rumble and Hodorff 1993). Of 15 adult females in south central South Dakota with unsuccessful nests, only 2 (13%) attempted to renest (Flake and Day 1995). In Arizona and New Mexico, only adults (18-35%) attempted to renest (Lockwood and Sutcliffe 1985, Schemnitz et al. 1985, Wakeling 1991).

Birds (35%) and mammals (26%) were the primary causes for failure of Merriam's turkey nests in South Dakota. Weather, e.g., late spring snow storms, can be an important factor affecting nest outcome. During some years, American crows (*Corvus brachyrhynchos*) accounted for complete loss of all first nesting attempts and 65 percent of total annual nest predation (Rumble and Hodorff 1993). Coyotes and, to a lesser degree, red fox were the primary mammalian predators in the Black Hills. In south central South Dakota, 17 of 39 (44%) of nesting attempts hatched and 86 percent of nest losses were attributed to mammalian predation (Flake and Day 1995). Probable nest predators included coyotes and black-billed magpies (*Pica pica*). American crows or black-billed magpies were primary nest predators in Montana (Thompson 1993).

In the southwestern U.S., nesting outcomes differed from those in northern latitudes. Only adults nested in Arizona where nest success averaged 68 percent (Wakeling 1991). Most nest losses in Arizona resulted from mammalian predation, although ravens (*C. corax*) were noted predators of nests (Wakeling et al. 1998). Renesting by females in Arizona was 18 percent of which only half were successful (Wakeling et al. 1998). In southeastern New Mexico, nest success averaged 31 percent for first nests and 55 percent for renests for an average hen success of 35 percent (Lockwood and Sutcliffe 1985).

Multiple microhabitat characteristics at the nest site influenced the outcome of nesting in Arizona; successful nest sites had greater horizontal screening and overhead cover (Wakeling et al. 1998). Rumble and Hodorff (1993) reported greater survival rates of third nest attempts than first or second attempts in the Black Hills; third nest attempts had greater horizontal screening and more vegetative cover than earlier attempts.

Poult Survival

We are unaware of a suggested level of reproductive success for maintaining populations of Merriam's turkey. Data on poult survival are limited and extrapolation beyond the areas where these studies were conducted must be done cautiously. Glidden and Austin (1975) suggested that poult survival should exceed 20 percent for maintaining eastern turkey (*M. g. silvestris*) populations, depending on nesting success, nesting rates for yearlings and adults, and renesting effort.

We can reasonably expect poult mortality for Merriam's turkey from hatch to August to vary from 60 to 70 percent; however, additional data are needed that quantify the effect of complete brood loss on these estimates. Mortality rates of eastern turkey poults vary from 50 to 75 percent during the first 14 days post hatch (Vangilder 1992). The period of highest poult mortality occurs while flightless—usually 7-9 days post hatch—when dietary protein requirements for growth are high. However, we have observed flightless poults 12 to 14 days post hatch when availability of invertebrates was low (M. Rumble, personal observation). Mortality of eastern turkey poults occurs primarily in the first 2 weeks post hatch with minimal losses thereafter (Vangilder 1996). All complete brood losses of Merriam's turkey in south-central South Dakota occurred ≤ 2 weeks post hatch (Flake and Day 1995). Predation accounts for about 80 percent of mortality of eastern turkey poults (Speake et al. 1985). Mortality of Merriam's turkey poults during the first 8 weeks post hatch averaged 64 percent in Wyoming (Hengel

1990). Based on personal observations, we conclude that predation and weather are important contributors to early mortality of Merriam's turkey poults. In the Black Hills, poult mortality estimates from late summer hen:poult ratios and average clutch size are >40 percent (unpubl. Pittman-Robertson Rep. W-95-R-31, South Dakota Department Game Fish and Parks 1998). In Arizona, brood surveys suggested poult mortality rates from 41 to 65 percent by August (Wakeling 1991). Brood surveys underestimate poult mortality; they do not account for entire brood losses because unsuccessful females and those with complete brood loss use habitats where they are less likely to be observed (Shaw and Mollohan 1992, Hoffman et al. 1993, Mollohan et al. 1995). In south-central South Dakota, poult mortality estimates from radio marked females ≤ 8 weeks post hatch was 57 percent including 35 percent complete loss of broods. (Flake and Day 1995).

Population Modeling

Because of the number of factors involved, modeling is useful for estimating vital rates necessary for sustaining turkey populations. Modeling successfully identified probable factors that limit populations of eastern turkeys in Wisconsin (Rolley et al. 1998). Demographic modeling suggested that greater survival of subadult females (Wakeling 1991) or adult females (Wakeling and Rogers 1998) in Arizona could potentially increase Merriam's turkey populations. Nonetheless, Wakeling and Rogers (1998) speculated that managers could more successfully increase nesting rates of yearling females through habitat manipulation than increase survival rates by controlling predators. Because of an apparent relationship between nesting and nutrition or food availability, habitat manipulation directed at improving body condition of females through improved abundance and distribution of food would likely improve nesting rates of Merriam's turkeys (e.g., Wakeling 1991, Wakeling and Rodgers 1995, Hoffman et al. 1996).

SUMMARY AND CONCLUSIONS

The likelihood that adult or yearling Merriam's turkeys attempt to nest varies spatially and temporally, probably in relation to population density or physiological condition of females at the onset of nesting. Food availability and nutrition may be the most direct link to nesting rates. In addition to installing food plots, silvicultural treatments are available to increase mast production of oak, pine and other mast producing species. Adult female Merriam's turkeys exhibit greater reproductive success than yearlings, i.e., after their second spring. In general, low reproductive output among yearling females results from low rates of success from the first nesting attempt with little or no likelihood of renesting. Renests have a greater chance of hatching, but renest rates are highly variable. Populations of Merriam's turkeys with a high percentage of nesting by yearling females are more resilient to population declines and nest loss than those in which yearling females are less likely to nest. Predators, weather, and habitat may interact to influence nesting success with coyotes, crows, ravens, and magpies being major nest predators.

Predation is the primary source of mortality to female Merriam's turkeys, most of which is attributed to coyotes. Merriam's turkeys commonly live 3-5 years and some >8 years. Because of their longevity, we hypothesize that mortality is only partially compensatory. Population models suggested that altering survival of adult females increases turkey populations in which yearlings do not nest. However, increased nesting by yearlings probably has the greatest potential to increase populations of Merriam's turkeys.

Survival of poults is generally quite low. While, low survival of poults is common among all subspecies of wild turkeys, indications are that some of the current Merriam's turkey range may lack high-quality brood habitat. Poults should be capable of flight in approximately 9 days. They occasionally remain flightless

for >2 weeks, which suggests less than optimal growth and development. Growth and development of turkey poults is linked to invertebrate abundance, which in turn is linked to the abundance of herbaceous vegetation in meadows.

Most of the information on Merriam's turkey populations is from studies of habitat relations. Except for Arizona, studies with sufficient sample sizes from which to estimate cause-specific mortality rates are lacking. Consequently, we recommend that future studies address cause-specific nest losses and mortality rates to Merriam's turkeys. Similarly, data are lacking on rates of poult survival, causes of mortality, and measures of survival related to habitat quality. We believe the need for these studies encompasses most of the current range of Merriam's turkeys. We believe population sensitivity modeling could identify the limiting factors to Merriam's turkey populations.

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