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SPATIAL POPULATION DYNAMICS OF WESTERN PAINTED TURTLES IN A WETLAND ECOSYTEM IN NORTHWESTERN MONTANA

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Spatial Population Dynamics of Western Painted Turtles in a Wetland Ecosystem in Northwestern Montana

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Population dynamics are driven by the interplay between the positive forces of births and immigration and the negative forces of deaths and emigration. Understanding dynamics at the local and metapopulation level is key in wildlife conservation. Although data on turtle survival and movement rates are available, few studies use rigorous statistical analyses and none include examination of stage-specific seasonal survival simultaneous with movement estimates.

I used capture-mark-recapture methods to estimate apparent survival rates and movement probabilities of adult and juvenile western painted turtles (*Chrysemys picta bellii*) across space and time in a wetland ecosystem in northwestern Montana. All wetlands within five complexes were sampled during three primary sessions a year from fall 2002 to spring 2005. I captured 1,072 individual adults 5,050 times and 442 individual juveniles 3,078 times.

Although both juvenile and adult apparent survival rates were influenced by pond, seasons, and year, I found very different patterns spatially and seasonally between age classes. Apparent annual survival was lowest for adults in shallow ponds and lowest for juveniles in deep ponds. This variation could be due to mobility of adults which allows them to seek refugia habitats during drought conditions. Juveniles were less mobile and less likely to leave ponds.

Movement probabilities of adults were influenced by distance between ponds and depth of originating pond. Only two juveniles were observed to move between complexes. Although the highest interpopulation movement probability was 3.8%, the probability for most interpopulation movements was very low (< 1%). Temporary emigration estimates were higher than estimates of interpopulation movement indicating the importance of refugia habitat.

I examined the potential impacts of road mortality on both the overall population size and population structure via sex and stage class ratios of this population. Road mortality averaged 185 individuals/year. Annual road mortalities ranged widely depending on pond characteristics but in general were higher than the 2-3% mortality suggested by other research to likely affect long-term viability in turtle populations. No highway-induced sex-bias occurred in this population.

Population growth rates were negatively influenced by the presence of roads and positively influenced by movements.

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CHAPTER 1. INTRODUCTION AND OVERVIEW: SPATIAL POPULATION DYNAMICS OF WESTERN PAINTED TURTLES IN A WETLAND ECOSYSTEM IN NORTHWESTERN MONTANA

Individuals within most wildlife species are distributed unevenly across the landscape due to variations in ecological characteristics (Stacey et al. 1997). These groups of individuals or patches form local populations which can have considerable influence on population dynamics (Pulliam 1988, Kareiva and Wennergren 1995). Population dynamics are driven by the interplay between the positive forces of births and immigration and the negative forces of deaths and emigration (Wilbur 1996). Understanding these dynamics at both the local and metapopulation levels is key in the management and conservation of wildlife species.

Movement of individuals between local populations is the process that connects local populations into a larger functional demographic unit on a regional scale (Merriam 1984). The distance and rate of movements among patches affects population dynamics, social behavior, rates of extinction and colonization, and genetic composition. Connectivity of a population across a landscape not only includes the probability of movement but also the probability of survival of animals moving between patches (Henein and Merriam 1990).

Within populations, survival is a critical vital rate influencing population growth rates, especially for long-lived species (Crouse et al. 1987, Heppell et al. 1999). Stage-specific survival rates are important for understanding population viability because different age-classes contribute differently to population growth. For many species, annual survival rates are lower and more variable over space and time for juveniles than for adults and different age classes often respond differently to changes in environmental factors. Seasonal survival rates can relate mortality to particular phases of the annual cycle such as reproduction, migration, or hibernation.

Wetland habitats offer unique opportunities to study questions of connectivity and metapopulation structure because discrete boundaries delineate suitable and unsuitable habitat. More than half of all wetlands in the continental United States have been lost, so understanding and maintaining the connectivity of wetland ecosystems is key in maintaining viable populations of wetland-associated species (EPA 2000). Wetland-associated populations are often naturally fragmented; thus, anthropogenic changes to the landscape could affect population connectivity and long-term viability. The painted turtle (*Chrysemys picta*), a species of special concern to the Confederated Salish and Kootenai Tribes, provides an excellent model system for studying the effects of connectivity and anthropogenic fragmentation such as a highway. This aquatic species is abundant, easily captured, and is known to move between ponds through dispersal as well as through seasonal migrations (Congdon and Gatten 1989, Ernst et al. 1994). Many aquatic turtle species, such as painted turtles, are especially vulnerable to barriers to movement and fragmentation, because although these turtles use terrestrial landscapes for nesting and seasonal movements, they have limited abilities to move effectively across the landscape (Mitchell 1988). While freshwater turtles have declined in abundance due to habitat loss and fragmentation, few quantitative studies have documented such a relationship (Mitchell and Klemens 2000).

Populations of painted turtles have been studied extensively (e.g., Cagle 1950, Gibbons 1968, Wilbur 1975, Tinkle et al. 1981, Mitchell 1988, Iverson and Smith 1993), yet few studies use rigorous statistical analyses that lead to reliable inferences (but see Lindeman 1990, Koper and Brooks 1998, Bowne et al. 2006). I used capture-mark-recapture (CMR) methods to simultaneously estimate survival and movements of adult and juvenile western painted turtles (*C. p. bellii*) across space and time (seasonal and annual) in a wetland ecosystem in western Montana. I simultaneously conducted road mortality surveys to assess the potential impacts of the highway on the population.

In Chapter 2, I estimated survival rates of adult and juvenile turtles as influenced by spatial and seasonal variation using multistate robust design models. Spatial variation was measured between five pond complexes and seasonal variation was measured between winter, early summer, and late summer. Knowing when mortality occurs within the annual cycle of activities is important in management and conservation. Survival was estimated in the presence of both interpopulation movements and temporary emigration.

In Chapter 3, using CMR modeling, I estimated both interpopulation movements and temporary emigration. Understanding factors that affect age- and sex-specific movement rates is important in determining what factors influence population dynamics and spatial structure. Interpopulation movement estimates allow us to evaluate connectivity and the spatial structure of the population while temporary emigration estimates shed light on use of habitats outside the study area and are important for conservation efforts.

Also in Chapter 3, I used a stage-based, multi-site, matrix population model (Morris and Doak 2002) to assess population-level consequences of movements, particularly in relation to the highway. I structured the population models using stage- and population-specific apparent survival rates estimated in Chapter 2 and road mortality data from Chapter 4.

Effects of roads on wildlife have gained attention over the last decade because of the ubiquitous network of roads and the visibility of road mortality. The effects can impact wildlife populations in a multitude of ways such as changes in quantity and quality of habitat, direct mortality, altered behavior, and reduction in landscape connectivity. Turtle species may be particularly susceptible to the effects of roads because of life history traits that make it difficult to respond to perturbations in survival rates. Most research on the effects of roads on turtle populations have focused on either the number of turtles killed on roads or the alteration of population structure through disproportionate road mortality by sex. In Chapter 4, I examined the potential impacts of road mortality on both the overall population size and population structure via sex- and stage-class ratios of this population. To accomplish this, I conducted the CMR study and road mortality surveys concurrently to estimate the percentage of the population killed on the road and to examine the potential alteration in population structure.

Although this wetland ecosystem has a high level of natural fragmentation, fragmentation due to anthropogenic factors is likely to increase given anticipated growth in development and traffic volumes (FHWA and MDT 2000). Currently, an 18 km (11.2 mi) section of roadway in the Ninepipe/Ronan section of the existing U.S. Highway 93 is proposed for improvements (FHWA et al. 2005). The highway project, which runs through my study area, may increase the width of the highway and allow for increased traffic flow, both of which could exacerbate the current issue of turtle mortality due to roads.

The majority of funding for my research was provided by the Montana Department of Transportation (MDT). One of the concerns of MDT is the affects of road mortality on turtle populations. Appendix 2 is the complete report submitted to MDT. This report included 1) data on the location of all turtles found dead on the road in the study area (Appendix 2, Fig. 5), 2) a review of available fencing methods used in herpetofauna-highway interaction projects, 3) an experiment to examine the effectiveness of flashing material as a barricade on low fencing, and 4) recommendations to guide design and placement of wildlife crossing structures during the Highway 93 reconstruction project.

Very little information is available on the hydrology of the ponds in the Mission Valley. The amount of water available on the landscape changes drastically from spring to fall with many temporary ponds available in spring and only a few permanent ponds holding water in fall (Fig. 1). This situation was exacerbated by drought conditions during my study. In appendix 1, I included a table of pond hydrology and depth measurements (when taken) of ponds within my study area from 2002 - 2007. Reference maps to the identification numbers of all ponds are also included.

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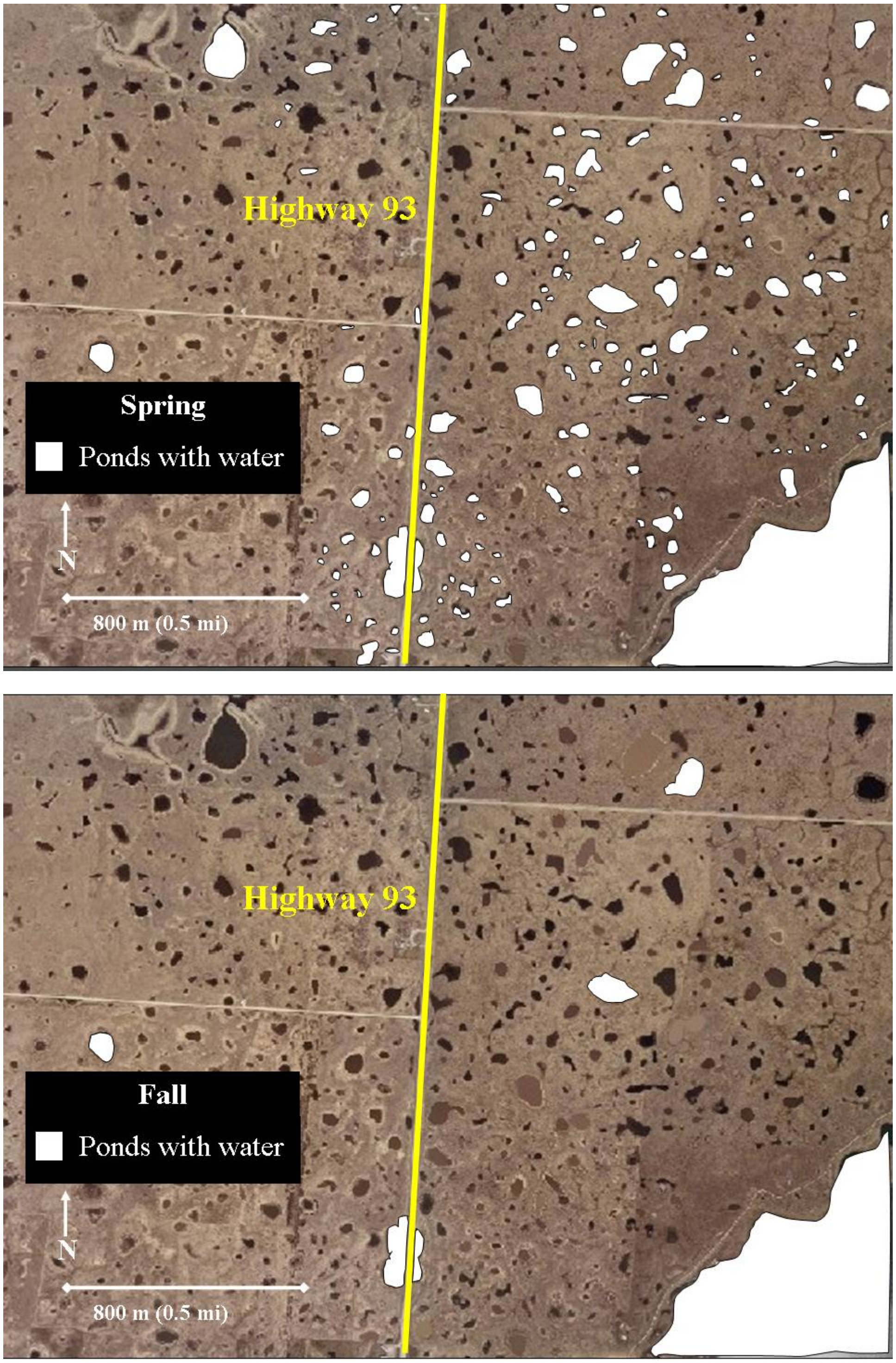

Fig. 1. Pond permanence on the study area in the Mission Valley, Montana. Top photo shows the available water (white ponds) on the landscape in spring (May 2002). Bottom photo shows the available ponds in fall (August 2003 – 2005). The underlying photo was taken in spring (April) 2001 which was a relatively wet year.

CHAPTER 2. SPATIAL AND SEASONAL VARIATION IN STAGE-SPECIFIC SURVIVAL RATES OF WESTERN PAINTED TURTLES IN NORTHWESTERN MONTANA

ABSTRACT

Stage-specific survival rates are important for understanding population viability of long-lived species because different age classes contribute differently to population growth. For many species, annual survival rates are lower and more variable over space and time for juveniles than for adults and different age classes often respond differently to changes in environmental factors. Seasonal survival rates can relate mortality to particular phases of the annual cycle such as reproduction, migration, or hibernation. Although data on turtle survival rates are available, few studies have used detailed statistical analyses and none have examined stage-specific seasonal survival. We used capture-mark-recapture methods and multistate robust models to estimate apparent survival rates of adult and juvenile western painted turtles (*Chrysemys picta bellii*) across space and time (seasonal and annual) in a wetland ecosystem in western Montana. Because not all resources may be contained within the aquatic habitat, we identified five pond "complexes" centered on a permanent pond. All wetlands within each complex were sampled during three primary sessions a year from fall 2002 to spring 2005. We captured 1,072 individual adults 5,050 times and 442 individual juveniles 3,078 times. Although apparent survival rates of both juvenile and adult turtles were influenced by site (pond), seasons (summer, winter), and year, patterns differed both spatially and seasonally between age classes. Apparent annual survival was lowest for adults in shallow ponds and lowest for juveniles in deep ponds. This variation could be due to the mobility of adults which allows them to seek refugia habitat off the study site (permanent emigration) during drought conditions. Juveniles were less mobile and less likely to leave pond complexes. The low survival of juveniles in deep ponds may have been due to high predation rates on juveniles. Our study provides further support for conservation across landscapes and inclusion of a variety of habitats that may be important for different age classes to maintain long-term population viability.

INTRODUCTION

Dynamics of animal populations are driven by interplay between the positive forces of births and immigration and the negative forces of deaths and emigration. Understanding these dynamics is key in the management and conservation of wildlife species. Historically, population ecology included the assumption of closed populations in which dynamics were determined only by births and deaths; if movements were included, immigration was assumed to be equal to emigration (Hanski and Simberloff 1997). Traditional theory also assumed these vital rates were constant in space and time. Since MacArthur and Wilson (1967) and Levins (1969) seminal papers on spatial dynamics, advances in ecological theory and improved field methods and computer technologies have enabled researchers to further explore population dynamics in more realistic terms that include space, time, and movements (Gilpin 1987, Wilbur 1996). Intuitively, we know that all natural environments vary temporarily and spatially at some scale. The significant challenge is to determine the role played by this variation in population dynamics, which ultimately determines viability of a population (Gilpin 1987).

Survival, one of the primary vital rates determining population growth rates, is especially important in long-lived species. Survival rates can be influenced by abiotic factors such as weather and habitats, and survival of males and females and different aged individuals can vary in both time and space independently (as reviewed in Ozgul et al. 2006). For many species, survival rates are lower and more variable over space and time for juveniles than for adults, and different age classes often respond differently to changes in environmental factors (Cooke et al. 2000, Ozgul et al. 2006).

Although several studies have recently addressed spatial and temporal variation simultaneously in age- or sex-specific survival rates (Ringsby et al. 1999, Graham and Lambin 2002, Casula 2006, Baker and Thompson 2007), the relationships are not well understood, especially for long-lived species (Ozgul et al. 2006). Understanding spatial and temporal variation in vital rates is important not only for conservation and management but also in developing and testing life history theories (Beissinger and Westphal 1998, Morris and Doak 2002, Tuljapurkar et al. 2003, Chaloupka and Limpus 2005). Much of life history theory assumes mortality risks vary in response to specific activities throughout the annual cycle of an animal (Gauthier et al. 2001). Many species have evolved strategies, such as migration or hibernation, to deal with spatial or temporal variation in resources or reproductive opportunities.

Biologists most often estimate average survival rate over the entire annual cycle of an animal. However, shorter intervals can relate survival, and therefore mortality, to particular phases of the annual cycle such as hibernation, reproduction, or migration (Schaub and Vaterlaus-Schlegel 2001, Crespin et al. 2002, Sillett and Holmes 2002, Sendor and Simon 2003). Variations in mortality risks can shape the evolution of basic life-history traits (Bodie and Semlitsch 2000) and can also be used in management decisions (Gauthier et al. 2001). Seasonal survival rates could be used in population matrix models to determine the importance of summer versus winter mortality rates to overall population growth. If summer survival rates are driving population growth, then focusing on factors that affect summer survival would be important. This information could then be used in conservation efforts. For example, implementing mitigation measures such as wildlife crossing structures may lower mortality in summer and be beneficial for long-term viability of the population. Seasonal survival rates also may be altered by other environmental disturbances, such as climate change, which may modify the hydrology or hydroperiods of ponds and thus affect overwinter survival.

The lack of survival data is particularly acute for turtles (Shine and Iverson 1995). Populations of painted turtles (*Chrysemys picta*) have been studied extensively (e.g., Cagle 1950, Gibbons 1968a, Wilbur 1975a, Tinkle et al. 1981, Mitchell 1988, Iverson and Smith 1993) yet few studies use rigorous statistical analyses which lead to reliable inference (but see Lindeman 1990, Koper and Brooks 1998, Bowne et al. 2006). Many observational studies suggest mortality of adults may be highest during winter (Sexton 1959b, Christiansen and Bickham 1989, Ultsch 1989), but none have rigorously examined seasonal survival. Capture-mark-recapture studies have been conducted on sea turtles (Kendall and Bjorkland 2001, Chaloupka and Limpus 2005), musk turtles (Fonnesbeck and Dodd 2003), box turtles (Converse et al. 2005), and diamondback terrapins (Tucker et al. 2001). However, only the latter study examined stage-specific survival rates in both space and time simultaneously and none examined seasonal survival.

The painted turtle is a small to medium-sized freshwater pond turtle that inhabits ponds, lakes, and slow-moving waters. Terrestrial activity is restricted to nesting by females, dispersal by juveniles, and seasonal movements between ponds by both sexes and age classes (Sexton 1959b, Gibbons 1968b, McAuliffe 1978, Congdon and Gatten 1989, Taylor and Nol 1989, Rowe et al. 2005). More northern populations of turtles may remain dormant at the bottom of ponds for six to seven months each year (Ernst et al. 1994). Like many turtle species, painted turtles possess a suite of life history characteristics (e.g., long-lived, delayed sexual maturity, high adult survival rates, and low recruitment rates) that combine to limit their ability to respond quickly to perturbations that increase mortality in any age group (Congdon et al. 1993, Heppell 1998, Heppell et al. 2000). Biology and life history of painted turtles are described in detail by Sexton (1959b), Gibbons (1968a and b), Wilbur (1975a), Mitchell (1988), and Ernst et al. (1994).

We used capture-mark-recapture methods to characterize spatial and seasonal variability in age-specific survival of western painted turtles (*C. p. bellii*) in western Montana. Although the survival analysis discussed here also includes simultaneous analysis of movements (e.g., between local populations and temporary emigration), movement parameters are addressed thoroughly in a companion paper.

The role movements play in population dynamics has been inferred from the inability to account for changes in populations solely based on birth and death rates (Hestbeck et al. 1991, Spendelow et al. 1995). When spatial aspects of populations are explored, information on movement is necessary to separate mortality from emigration, thus improving estimates of survival (Hestbeck et al. 1991, Lebreton et al. 1992, Kendall and Nichols 1995, Kendall and Bjorkland 2001, Lebreton and Pradel 2002) and shedding light on the potential for metapopulation structure (Spendelow et al. 1995).

METHODS

Study Area

Our study area is located in the Mission Valley of northwestern Montana (47° 27' N, 114° 04' W; elevation 920 - 940 m), and contains glaciated, depressional wetlands that resemble the prairie pothole region of the mid-western United States (US Fish and Wildlife Service 2007). Historically, the Mission Valley was Palouse prairie but over time it has been extensively modified by agriculture and development. The study site is an area of high-density wetlands with over 2,000 permanent and ephemeral wetlands in an area of approximately 78 km^2 (Fowle 1996). The wetlands are primarily palustrine emergent basins with various water regimes ranging from permanent to seasonally flooded (Cowardin et al. 1979). The permanent ponds are characterized by open water with very little emergent vegetation although some cattails (*Typha* spp.) and rushes (*Juncus* spp.) occur along the edges of some ponds. Aquatic vegetation in the permanent ponds is sparse and consists mostly of milfoil (*Myriophyllum* spp.) and duckweed (*Lemna* spp.). The ponds are surrounded by grasslands, some of which were heavily grazed by cattle until 2001. Currently, the grasslands are ungrazed by livestock and dominated by western wheatgrass (*Agropyron smithii*), fescue (*Festuca* spp.) and invasive species such as Kentucky bluegrass (*Poa pratensis*), spotted knapweed (*Centaures maculosa*), erect cinquefoil (*Potentilla recta*), whitetop (*Cardaria draba*), mustard (*Brassica* spp.), and thistle (*Cirsium* spp.) (Anderson 2003).

We identified five permanent ponds classified as palustrine with intermittent exposure which indicates “surface water is present throughout the year except in years of extreme drought” (Cowardin et al. 1979:22). These five ponds, ranging in size from 0.6 ha to 1.6 ha, were important overwintering ponds for turtles and were separated from the next nearest permanent pond by at least 800 m, which exceeds the average reported movement distance of painted turtles (McAuliffe 1978, Rowe et al. 2003). One exception was that we treated two ponds (B and C) that were 80 m apart as separate populations because they were separated by Highway 93 (Fig. 1). Because not all required resources may be contained within the aquatic habitat (Pope et al. 2000), we identified a “complex” around each permanent pond. A complex was defined as the area within a 300-m radius from the center of the permanent pond (Fig. 1). This distance incorporated typical movements that include most terrestrial activities such as nesting and seasonal use of temporary ponds (Gibbons 1968b, McAuliffe 1978, Rowe 2003). All wetlands that held water within each complex were surveyed during each trapping session.

Three roads occur within the study area: U.S. Highway 93, Mollman Pass Trail, and Duck Road (Fig. 1). Road density within our study area was relatively low (0.72 km/km^2). Traffic volumes on Highway 93 (2-lanes) were considered high with an average of 290 vehicles/lane/hour during daylight hours when turtles were most likely to move.

Field Methods

Capturing and Marking Turtles

We captured painted turtles using seine nets (Lindeman 1990), basking traps (MacCulloch and Gordon 1978), muddling (Wilbur 1975a), and dip nets (Congdon and Gatten 1989) to minimize the potential for sampling bias by sex or stage class (Ream and Ream 1966, Gibbons 1990, Koper and Brooks 1998). We recorded the following data the first time a turtle was captured each year: location, plastron length and width (mm), carapace length and width (mm), weight (g), sex, and age, if possible. Shell measurements were all straight-line measurement taken with calipers and weight was measured using spring scales. On subsequent recaptures within a year, we recorded only turtle identification, location, and sex. Sex was determined by examining secondary sexual characteristics (elongated foreclaws and elongated preanal region of the tail, [Frazer et al. 1993]) and age was determined by annuli aging techniques on turtles less than 4 - 5 years old (Graham 1979).

Each turtle was individually marked by drilling the margins of the carapace (Cagle 1939, McAuliffe 1978) as well as injecting a Biomark™ passive integrated transponder (PIT) tag into the body cavity (Camper and Dixon 1988, Buhlmann and Tuberville 1998). Turtles smaller than 50 mm plastron length (PL) (about 30 g) did not receive a PIT tag. Hatchlings and some juveniles were notched using nail clippers rather than drilling because some shells were not yet fully ossified (McAuliffe 1978, Camper and Dixon 1988).

Classification of Turtles into Sex and Stage Classes

We grouped turtles into stage classes because reliability of aging techniques decreases with age due to shedding of the scutes (Sexton 1959a, Wilbur 1975b). Three stage classes were defined: hatchling, juveniles, and adults. Hatchlings were turtles with a PL ≤ 50 mm and are not discussed in this paper. Juveniles were turtles with a PL >50 mm and ≤ 104 mm, and sex was treated as unknown in all analyses. However, 82 mm was the smallest PL where we observed male secondary sexual characteristics; therefore, the juvenile category included some (< 1.8%) known male turtles that exhibited secondary sexual characteristics. Adults were turtles with a PL ≥ 105 mm. Any individual that was at least 105 mm PL and not showing signs of secondary sexual characteristics was considered female (Mitchell 1985). Based on subsequent recaptures, all male turtles exhibited secondary sexual characteristics by the time they reached 105 mm PL.

Pond Measurements

We measured pond depth during each trapping session using a graduated pole. Small, uniformly-shaped ponds were measured in the center and larger, irregularly shaped ponds were measured three times across the pond and averaged. We calculated pond volume using our depth measurements and pond circumference determined from Geographic Information System (GIS) data layers at a high-water period (April 2001); therefore, calculated volumes represent a relative measure of volume based on the high water mark.

Sampling Sessions

Pond complexes were sampled intensively during three sessions per year: spring (May 21 - June 1), summer (July 2 – 13) and fall (August 13- 24). Spring sessions were timed to capture turtles before they moved out of their overwinter ponds and fall sessions were timed to occur when turtles presumably had moved back to overwinter ponds. Following the multistate robust design capture-mark-recapture methodology (described below), we had eight trapping sessions (primary periods) between 2002 and 2005. In 2002, we had only the fall trapping session; in 2003 and 2004, all three sessions were conducted; and in 2005, we conducted only the spring session. Primary periods lasted 12 – 13 days during which we sampled all ponds in all complexes between two and four times (secondary periods). In spring, ponds were generally only sampled twice because of the large number of temporary ponds within the complexes due to spring rains and snow melt. By summer and fall sessions, virtually all temporary ponds had dried; consequently, we were able to sample all remaining ponds four times.

Analytical Methods

We used an information-theoretic approach (Burnham and Anderson 2002) to simultaneously evaluate relative support of multiple models describing relationships between survival and movement. *A priori* models were developed to address biological questions regarding survival and movement and were implemented in Program MARK (White and Burnham 1999, Cooch and White 2002). We analyzed adults and juveniles in separate models to keep the parameters to a number that could be handled by Program MARK.

Adults

We used multistate robust models to model survival within sites, movements between sites, and temporary emigration (Arnason 1973, Pollock 1982, Hestbeck et al. 1991, Brownie and Robson 1993, Kendall and Nichols 1995, Kendall et al. 1995, Kendall et al. 1997). These models estimate apparent survival (ϕ), movement (Ψ), and capture probabilities (*p*) simultaneously. Apparent survival (ϕ_t^A) is the probability that an animal in location A (i.e., pond complex A) in primary period *t* is alive and in one of the five complexes in primary period $t + 1$; capture probability (p_t^A) is the probability of capturing an animal that was alive at time *t* and associated with location A; movement (ψ_t^{AB}) is the probability that an animal alive in location A at primary period *t* is in location B at time $t + 1$, given that it survives until $t + 1$. Within Ψ, we modeled an unobservable state to examine temporary emigration (Kendall et al. 1997). Modeling strategy and model notation generally followed the approach of Lebreton et al. (1992). Sex was treated as an individual covariate to keep the number of parameters in the models manageable. Linear constraints (i.e., logit scale) were used for modeling relationships between survival and covariates.

We used “multistate” to refer to the five pond complexes (Ponds A – E; Fig. 1). We treated each pond complex as a geographical isolate and designated each as a local population because the distance between complexes was greater than normal daily movements which are usually less than 200 m (Gibbons 1968b). One exception was that we treated two ponds (B and C) that were 80 m apart as separate populations because they were separated by a Highway 93 (Fig. 1).

Juveniles

Any individual first captured as a juvenile (≥ 50 and ≤104 mm PL) was considered a juvenile throughout the study and only included in the juvenile analysis. Because transitioning from juvenile to adult is based on growth and, thus, is not deterministic, we were unable to model this transition and still keep the number of parameters to a reasonable number. Only two juvenile turtles moved between pond complexes; therefore, we restricted our juvenile analysis to Pollock’s robust design model (Pollock 1982) which does not include movement between local populations (i.e., pond complexes) yet allows for temporary emigration (γ_t) (Kendall and Nichols 1995, Kendall et al. 1995, Kendall et al. 1997). Parameters ϕ and p were defined and modeled in the same process as the adult analysis. Of the temporary emigration parameters; γ_t'' is the probability that an animal is absent from the pond complex at time t if absent at time t - 1, and γ_t' is the probability that an animal is absent at time t if present at time t – 1. We also used the same covariates as in the adult analysis to examine whether they varied over time (season and year), space (pond complex), and habitat quality (depth and volume).

Models of Capture, Movement, and Survival Probabilities

We followed a sequential modeling process for both the adults and the juveniles in which we first sought parsimonious models for p and Ψ and then used resulting parameterizations as the basis for developing models of survival probabilities. Because p can strongly influence estimates of other parameters, it was modeled first. In this first step, we asked whether p differed across populations, time, or sex. The robust design also allowed us to examine capture heterogeneity (e.g., trap happy or trap shy). In the second step, we modeled potential predictor variables for Ψ including time (season and year), distance (linear distance), habitat quality (as measured by pond depth and volume), sex, and temporary emigration. Once we found a parsimonious model on Ψ, we held movement constant. For our survival analysis, movement was modeled as a function of distance between ponds, pond depth, and seasons (i.e., winter, early summer, and late summer) and temporary emigration was modeled as random and as a function of seasons (i.e., winter, early summer, and late summer). Movement probabilities (both between populations and temporary emigration) are fully examined in a companion paper (Chapter 3).

Finally, survival probabilities were modeled to examine variation over time (season and year), space (pond complex), habitat quality (as measured by pond depth and volume), sex, and distance to the highway (site specific covariate). "Season" consisted of the intervals between trapping sessions: "winter" was 9 months from September to May; "early summer" was 1.5 months from late May to July; and "late summer" was 1.5 months from mid-July to late August. We also modeled "season" as only two seasons (winter and summer) which combined data from early and late summer.

Annual survival probability is the product of survival probabilities during the three seasons of the annual cycle, i.e., $\phi_{\text{annual}} = \phi_{\text{winter}} * \phi_{\text{early summer}} * \phi_{\text{late summer}}$. The associated variance in ϕ_{annual} was estimated with the delta method (Seber 1982, Williams et al. 2002).

Model Selection and Goodness of Fit

Hypotheses were evaluated using model selection based on Akaike's Information Criteria (AIC) (Akaike 1973). Models with low AIC values are parsimonious in that they fit the data reasonably well with a relatively small number of parameters. We used AIC_c which includes a small sample-size, second-order bias adjustment which is recommended when the number of estimated parameters is large relative to the sample size (Burnham and Anderson 2002). Models within two AIC values of the best approximating model were considered in the discussion (Burnham and Anderson 2002). Model selection uncertainty in the parameter estimates was incorporated by model averaging all models within two AIC values.

We used goodness-of-fit as a diagnostic procedure for testing the assumptions underlying the models. The assumptions for these models included those for the respective closed and open models (Seber 1982, Pollock et al. 1990). When a lack of fit or overdispersion was found in the data, this reflected either a lack of independence or heterogeneity among individuals (Pollock et al. 1990). Currently, no formal goodness-of-fit test is available for multistate capture-mark-recapture models. For both the adult and juvenile analyses, we tested for overdispersion using the variance inflation factor ($\hat{c}$) from the Pearson goodness-of-fit chi-square statistic of the most general model and its degrees of freedom ($\hat{c} = \chi^2/\mathrm{df}$) (Lebreton et al. 1992) using MSSRVRD (Multi-Stratum Survival and Robust Design; available on-line at www.mbr-pwrc.usgs.gov/software.html). Individual covariates cannot be included in the MSSRVRD program; therefore, $\hat{c}$ was estimated using the most highly parameterized model possible for each analysis without including covariates.

When overdispersion was detected (i.e., $\hat{c} > 1$), we used the quasi-likelihood AIC (QAIC) which inflates the sampling variance by multiplying those values by $\hat{c}$ (Burnham and Anderson 2002). When QAIC was used, we also increased the number of parameters by 1 to incorporate $\hat{c}$ (Burnham and Anderson 2002).

RESULTS

Environmental Covariates

The center ponds within each complex ranged in size from 0.64 to 1.60 ha (0.71, 1.60, 0.64, 1.22, 1.24, ponds A – E, respectively). All ponds lost water over the study period due to drought (Fig. 2). The deepest ponds (B and C) lost water yet still remained greater than 1.5 m deep at the end of the study; ponds A, D, and E started out much shallower and ended with less than 1 m of water (Fig. 2). Ponds B and C, hereafter, are referred to as “deep” and ponds A, D, and E, hereafter, are referred to as “shallow” (i.e., less hydrologically stable) ponds. Pond volume followed the same pattern as depth and ranged widely within and between ponds (range from fall 2002 to spring 2005: A, 9.9 – 2.2; B, 66.7 – 40.0; C, 15.4 – 9.6; D, 20.7 – 8.0; E, 10.4 – 1.3, all values x 1,000 m^3).

Virtually all temporary ponds within each complex dried out by the summer (July) trapping sessions.

Sample Size and Goodness of Fit

We captured and released 1,072 individual adult painted turtles 5,050 times: 517 males with 2,488 captures and 555 females with 2,562 captures. We captured and released 442 juveniles, 3,078 times. Of the 442 juveniles, 17 (< 4%) transitioned into the adult size class during the course of our study. Most of the turtles in the juvenile category were immature, however, 46 (10%) males matured during the course of our study. We did not model these transitions between stage-classes to keep the number of parameters manageable.

The Pearson's goodness of fit test statistics under our most parameterized models indicated overdispersion in both the adult and juvenile data: adult $\hat{c}$ value was 2.48 ($\chi^2 = 1248.9$, df = 504, P = 0.0) and the juvenile $\hat{c}$ value was 2.05 ($\chi^2 = 444.2$, df = 217, P = 0.0). We, therefore, applied these $\hat{c}$ values in all subsequent model fitting in adult and juvenile analyses.

Probability of Capture

In both the adult and juvenile analyses, the top model for *p* was an interaction between pond and trapping session. Sex was not an important factor in capture probability of adults. Although the model that included sex was within 2 QAICc ($\Delta QAIC_c = 1.03$), the lower and upper confidence intervals overlapped 0 ($\beta_{sex} = 0.7$, SE = 0.7, LCI and UCI = -0.07-0.22, respectively). We modeled variations of time, season, and pond, and no other models were within 2 QAICc of the top models for either adults or juveniles.

Estimates of capture probabilities in the top model ranged widely within and between ponds for both adults (Fig. 3) and juveniles (Fig. 4). Pond B, the largest and deepest pond, generally had the lowest capture probabilities for both juveniles and adults in each capture session.

Probability of Survival

In the adult analysis, two models were virtually within 2 $QAIC_c$. The most parsimonious model ($\phi_{pond*season2+year}$) indicated survival rate of adults varied significantly among ponds by two seasons (summer and winter) and year (Table 1). The second model ($\Delta QAIC_c = 2.01$) was the same as the first except sex was also included (Table 1). However, the 95% confidence intervals of the β_{sex} value overlapped 0 ($\beta_{sex} = 0.052$, SE = 0.261, 95% CI = -0.460, 0.563) indicating survival estimates for males and females overlap and, therefore, the difference is not biologically significant. Other factors had little influence on survival estimates; depth ($\Delta QAIC_c = 109.4$), volume ($\Delta QAIC_c = 128.0$), distance to road ($\Delta QAIC_c = 135.3$) (Table 1).

Only the top model was used to estimate apparent survival probabilities. Adult apparent survival rates were relatively high in the two "deep' pond (B and C) compared with the "shallow" ponds (A, D, and E) (Fig. 5). In the "deep" ponds, apparent survival rates followed the general pattern of higher survival probabilities in the winter than in the summer with an overall decline over the years (Fig. 5). Rates ranged from a high of 0.99 (SE = 0.008) in pond B in winter 2003 to a low of 0.63 (SE = 0.074) in pond C in winter 2005. Apparent survival rates in the "shallow" ponds varied greatly among and within ponds and did not follow any particular pattern (Fig. 5). Pond D had higher survival in winter ($\phi = 0.99$, SE = 0.02) than summer ($\phi = 0.52$, SE = 0.048), but pond A had higher survival ($\phi = 0.89$, SE = 0.034) in summer than winter ($\phi = 0.11$, SE = 0.072). Seasonal survival estimates for adults in the last interval (winter 2005) were lower than previous interval estimates. At the end of the analysis series, animals that may have temporarily emigrated do not have the opportunity to return to the study area; therefore, the last estimates of survival may appear to be lower than previous estimates (Converse et al. 2005).

Annual survival rates for adults decreased from 2003 to 2004. We found considerable spatial variation with survival in "deep" ponds higher than survival in "shallow" ponds (Fig. 6).

In the juvenile analysis, the top model, $\phi_{pond*season2+year}$ had a weight of 0.946 and was the same as the top model for adults (Table 2). Apparent survival probabilities for juveniles varied greatly within and among ponds but, in contrast to the adult estimates, the “shallow” ponds had generally higher and less varied survival estimates than “deep” ponds. The “deep” ponds (B and C) had similar patterns of high summer survival (0.911, SE = 0.063; 0.971, SE = 0.024, respectively) and low winter survival (0.381, SE = 0.086, 0.407, SE = 0.090, respectively) (Fig. 7). The “shallow” ponds had generally higher survival of juveniles and less variation than the “deep” ponds.

Annual survival rates for juveniles increased from 2003 to 2004 in most ponds, contrary to the adult estimates. Similar to adults, we also found considerable spatial variation in annual survival rates of juvenile; however, the pattern was reversed with “shallow” ponds having higher rates than “deep” ponds (Fig. 8). Pond A was the only pond where juvenile annual survival decreased.

DISCUSSION

Ours is the first study to examine seasonal survival rates simultaneously within different populations (pond complexes) using rigorous statistical methods for any turtle species. Overall, apparent survival rates of western painted turtles varied both spatially and seasonally. Patterns of variation differed between juveniles and adults.

Annual Apparent Survival

Although similar factors (i.e. pond, seasons, and year) influenced apparent survival rates in both juveniles and adults, we found very different patterns spatially and annually between the stage classes. Pond depth differentially affected class-specific apparent survival rates. Adults had higher apparent survival in deep ponds than in shallow (i.e., less hydrologically stable) ponds but the pattern for juveniles was reversed; juveniles in shallow ponds had higher apparent survival rates than those in deep ponds (Figs. 7 and 8).

Reported annual survival rates for painted turtles vary greatly. In general, adults have higher survival rates than juveniles. Annual survival rates for adults range from 0.29 to 0.96 while juveniles range from 0.21 to 0.98 (Wilbur 1975a, Mitchell 1988, Zweifel 1989, Frazer et al. 1991). We found considerable spatial variation with the highest annual survival rates for adults occurring in “deep” ponds (range: 0.57 [SE =

0.02] to 0.93 [SE = 0.16]) and the lowest survival rates occurring in “shallow” ponds (range: 0.12 [SE = 0.03] to 0.61 [SE = 0.11]). Annual survival of juveniles ranged from a low of 0.34 (SE = 0.08) in “deep” ponds to a high of 1.0 (SE = 0) where no mortality occurred in a shallow pond.

In other studies, females generally have lower survival rates than males (0.84 female/0.86 male, Wilbur 1975a; 0.29 – 0.50 female/0.64-0.83 male, Frazer et al. 1991). No estimates of variance were provided; therefore, it is difficult to definitively determine if the differences were statistically significant. Differential mortality in females on nesting forays may increase chances of mortality due to roads (Haxton 2000, Steen and Gibbs 2004, Aresco 2005, Gibbs and Steen 2005). However, we found no difference between the sexes in apparent survival rates. Our study may exhibit different results because in a drought situation both males and females may move out of drying ponds whereas in normal water years females may make more terrestrial movements because of the need to nest on land.

The effects of road mortality on population dynamics of turtles is a growing concern (Gibbs and Shriver 2002, Steen and Gibbs 2004, Aresco 2005, Gibbs and Steen 2005, Steen et al. 2006). We expected ponds adjacent to the highway to have lower survival rates than ponds far from the highway. However, ‘distance from highway’, a pond-specific covariate, did not influence apparent survival rates in our ponds. This may be because the ponds furthest from the road lost the most water, forcing turtles to move. This movement may have increased road mortality in ponds far from the highway while ponds adjacent to the highway had less forced movements because they retained water. Road mortality associated with each pond complex is discussed in chapter 3.

Apparent survival models can not separate between mortality and permanent emigration, so only survival within the study area is estimated; true survival is at least equal to, and expected to be higher than, apparent survival. We attempted to include the entire population (metapopulations) and movements between all local populations in this study; however, even on this relatively small scale it was difficult to identify and sample all important habitats simultaneously. To minimize the effects of emigration, we modeled temporary emigration; nevertheless, it is not likely that all turtles that emigrated temporarily returned to the area because water levels had not yet begun to recover by the end of our study. After data collection ended, some adults were observed moving back into the shallow ponds. Only longer-term studies would help to elucidate the role of movements to refugia sites off the study site. Buhlmann and Gibbons (2001) observed site fidelity to refugia in successive years for some turtle species.

In deep ponds, annual survival of adults was much greater than survival of juveniles; however, this pattern was reversed in shallow ponds with juveniles having higher survival than adults (Figs. 7 and 8). Annual survival estimates for adults in shallow ponds may be artificially low due to high rates of emigration. Turtles likely emigrated during the drought and shallow ponds experienced a greater exodus than deeper ponds, thus, confounding survival rates especially in the drying ponds. Adults were more likely to move off the study site than juveniles. No juveniles were observed to move between complexes during the study and the abundance of juveniles remained relatively constant over the study while adults were observed to move and the abundance of adults had a negative trend, particularly in the shallow ponds.

Seasonal Apparent Survival

The annual cycle of painted turtles includes overwinter hibernation and summer activities that may involve both short- and long-distance movements including nesting by females, mate seeking by males, and seasonal use of temporary habitats (Gibbons et al. 1990). During drought conditions, movements out of unsuitable habitats may also be required.

In general, adult turtles in all ponds experienced lower apparent survival in summer than in winter for each year. Adults in deep ponds had higher and less variable apparent survival rates over the seasons than adults in shallow ponds. This pattern is expected given the potential for greater risks of mortality in summer due to increased movements which increases the chance of mortality from roads and exposure to predators. Only aquatic predators are able to locate and consume turtles overwinter during hibernation.

Adult turtles in shallow ponds experienced greater variation between summer and winter apparent survival rates than adults in deep ponds where turtles were less likely to emigrate. Turtles in shallow ponds either moved, thereby increasing mortality due to roads or increased exposure to predators, or they remained in the ponds with potentially suboptimal hibernation habitat, thus increasing the risk of overwinter mortality.

One shallow pond (pond A) did not follow the above patterns. Adults in this pond had lower survival in winter than summer. It is likely that this pond froze to the bottom or experienced prolonged anoxic conditions in winter 2004. In spring, we collected 13 dead turtles (juveniles and adults) in our nets. All these turtles were fully intact; therefore, mortality was not due to predation.

We also found a pattern of lower apparent survival over time; therefore, apparent survival rates in 2004 were lower than corresponding seasons in 2003. This was likely due to a combination of truly lower survival because of lower quality habitats and permanent emigration.

Juveniles in shallow ponds experienced higher and less variable survival than juveniles in deep ponds (Fig. 6) which is the reverse of adult estimates. Apparent survival in winter in shallow ponds was higher than summer which is similar to the adult pattern. Juveniles were less likely than adults to emigrate from shallow ponds which could account for the higher survival and less variation of juvenile estimates compared with adults. Similar to the adults, one shallow pond (pond A) did not follow the same pattern as the other shallow ponds. Three dead juvenile turtles were also found fully intact in this pond the following spring.

Unexpected results occurred in deep ponds where juveniles experienced significantly lower apparent survival during winter than summer. This could be due to two possible reasons: 1) intraspecific competition for optimal hibernation sites, or 2) size-specific predation. In the first case, both adults and juveniles overwintered in the deep ponds, whereas, most adults had emigrated from the shallow ponds. Therefore, adults could be taking the best hibernation sites in the deep ponds. Although painted turtles do choose hibernation sites that differ from random (Taylor and Nol 1989), I could find no literature regarding intraspecific competition for hibernation sites. Competition would require hibernation sites to be a limited resource, which seems unlikely given the size of the ponds and the density of turtles. The second case of size-specific predation seems more probable. Only the deep ponds were observed to have muskrats (*Ondatra zibethicus*) and mink (*Mustela vison*) which are the only resident aquatic predators in this ecosystem. River otter (*Lutra canadensis*) are also known to use ponds in this area from time to time, although none were observed during our study. These three species are more likely to feed on juveniles than adults (Brooks et al. 1991, Brown and Brooks 1994, Ernst et al. 1994).

Drought Conditions Confound Mortality and Permanent Emigration

Survival patterns were dictated in part by local environmental conditions such as the hydrology of ponds (i.e., pond depth). Drought, with the subsequent drying of ponds, forces turtles to either move or potentially hibernate in suboptimal habitats. Increased emigrations by turtles in response to drought has been documented by McAuliffe (1978), Christiansen and Bickham (1989), Gibbons et al. (1983), and Lindeman and Rabe (1990). Very little movement (0 - 4%) was observed between the pond complexes (Chapter 3); therefore, it is likely turtles moved to permanent waters off the study area (Fig. 1). Pond drying in winter can also result in an increased rate of mortality due to exposure of hibernating turtles to freezing temperatures or prolonged anoxic conditions (Christiansen and Bickham 1989, Ultsch 2006). We observed overwinter mortality when dead turtles were collected in our nets during the spring trapping sessions. Overwinter mortality has also been documented by Taylor and Nol (1989), Brooks et al. (1991), and Bodie and Semlitsch (2000). Drought conditions complicate survival estimates because of the potential for both increased permanent emigration and increased overwinter mortality and models are not able to separate these out. Increasing the sampling area to incorporate possible locations of emigration off the study site is one way to distinguish between these two outcomes, yet this is often logistically infeasible.

Implications of variability in long-term population viability

Life history theory predicts more variability in vital rates that are not as important to individual fitness or future population growth (Pfister 1998). Adult survival tends to have greater influence than juvenile survival on the population dynamics of long-lived species such as sea turtles (Crowder et al. 1994, Heppell et al. 2000); however, population viability analysis on European pond turtles (*Emys orbicularis*) indicated that models were sensitive to both adults and juveniles survivorship (Rivera and Fernández

2004). Given the high variability in adult and juvenile survival in our study, future modeling attempts should thoroughly incorporate the spatial/temporal variation in survival of both age classes and carefully examine the population dynamic consequences of this variation (Ozgul et al. 2006). We provide empirical information that can be used to generate realistic population viability and metapopulation models for painted turtles as a conservation planning tool.

Future Analyses

No modeling techniques currently exist that allow modeling of survival as a function of movement. Given that turtles are likely to be killed in the process of moving, this could be an important development to determine the actual "cost" associated with movement. Although few fields in modern ecology have developed as fast as the techniques of analyses of marked individuals in the study of populations (Seber and Schwartz 2002) the need for new and more realistic modeling scenarios appears insatiable. Barker and White (2004) considered the construction of the "mother-of-all-models" which would allow the researcher to customize the model design to the available data.

Summary

Survival rates of painted turtles exhibit both spatial and seasonal variation and the pattern of variation is different between stage-classes. The conservation of aquatic turtle species, requires a mosaic of wetland types across the landscape. The value of small, less hydrologically stable, wetlands to long-term population persistence of turtles could be very important given their importance for juvenile survival. These small wetlands have proven important for other taxa as well, such as amphibians (Skelly et al. 1999), waterfowl (Batt et al. 1989, Yerkes 2000), small mammals, and birds (Gibbs 1993, Farmer and Parent 1997). Wetland complexes differ in their potential to provide suitable habitat because different species, and sometimes stage-classes within a species, have life histories that influence how each interacts with the landscape (Naugle et al. 2005).

Another conservation measure that could be important for some populations is the installation of wildlife crossing structures such as culverts that could minimize the effects of road mortality on the population. Mortality due to roads is likely influencing survival rates of turtles given that apparent survival rates were lowest in summer when adult turtles were moving. This is especially true in drought years when more turtles are forced to move across the landscape.

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Table 1. List of candidate set of survival models of capture-mark-recapture data collected on adult painted turtles within 5 pond complexes using multistate robust models in Montana 2002-2005. Factors affecting movement and capture probabilities were held constant at $\Psi_{\text{depth+distance+season3}}$ + temporary emigration $_{\text{random+season3}}$ and $p_{\text{pond*session}}$. Models are listed in ascending order of QAIC$_c$, with the lowest values indicating the best models. The most parsimonious models are highlighted in bold.

Model	QAIC$_c$	ΔQAIC$_c$	w$_i$	K
ϕ pond*season2+year	**7083.36**	**0**	**0.7305**	**60**
ϕ pond*season2+year+sex	7085.37	2.01	0.2674	61
ϕ pond+time	7096.45	13.09	0.0011	59
ϕ pond+season2+year	7097.20	13.84	0.0007	56
ϕ pond+season3+year	7098.76	15.40	0.0003	57
ϕ pond*season2	7110.71	27.35	0	58
ϕ pond+season3	7124.51	41.15	0	55
ϕ season3	7167.89	84.53	0	51
ϕ pond+depth	7191.57	108.20	0	54
ϕ depth	7192.80	109.44	0	50
ϕ pond+volume	7196.83	113.47	0	54
ϕ pond+year	7207.17	123.81	0	55
ϕ volume	7211.38	128.02	0	50
ϕ pond	7215.51	132.15	0	53
ϕ distance to highway	7218.66	135.30	0	50
ϕ constant	7228.57	145.21	0	49
ϕ sex	7230.60	147.24	0	50

Notes: Akaike's Information Criterion corrected for small sample size and overdispersion (QAIC$_c$), differences in QAIC$_c$ values (ΔQAIC$_c$), QAICc weights (w$_i$), and number of parameters (K) are given for each model. Subscripts give parameterization for ϕ: constant = constant over space and time; "time" = variation by sampling period; "pond" = variation over space (i.e., pond complex); "season2" = variation over winter and summer (combines early summer and late summer); "season3"

= variation over 3 seasons (winter, early summer, and late summer); “year” = variation by 2003, 2004, and 2005; “sex” = variation between males and females; “volume” = variation by pond volume each session; “depth” = variation by pond depth each session; and “distance to highway” = variation by distance between pond center and closest point on the highway. Subscripts joined by “+” indicate an additive model and “*” indicates a factorial model. Not all models shown. Models that did not converge or had parameters estimated with singular values are not shown.

Table 2. List of candidate set of survival models for juvenile painted turtles collected within 5 pond complexes using capture-mark-recapture data, Montana 2002-2005. Factors affecting random temporary emigration and capture probabilities were held constant at $\gamma' = \gamma''_{\text{early summer – late summer/winter}}$ and $p_{\text{pond*session}}$, respectively. Models are listed in ascending order of QAIC$_c$, with the lowest values indicating the best models. The most parsimonious models are highlighted in bold.

Model	QAIC$_c$	ΔQAIC$_c$	w_i	K
$\phi_{\text{pond*season2+year}}$	**3670.85**	**0**	**0.9462**	**52**
$\phi_{\text{pond*season3+year}}$	3676.79	5.93	0.0487	56
$\phi_{\text{pond+season3+year}}$	3681.73	10.88	0.0041	49
$\phi_{\text{pond+season2+year}}$	3684.99	14.14	0.0008	48
$\phi_{\text{pond+ time}}$	3685.01	14.15	0.0008	51
$\phi_{\text{pond*season2}}$	3685.03	14.18	0.0008	50
$\phi_{\text{pond*season3}}$	3689.17	18.31	0.0001	54
$\phi_{\text{pond+season3}}$	3692.92	22.07	0	47
$\phi_{\text{pond+year}}$	3694.89	24.04	0	47
$\phi_{\text{pond+season2}}$	3695.22	24.36	0	46
$\phi_{\text{pond+depth+year}}$	3696.96	26.10	0	48
$\phi_{\text{pond+depth}}$	3697.27	26.42	0	46
$\phi_{\text{pond+volume}}$	3701.39	30.54	0	46
ϕ_{pond}	3701.86	31.00	0	45
ϕ_{depth}	3708.36	37.51	0	42
ϕ_{season3}	3714.42	43.57	0	43
ϕ_{season2}	3716.09	45.24	0	42
ϕ_{volume}	3716.39	45.53	0	42
ϕ_{constant}	3722.56	51.71	0	41
$\phi_{\text{pond*season2*year}}$ sin - link	4092.59	421.74	0	60
$\phi_{\text{pond*time}}$ sin - link	4102.67	431.82	0	69

Notes: Akaike's Information Criterion corrected for small sample size and overdispersion (QAIC$_c$), differences in QAIC$_c$ values (ΔQAIC$_c$), QAICc weights

(w_i), and number of parameters (K) are given for each model. Subscripts give parameterization for ϕ: constant = constant over space and time; “time” = variation by sampling period; “pond” = variation over space (i.e., pond complex); “season2” = variation over winter and summer (combines early summer and late summer); “season3” = variation over 3 seasons (winter, early summer, and late summer); “year” = variation by 2003, 2004, and 2005; “sex” = variation between males and females; “volume” = variation by pond volume each session; “depth” = variation by pond depth each session; and “distance to highway” = variation by distance between pond center and closest point on the highway. Subscripts joined by “+” indicate an additive model and “*” indicates a factorial model. Not all models shown. Models that did not converge or had parameters estimated with singular values are not shown.

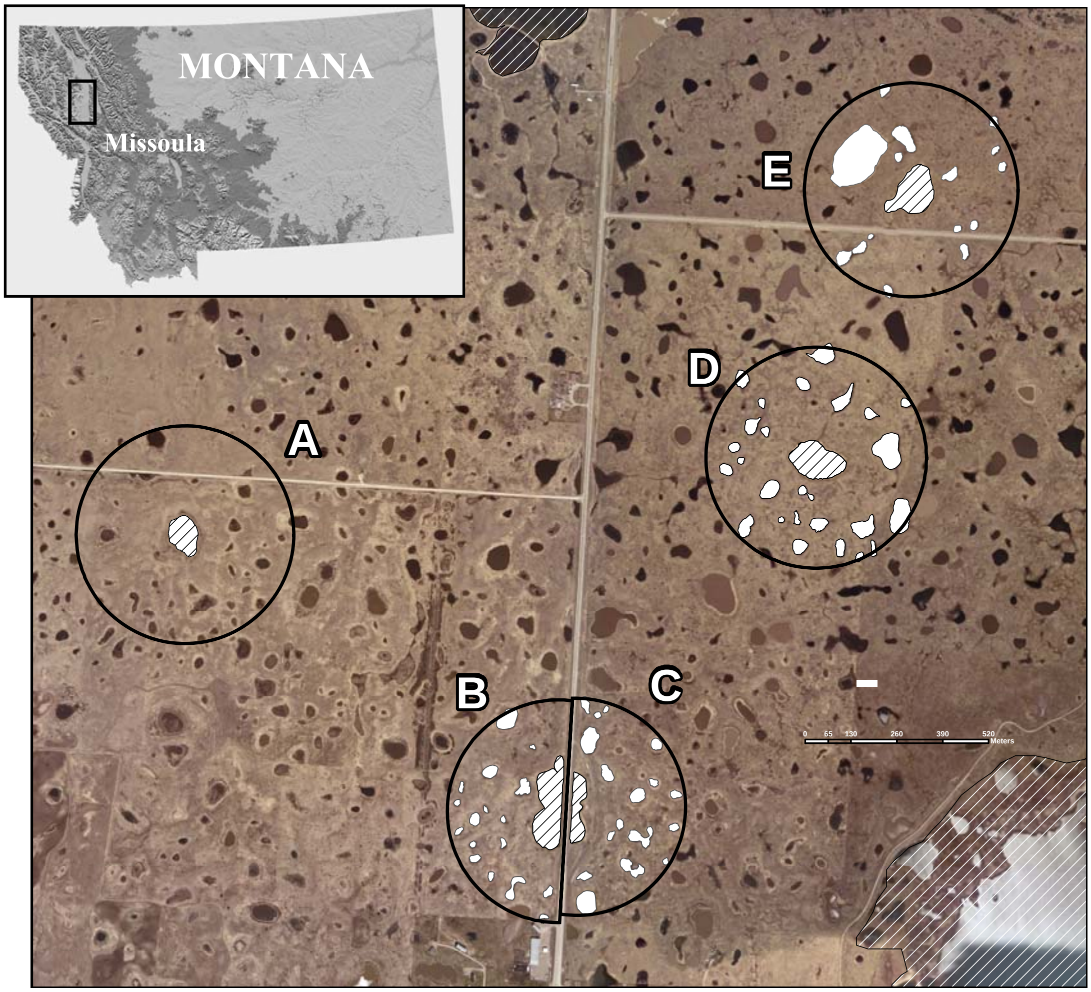

Fig. 1. Aerial photo of study area in the Mission Valley of Montana. Pond complexes are centered on “permanent” overwinter ponds (white with black hatch marks) and are labeled A – E. All temporary ponds within complexes (white) were sampled when water was present. Note: temporary ponds in Complex A never held water during my study. The rest of the photo shows temporary ponds outside the complexes. Virtually all temporary ponds were dry by the end of July each year. Two permanent bodies of water occur in the area, Kicking Horse Reservoir and an irrigation pond (white hatched areas, upper center and lower right of photo). Also, note that U.S. Highway 93 runs north – south through the study area.

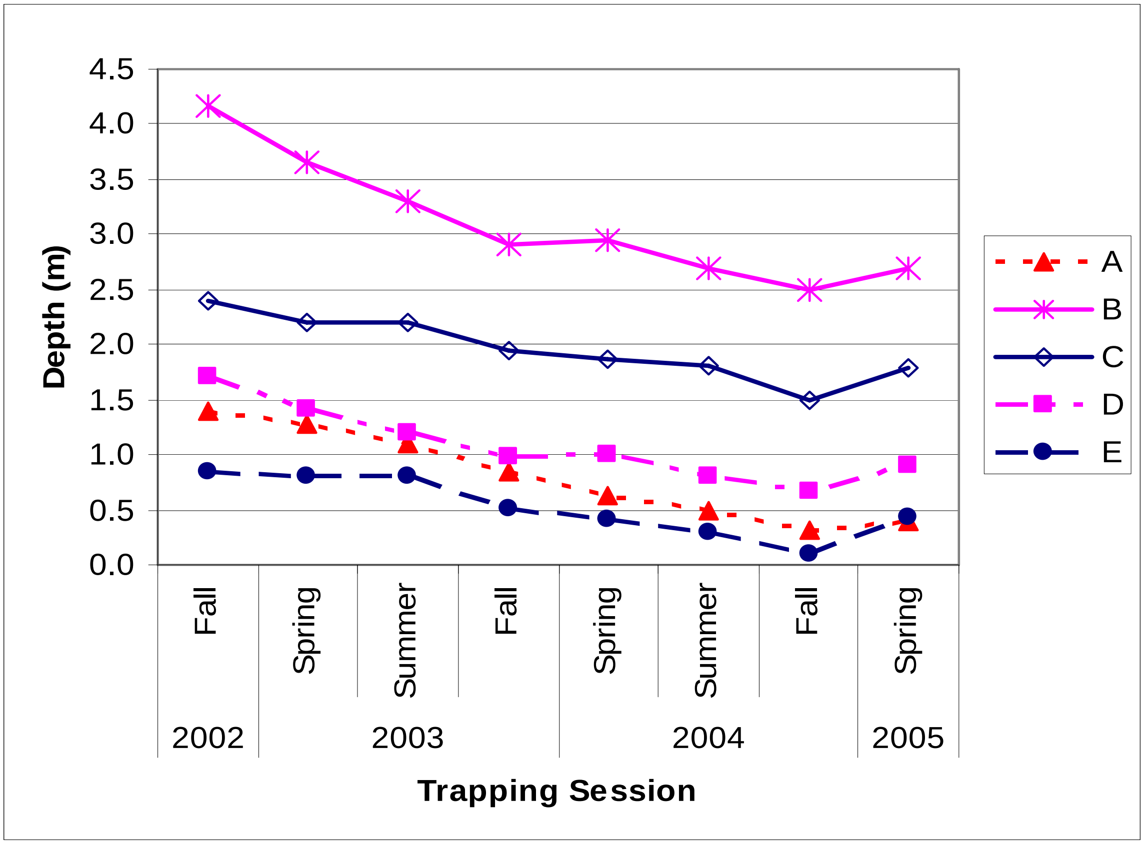

Fig. 2. Depth of water in the center pond of each complex from fall 2002 to spring 2005 in western Montana. Dashed lines represent “shallow” ponds (A, D, and E) and solid lines represent “deep” ponds (B and C) in all subsequent graphs.

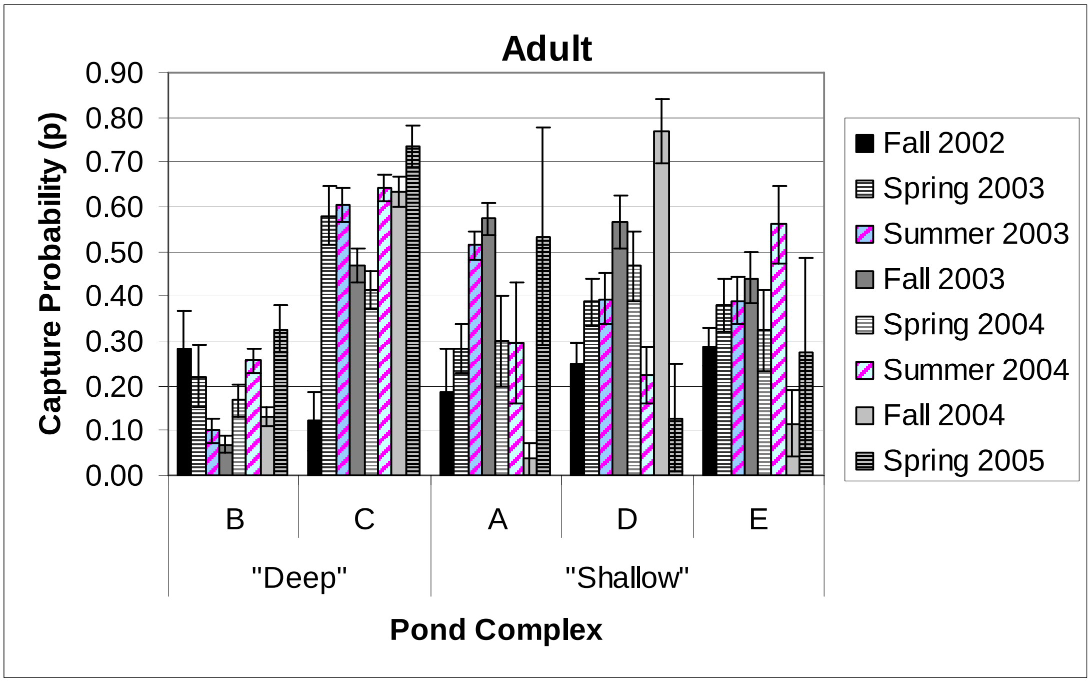

Fig. 3. Estimates of capture probability for adult painted turtles by pond complex and trapping session in western Montana, 2002-2005. Bars represent standard errors.

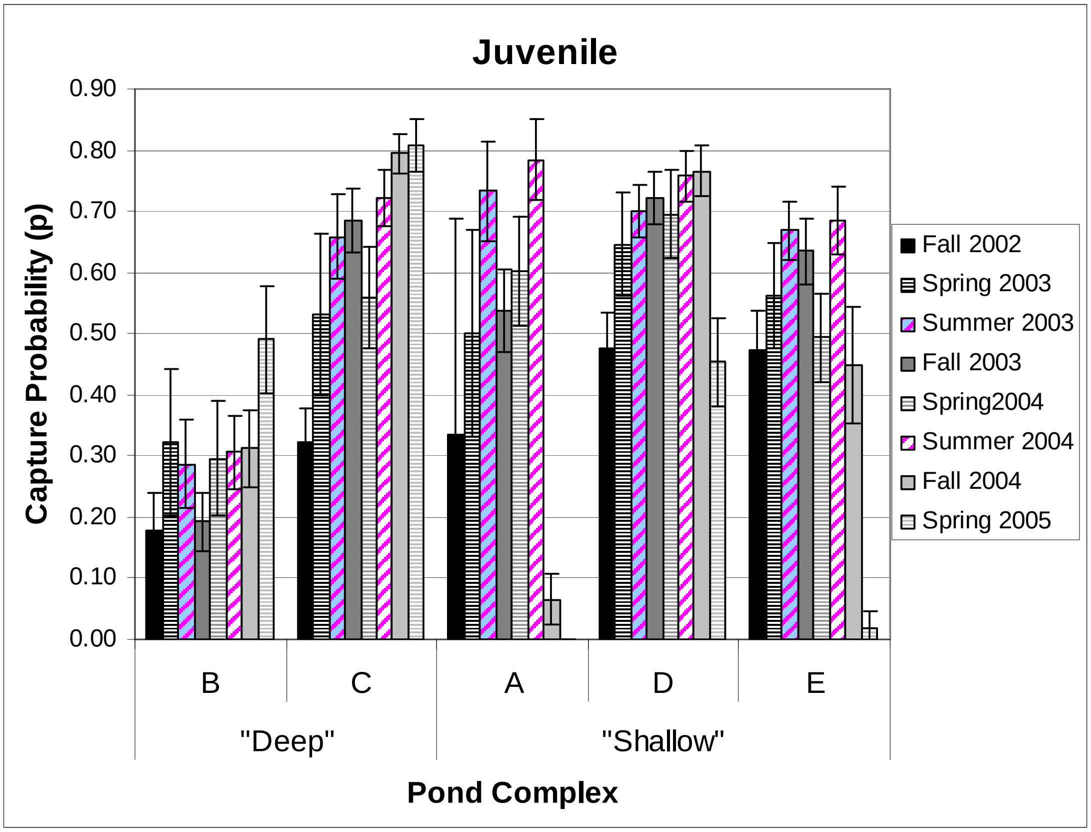

Fig. 4. Estimates of capture probability for juvenile painted turtles by pond complex and trapping session in western Montana, 2002-2005. Bars represent standard errors.

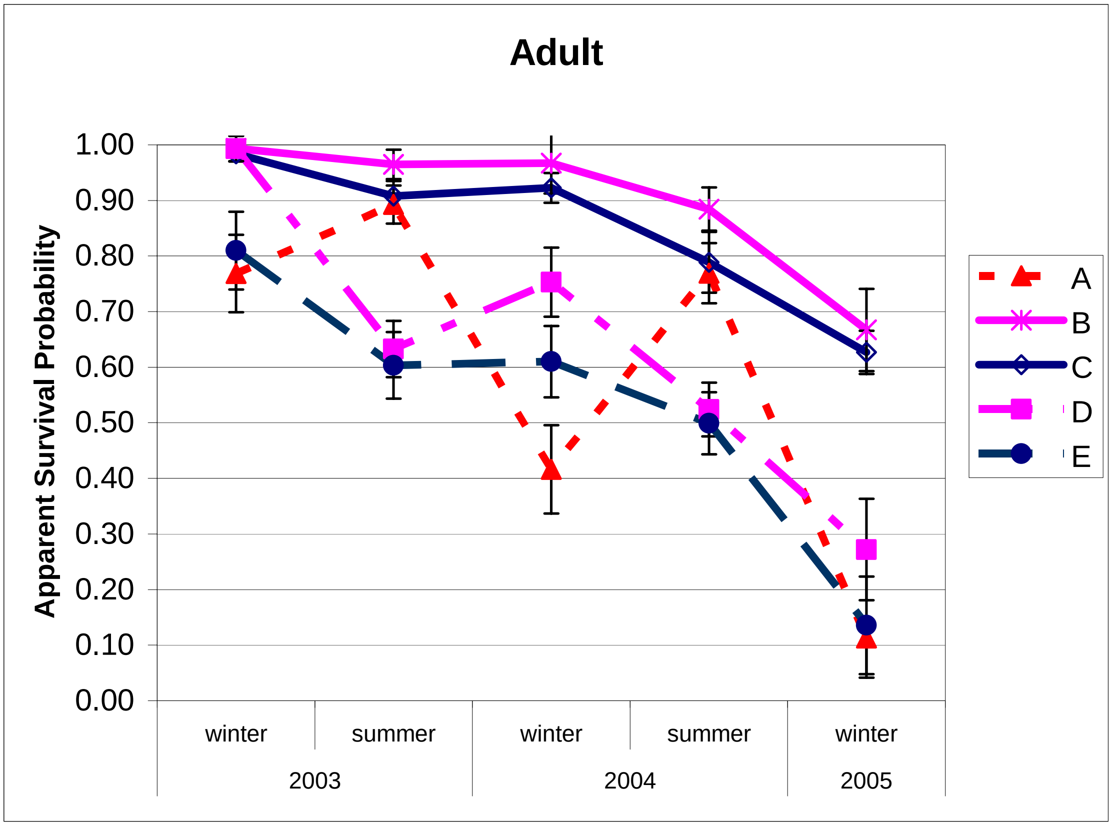

Fig. 5. Seasonal estimates of apparent survival of adult painted turtles by pond complex and year (estimates are based on top model) in western Montana, 2002-2005. Solid lines represent ponds that retained water (B and C) during the drought and dashed lines represent ponds that lost substantial water (A, D, and E). Bars represent standard errors.

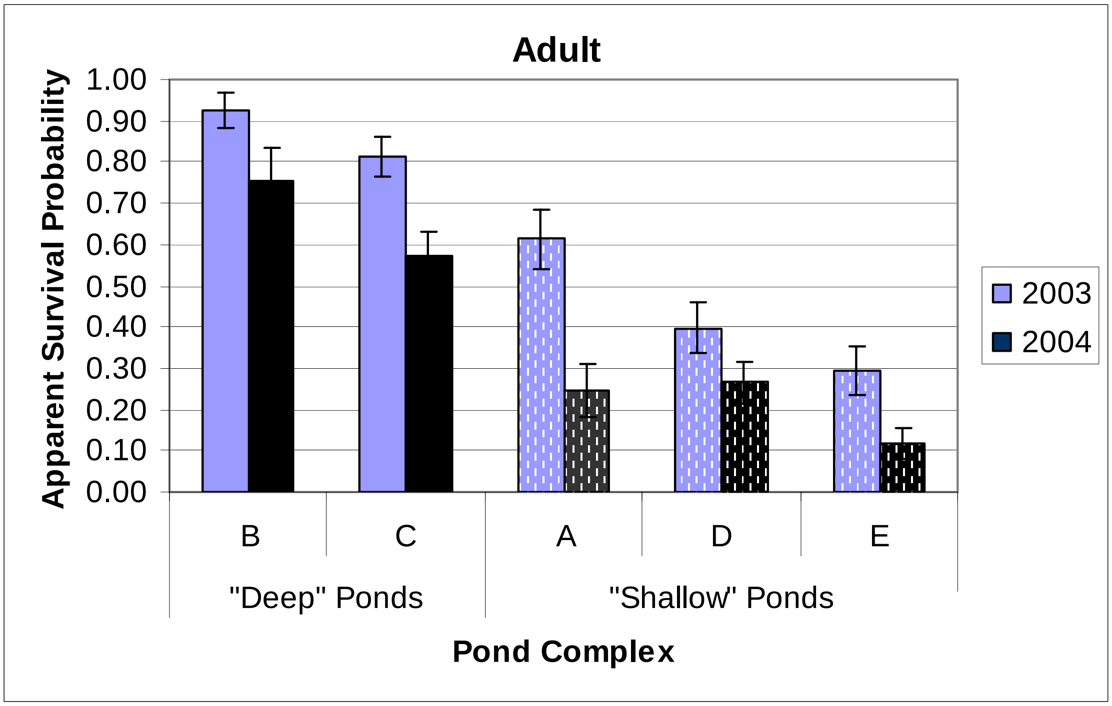

Fig. 6. Annual estimates of apparent survival of adult painted turtles by pond complex and year in western Montana, 2003-2004. Stippled boxes represent “shallow” ponds and solid boxes represent “deep” ponds. Bars represent standard errors.

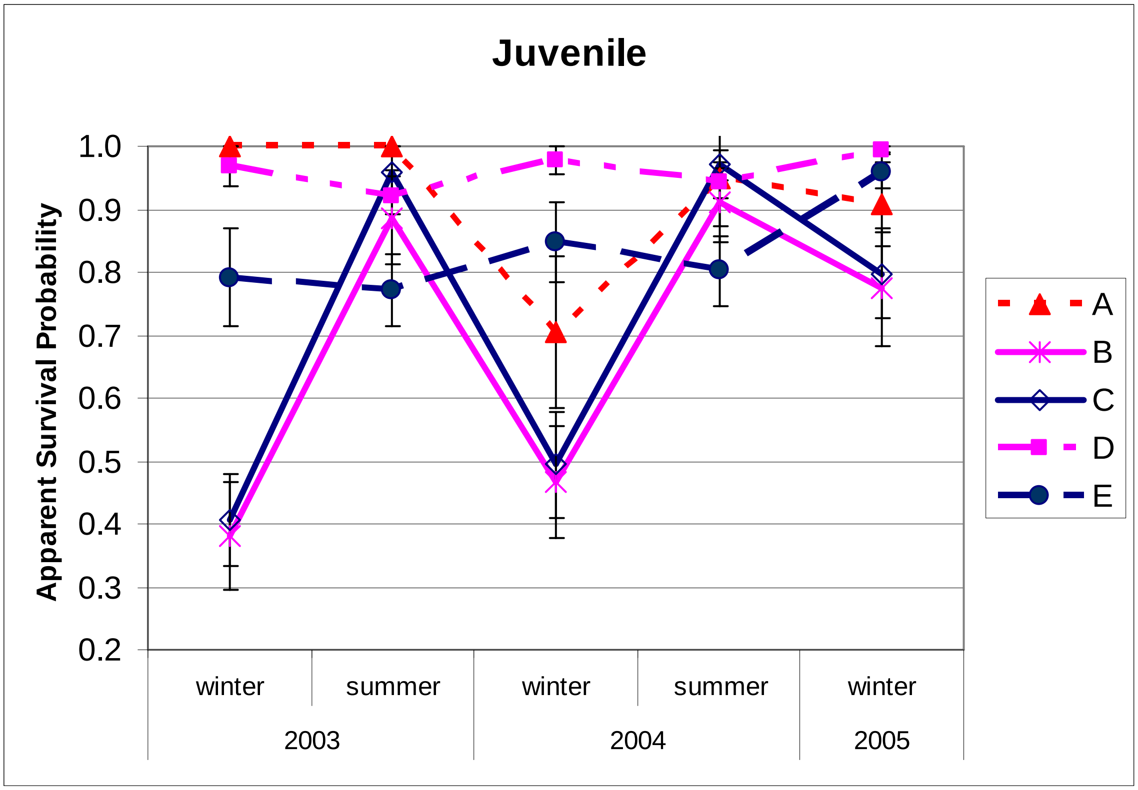

Fig. 7. Seasonal estimates of apparent survival of juvenile painted turtles by pond complex and year in western Montana, 2002-2005. Solid lines represent ponds that retained water (B and C) during the drought and dashed lines represent ponds that lost substantial water (A, D, and E). Bars represent standard errors.

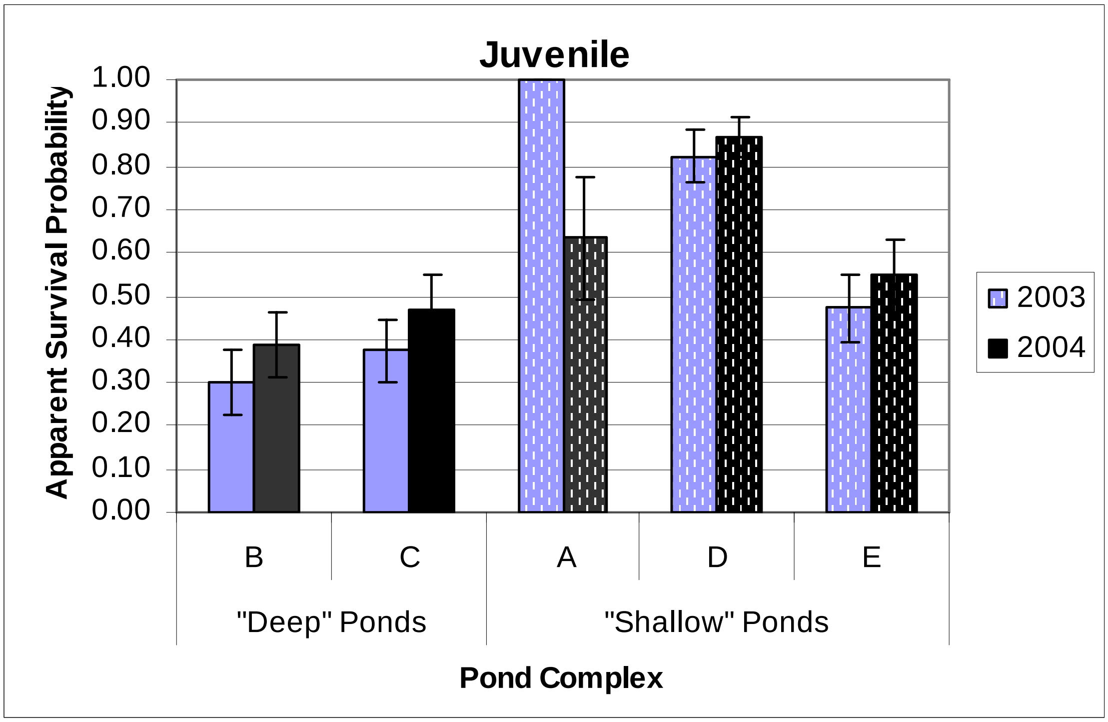

Fig. 8. Annual estimates of apparent survival of juvenile painted turtles by pond complex and year in western Montana, 2003-2004. Stippled boxes represent “shallow” ponds and solid boxes represent “deep” ponds. Bars represent standard errors.

CHAPTER 3. MOVEMENT AND POPULATION GROWTH RATE OF WESTERN PAINTED TURTLES IN A WETLAND ECOSYSTEM IN MONTANA

ABSTRACT

Individuals within most wildlife species are distributed unevenly across the landscape due to variations in ecological characteristics. The distance and rate of movements among patches can affect population dynamics of the larger regional population. Understanding factors that affect age- and sex-specific movement rates is important in determining what factors influence population dynamics and spatial structure. In spite of the critical importance of movement, few empirical estimates of movement rates or their effect on spatially structured populations have been conducted on most taxonomic groups.

We used capture-mark-recapture (CMR) methods to estimate movement probabilities of western painted turtles (*Chrysemys picta bellii*) in a wetland ecosystem in western Montana. We used multistate robust models for adults and Pollock's robust models in juveniles to estimate both interpopulation movements and temporary emigration in adults and temporary emigration in juveniles. Ours is the first study to examine interpopulation and temporary emigration movement probabilities for a freshwater turtle species using statistically rigorous methods.

We used a stage-based, multi-site, matrix population model to assess the population-level consequences of movement and roads. We used apparent survival and movement rates generated by CMR analyses and road mortality rates from surveys conducted over the same time period.

Overall, interpopulation movement probabilities were very low (< 0.04). Temporary emigration rates were slightly higher (0.069 for adults and 0.047 for juveniles). The probability of interpopulation movement of adults was influenced most by distance between ponds and depth of pond of origin. The presence of the highway had a strong negative effect on movement probabilities and contrary to expectations, sex did not influence the probability of movement. Population growth rates were negatively influenced by the presence of roads and positively influenced by movements.

INTRODUCTION

Individuals within most wildlife species are distributed unevenly across the landscape due to variations in ecological characteristics (Stacey et al. 1997). These groups of individuals or patches form local populations which, at the landscape scale, can have considerable influence on population dynamics (Pulliam 1988, Kareiva and Wennergren 1995). Movement of individuals between local populations connects local populations into a functional demographic unit on a regional scale (Merriam 1984). The distance and rate of movements among patches creates spatial structure such as metapopulations and, thus, can affect population dynamics of the larger regional population (Wiens et al. 1993).

Movement rates are often difficult to estimate due to substantial logistical constraints such as requiring marked individuals in several locations or patches and simultaneous study in these patches (Spendelow et al. 1995). Advances in technology and analytical tools have allowed more reliable estimates of the probability of movement only recently (e.g., Spendelow et al. 1995, Blums et al. 2003, Nichols et al. 2004, Breton et al. 2006).

Capture-mark-recapture (CMR) models are statistically rigorous, can estimate the probability of movement, and allow the exploration of temporary emigration. An assumption of CMR models for open populations is that all individuals have identical capture probabilities (Seber 1982, Pollock et al. 1990). This assumption can be difficult to meet if some animals leave the study area and return during later sampling sessions. Biologically, temporary emigration can explain patterns in which 1) not all individuals return to the breeding area each year, 2) the sampling area may not include the entire home range of some individuals, and 3) activities of some individuals may prevent their detection in a given period such as when animals are underground or in torpor (Kendall et al. 1997, Kendall 1999). For example, if sampling a population at the breeding site (such as birds in a colony or amphibians in a pond) then individuals not breeding will not be available for capture that year. This situation causes variation in capture probabilities among individuals and can lead to biases and low precision of survival estimates in some model designs (Kendall et al. 1997). The most common use of temporary emigration analyses has been to determine breeding probabilities (Lindberg et al. 2001, Bailey et al. 2004a, Bailey et al. 2004b, Fretey et al. 2004, Kendall 2004, Muths et al. 2006).

In spite of the critical importance of movement, few empirical estimates of movement rates or their effect on spatially structured populations have been conducted on most taxonomic groups (Bowne and Bowers 2004). Few studies of interpopulation movements of freshwater or terrestrial turtles currently exist that adequately describe the connectivity of habitats at a landscape scale (but see Tucker et al. 2001, Dodd et al. 2006, Bowne et al. 2006). Painted turtle (*Chrysemys picta*) movements have been addressed (e.g., Sexton 1959, McAuliffe 1978, Taylor and Nol 1989, Zweifel 1989, Rowe et al. 2005), but few investigations have used statistically rigorous methods (Shine and Iverson 1995); but see (Rowe 2003, Bowne et al. 2006).

The painted turtle is an aquatic turtle that exhibits high fidelity to specific ponds and uses terrestrial habitats in a limited manner. This patchy distribution of habitat and limited dispersal capabilities may be indicative of a metapopulation structure (Sjögren 1991, Sjögren-Gulve 1994, Hecnar and M'Closkey 1996, Trenham 1998, Skelly et al. 1999). Terrestrial activity includes seasonal movements for reproduction (nesting or mate-seeking), feeding, and departure to and return from ponds as water levels change (Sexton 1959, Gibbons 1968, McAuliffe 1978, Congdon and Gatten 1989, Taylor and Nol 1989, Gibbons 1990a, Rowe et al. 2005).

We used CMR methods to estimate movement probabilities of western painted turtles (*C. p. bellii*) in a wetland ecosystem in western Montana. We estimated both interpopulation movements and temporary emigration using CMR modeling. Understanding factors that affect age- and sex-specific movement rates is important in determining what factors influence population dynamics and spatial structure (Converse et al. 2005). Interpopulation movement estimates allow us to evaluate connectivity and the spatial structure of the population while temporary emigration estimates shed light on use of adjacent habitats outside the study area and is important for conservation efforts. Temporary emigration has received little qualitative attention in turtle demographic studies except in the context of breeding probabilities of sea turtle (Kendall and Bjorkland 2001, Fujiwara and Caswell 2002, Kendall and Nichols 2002).

Finally, we used a stage-based, multi-site, matrix population model to assess the population-level consequences of movement and roads. We used survival and movement rates generated by CMR analyses for each pond population and road mortality rates from surveys conducted over the same time period as the CMR data collection.

METHODS

Study Area

The study was conducted from August, 2002 to May, 2005 in the Mission Valley of northwestern Montana (47° 27' N, 114° 04' W; elevation 920 - 940 m). The valley contains glaciated, depressional wetlands in high-densities: over 2,000 permanent and ephemeral wetlands in an area of approximately 78 km^2 (Fowle 1996). The wetlands are primarily palustrine emergent basins with various water regimes ranging from permanent to seasonally flooded (Cowardin et al. 1979). Permanent ponds are characterized by open water with very little vegetation. The surrounding matrix consists of grasslands that are ungrazed by livestock and dominated by western wheatgrass (*Agropyron smithii*), fescue (*Festuca* spp.) and invasive species such as Kentucky bluegrass (*Poa pratensis*), spotted knapweed (*Centaures maculosa*), erect cinquefoil (*Potentilla recta*), whitetop (*Cardaria draba*), mustard (*Brassica* spp.), and thistle (*Cirsium* spp.) (Anderson 2003). A full description of the study area and pond habitat can be found in Chapter 2.

We identified five permanent ponds classified as palustrine with intermittent exposure which indicates “surface water is present throughout the year except in years of extreme drought” (Cowardin et al. 1979:22). These five ponds ranged in size from 0.6 ha to 1.6 ha, were important overwintering ponds for turtles, and were separated from the next nearest permanent pond by a distance that exceeded the average reported movement distance of painted turtles (McAuliffe 1978, Rowe et al. 2003) (Fig. 1). We identified a “complex” around each permanent pond because not all required resources may be contained within the aquatic habitat (Pope et al. 2000, Marsh and Trenham 2001, Semlitsch and Bodie 2003, Roe and Georges 2007). Complexes were defined as the area within a 300 m radius circle around the center of each permanent pond (Fig. 1). This distance incorporated typical movements that included most terrestrial activities such as nesting and seasonal use of temporary ponds (McAuliffe 1978, Burke and Gibbons 1995, Rowe 2003, Semlitsch and Bodie 2003).

Road density within our study area was relatively low (0.72 km/km^2), even though the area contains three roads: U.S. Highway 93, Mollman Pass Trail, and Duck Road (Fig. 1). Traffic volumes on Highway 93 (2-lanes) were considered high with an average of 290 vehicles/lane/hour during daylight hours when turtles were most likely to move. Road mortality rates from 2003-2005 averaged 345 turtles/year on Highway 93, 6 turtles/year on Mollman Pass Trail, and 0.33 turtles/year on Duck Road (Chapter 4).

Field Methods

We captured painted turtles using a variety of methods including seine nets, basking traps, and muddling to maximize captures and minimize the potential for sampling bias (Ream and Ream 1966, Gibbons 1990b, Koper and Brooks 1998). We recorded the location, plastron length (PL) and width (mm), carapace length and width (mm), weight (g), sex, and age, if possible. Sex was determined by examining secondary sexual characteristics (elongated foreclaws and elongated preanal region of the tail, [Frazer et al. 1993]).

We individually double-marked each turtle by 1) drilling the margins of the carapace (Cagle 1939, McAuliffe 1978) and 2) injecting a Biomark™ passive integrated transponder (PIT) tag into the body cavity (Camper and Dixon 1988, Buhlmann and Tuberville 1998). Some juveniles were notched using nail clippers rather than drilling because some shells were not yet fully ossified (McAuliffe 1978, Camper and Dixon 1988).

We grouped turtles into three stage classes: hatchling, juvenile, and adult, based on PL. Hatchlings were turtles with a PL $\leq$ 50 mm and are not discussed in this paper. Juveniles were turtles with a PL >50 mm and $\leq$ 104 mm and sex was treated as unknown in all analyses. However, we observed male secondary sexual characteristics in a few (<1.8%) juveniles. Adults were turtles with PL > 104 mm. Any individual that was > 104 mm PL and not exhibiting secondary sexual characteristics was considered female (Mitchell 1985). Based on subsequent recaptures, all male turtles exhibited secondary sexual characteristics before reading a PL of at least 105 mm.

Pond Measurements

We measured pond depth each trapping session using a graduated pole. Small ponds occupied simple basins and were measured in the center. Larger ponds with more complex topography were measured three times across the pond and averaged. We calculated pond volume using our depth measurements and pond circumference determined from Geographic Information System (GIS) data at a relatively high-water period (April 2001); therefore, calculated volumes represent a relative measure of volume based on the high water mark.

Sampling Sessions

Pond complexes were sampled intensively during three sessions per year: “May” (May 21 - June 1), “July” (July 2 – 13) and “August” (August 13 - 24) (Fig. 2). We had eight trapping sessions (primary periods) between 2002 and 2005. In 2002, we conducted only the August trapping session; in 2003 and 2004, all three sessions were conducted; and in 2005, we conducted only the May session. Primary periods lasted 12 – 13 days during which we sampled all wetlands that held water within each complex between two and four times (secondary periods). In May, ponds were generally only sampled twice because of the large number of temporary ponds within the complexes due to spring rains and snow melt. By July and August sessions, virtually all temporary ponds had dried; consequently, we were able to sample all remaining ponds four times. Ideally, we sampled just before the onset of winter (August session) when turtles had returned to overwinter ponds and just prior to the initiation of spring activity (May session) before turtles moved out of the overwinter pond.

More detailed information on study site and field methods is provided in a companion paper (Chapter 2).

Analytical Methods

We used an information-theoretic approach (Burnham and Anderson 2002) to simultaneously evaluate relative support of multiple models describing relationships between survival and movement. *A priori* models were developed to address biological questions regarding survival and movement and were implemented in Program MARK

(White and Burnham 1999, Cooch and White 2002). We analyzed adults and juveniles separately because only two juveniles were observed to move between complexes; therefore, multistate modeling was unnecessary for juveniles.

Adults

We used multistate robust models to estimate survival within sites and movements (both between site movements and temporary emigration) (Arnason 1973, Pollock 1982, Hestbeck et al. 1991, Brownie and Robson 1993, Kendall and Nichols 1995, Kendall et al. 1995, Kendall et al. 1997). These models estimate apparent survival (ϕ), movement (Ψ), and capture probabilities (p) simultaneously. Apparent survival (ϕ_t^A) is the probability that an animal in location A (i.e., pond complex A) in primary period t is alive and in one of the five complexes in primary period $t + 1$; capture probability (p_t^A) is the probability of capturing an animal that was alive at time t and associated with location A; movement (ψ_t^{AB}) is the probability that an animal alive in location A at primary period t is in location B at time $t + 1$, given that it survives until $t + 1$. Within Ψ, we modeled an unobservable state to examine temporary emigration (Kendall et al. 1997, Bailey et al. 2004a). Modeling strategy and model notation generally followed the approach of Lebreton et al. (1992). Sex was treated as an individual covariate to keep the number of parameters in the models manageable.

We used "multistate" to refer to the five pond complexes (Ponds A – E; Fig. 1), therefore the transition probability represented the likelihood of movement between the five pond complexes. We treated each pond complex as a geographical isolate and designated each as a local population because the distance between complexes was greater than normal daily movements (less than 200 m, Gibbons 1968). One exception was that we treated two ponds (B and C) that were 80 m apart as separate populations because they were separated by a Highway 93 (Fig. 1) (sensu Petranka et al. 2004).

Juveniles

Any individual first captured as a juvenile (≥ 50 and <104 mm PL) was considered a juvenile throughout the study and only included in the juvenile analysis.

Only two juvenile turtles moved between pond complexes; therefore, we restricted our juvenile analysis to Pollock's robust design model (Pollock 1982) which does not include movement between local populations (i.e., pond complexes) yet allows for temporary emigration (γ_t) (Kendall and Nichols 1995, Kendall et al. 1995, Kendall et al. 1997). Parameters ϕ and p were defined and modeled in the same process as the adult analysis. Of the temporary emigration parameters, γ_t'' is the probability that an animal is absent from the pond complex at time t if absent at time t - 1, and γ_t' is the probability that an animal is absent at time t if present at time $t – 1$. We used the same variables as in the adult analysis to examine which factors most influence temporary emigration rates.

Models of Capture, Survival, and Movement Probabilities

We followed a sequential modeling process for both adults and juveniles in which we first sought parsimonious models for p and ϕ, and then used resulting parameterizations as the basis for developing models of movement probabilities. Because p can strongly influence estimates of other parameters, it was modeled first. In this first step, we asked whether p differed across populations, time, or sex. The robust design also allowed us to examine capture heterogeneity (i.e., trap happy or trap shy). In the second step, we modeled potential predictor variables for ϕ including time (season and year), space (pond complex), habitat (as measured by pond depth and volume), sex, and distance to the highway (site specific covariate). Once we found a parsimonious model on ϕ, we held survival constant. For our movement analysis, survival was modeled as an interaction between pond and season (i.e., winter and summer) and year. Survival is fully examined in a companion paper (Chapter 2).

Three main types of metapopulation models of movement have been developed over the years; the island model assumes that movement rates are constant and equal between all pairs of populations (Wright 1931); the stepping-stone model assumes that adjacent populations share a common movement rate which is higher than non-adjacent populations (Hanski and Simberloff 1997); and the isolation by distance model assumes movement from one population to another varies inversely with the distance between them (Wright 1943). We modeled movement probabilities examining each of these models. Both linear logistic and negative exponential distributions have been used to model movement probabilities (Spendelow et al. 1995, Hanski et al. 2000, Trenham et al. 2001). We modeled distance as a function of the distance between the center ponds in each complex using either distance itself (represented as Ψ_{distance}) or the negative exponential of distance (represented as $\Psi\ e^{-\text{distance}}$) (Skvarla et al. 2004). We developed habitat models of movement by permitting different movement probabilities based on the depth (m) or volume (m^3) of the originating pond. We also developed "road models" by modeling the presence of an intervening road when a straight line between two complexes intersected the highway. Some complexes were also separated by the presence of secondary roads which were not included in the "road" model because relatively little mortality occurred on these secondary roads.

Temporal variation was modeled as season and year. "Season" consisted of the intervals between trapping sessions: "winter" was 9 months from September to May; "early summer" was 1.5 months from late May to July; and "late summer" was 1.5 months from mid-July to late August (Fig. 2). We modeled movement as a function of three seasons (winter, early summer, and late summer) and also as two seasons (winter and summer) which combined data from early and late summer. Finally, movement was modeled as a function of sex. We expected males to make interpopulation movements more frequently than females (e.g., Gibbons 1986, Tuberville et al. 1996).

Temporary Emigration

Temporary emigration could result from turtles of either sex using areas outside our study site (e.g., using temporary ponds for foraging or mate seeking) or females nesting on land both on and off our study site. We expected a female bias in temporary emigration because females on nesting forays in terrestrial habitats would not be available for capture within the pond.

We constrained our considerations to eight models for temporary emigration in both the adult and juvenile analyses because temporary emigration parameters are often difficult to estimate. These models included a "no temporary emigration" model ($\gamma'' = \gamma' = 0$); five random emigration models that included one constant $\gamma''(.) = \gamma'(.)$, one dependent on site, $\gamma''(\text{pond}) = \gamma'(\text{pond})$, one dependent on two seasons γ''(winter/early summer vs. late summer) = γ'(winter/early summer vs. late summer), one dependent on two seasons γ''(winter vs. summer) = γ'(winter vs. summer), and one dependent on three seasons γ''(winter, early summer, late summer) = γ'(winter, early summer, late summer); and two Markovian models, the first, constant γ''(.), γ'(.), the second, site dependent, γ''(pond), γ'(pond).

Model Selection and Goodness of Fit

Hypotheses were evaluated using model selection based on Akaike's Information Criterion (AIC) (Akaike 1973). Models with low AIC values are parsimonious in that they fit the data reasonably well with a relatively small number of parameters. I used AIC_c which includes a small sample-size, second-order bias adjustment which is recommended when the number of estimated parameters is large relative to the sample size (Burnham and Anderson 2002). Models within two AIC values of the best approximating model were considered in the discussion (Burnham and Anderson 2002). Model selection uncertainty in the parameter estimates was incorporated by model averaging all models within two AIC values.

We used goodness-of-fit as a diagnostic procedure for testing assumptions underlying the models. The assumptions for these models included those for the respective closed and open models (Seber 1982, Pollock et al. 1990). When a lack of fit or overdispersion was found in the data, this reflected either a lack of independence or heterogeneity among individuals (Pollock et al. 1990). Currently, no formal goodness-of-fit test is available for multistate capture-mark-recapture models. For both adult and juvenile analyses, we tested for overdispersion using the variance inflation factor ($\hat{c}$) from the Pearson goodness-of-fit chi-square statistic of the most general model and its degrees of freedom ($\hat{c} = \chi^2/\text{df}$) (Lebreton et al. 1992) using MSSRVRD (Multi-Stratum Survival and Robust Design; available on-line at www.mbr-pwrc.usgs.gov/software.html). Individual covariates cannot be included in the MSSRVRD program; therefore, $\hat{c}$ was estimated using the most highly parameterized model possible for each analysis without including covariates.

When overdispersion was detected (i.e., $\hat{c} > 1$), we used the quasi-likelihood AIC (QAIC) which inflates the sampling variance by multiplying those values by $\hat{c}$ (Burnham and Anderson 2002). When QAIC was used, we also increased the number of parameters by 1 to incorporate ĉ (Burnham and Anderson 2002).

Population Growth Models

We used a stage-based, multi-site, matrix population model (Morris and Doak 2002) to assess the population-level consequences of movements of painted turtles, particularly in relation to the highway. We structured our population models using stage- and population-specific apparent survival rates estimated from CMR analyses (Table 1) (For details on modeling see Chapter 2). We used three data sets of vital rates representing relatively "good", "bad", and average year data. We defined 2003 estimates as a relatively "good" year when more water was available on the landscape and 2004 estimates as a relatively "bad" year when less water was available (Table 2). Apparent survival rates of adults were higher in 2003 than in 2004 for all ponds (Table 1). This relationship did not necessarily follow the same pattern for apparent survival of juveniles in all ponds (Table 1). We defined "average" as the average of 2003 and 2004 estimates.

Movement probabilities were estimated from the above analyses. Fecundity and breeding frequency estimates were held constant for all runs and were determined from the literature. We assumed fecundity to be 28 eggs/year based on two clutches/year of 14 eggs each (Iverson and Smith 1993, Lindeman 1996) and 80% of females are assumed to breed per year (Tinkle et al. 1981, Iverson and Smith 1993).

To incorporate the wide variation in estimates of survival from egg through hatchling stages, we used worst-case scenario estimates (0.048) for the "bad" year replicates and best-case estimates (0.399) for the "good" year replicates. To obtain these values, we combined estimates of egg survival from the literature (0.08 to 0.67; Gibbons 1968, Tinkle et al. 1981) with hatchling survival estimated from our CMR data (0.42 in 2003 and 0.77 in 2004; K. Griffin unpublished data). We then averaged the two years. We assumed hatchlings remained hatchlings for one year and female juveniles became adults (matured) at 6 years of age.

We calculated the deterministic, annual population growth rate (λ) of the overall population (i.e., all five pond complexes) for all three data sets (i.e., "good", "bad", and average) under three modeling scenarios. The "current situation" model uses current survival (Table 1) and movement probabilities estimated in our CMR analyses. In the "no movement" scenario, we set all movement probabilities equal to zero which represents the loss of all connectivity.

The "no road mortality" scenario represents full connectivity between the ponds by simulating that roads are not present. We modeled this by altering both movement and survival probabilities based on road kill data. First, we assumed all road mortalities of marked individuals were successful movements. Therefore, we increased movement probabilities by the percentage of individuals from each pond killed on the road each year to simulate successful movements (Table 1). These movement values were assigned a destination pond based on the movement probabilities between each pond. The percentage of the population killed on the road for each pond was adjusted to include carcasses known to be marked but that we were not able to individually identify (Table 1). Therefore, carcasses that were known marked but not identified were assigned ponds of origin based on the percentage of known road mortalities from each pond. In this scenario, we also increased survival rates within each pond using the same road mortality estimates as above. Therefore, individuals found dead-on-the-road were assumed to be alive.

RESULTS

Pond Characteristics

All ponds lost water over the study period due to drought (Table 2). The deepest ponds (B and C) lost water yet still remained greater than 1.5 m deep at the end of the study; ponds A, D, and E started out much shallower and ended with less than 1 m of water (Table 2). Pond volume followed the same pattern as depth and ranged widely within and between ponds (Table 2). Virtually all temporary ponds within each complex dried out by the "July" trapping sessions.

Sample Size and Goodness of Fit

We captured and released a total of 1,072 adults 5,050 times: 517 males for a total of 2,488 captures and 555 females for a total of 2,562 captures. We captured and released a total of 442 juveniles a total of 3,078 times.

The Pearson's goodness of fit test statistics under our most parameterized models indicated overdispersion in both the adult and juvenile data: adult $\hat{c}$ value was 2.48 (χ^2 = 1248.9, df = 504, P << 0.001) and the juvenile $\hat{c}$ value was 2.05 (χ^2 = 444.2, df = 217, P << 0.001). We, therefore, applied these $\hat{c}$ values in all subsequent model fitting in adult and juvenile analyses, respectively.

Probability of Capture and Survival

Details on capture and survival probabilities are discussed in a companion paper (Chapter 2). In both the adult and juvenile analyses, the top model for *p* was an interaction between pond and trapping session ($p_{\text{pond*session}}$). Estimates of capture probabilities in the top model ranged widely both within and between ponds for both adults and juveniles (Chapter 2). Within pond, median capture probabilities ranged from 0.19 in pond B to 0.59 in pond C for adults, and from 0.30 in pond B to 0.70 in pond D for juveniles.

For this analysis, survival probability was held constant at the most parsimonious model determined in Chapter 2. In both the juvenile and adult analyses, the top model was a function of pond, season, and year ($\phi_{\text{pond * season2 + year}}$). Survival estimates varied widely between ponds and across seasons and the pattern of variation between the age-classes was very different. Annual apparent survival in adults ranged from 0.925 (0.05) to 0.118 (0.03) and juveniles ranged from 0.337 (0.08) to 1.0 (Chapter 2).

Probability of Movement

Of the 1,072 individual adults, 48 individuals (4.4%) made interpopulation movements (between complexes) and only six of these individuals moved more than once. Of the six that moved twice, only two individuals potentially moved twice in one year based on capture histories. Five of the six individuals that moved more than once made out-and-back movements between two complexes; the other moved between three complexes. One hundred and thirty-nine individual adults (13.0%; 68 males, 71 females) and 22 juveniles (5.0%) made movements among ponds within the complexes (e.g., used temporary ponds within complexes) over the course of the study.

Interpopulation movements (Between pond complexes)

Interpopulation movements were not modeled for juveniles because only two were observed to move between pond complexes. Therefore, the interpopulation movement results refer only to adults.

Within the candidate set of models, three models with alternative movement variables were within 2 $\Delta QAIC_c$ of the best approximating model (Table 3). The most parsimonious model ($\Psi_{distance + depth}$) indicated the probability of movement was influenced by depth of pond of origin and linear distance between pond complexes (Table 3). The second best model included depth, distance, and two seasons (summer and winter). The third model was similar to the second except three seasons were included (early summer, late summer, and winter). The fourth model was the same as the top model but also included the presence of an intervening road.

Of the three types of metapopulation models, the isolation by distance model was best supported by the data with the probability of movement from one population to another varying inversely with the distance between the pond complexes ($\beta_{distance} = -2.67$, SE = 0.34). The negative exponential distribution of distance was less supported by the data ($\Delta QAIC_c = 5.5$). The island model was not supported by the data ($\Delta QAIC_c > 27.6$). We could not realistically model the stepping-stone model because our pond complexes were not linear on the landscape and we observed movement between non-adjacent complexes. Our time interval between sampling sessions was sufficiently long to allow movements to adjacent populations to be missed.

Habitat models indicated water depth in pond of origin had greater influence ($\beta_{depth} = -1.01$, SE = 0.21) on movement than volume ($\Delta QAIC_c = 2.5$). Movement was directional based on the water depth in the pond of origin. That is, more movement occurred out of drying ponds to those ponds less affected by the drought.

As predicted, the presence of the intervening highway had a negative affect on the probability of interpopulation movement ($\beta_{road} = -1.22$, SE =0.56; 95% CI = -2.3, -0.13).

We expected sex to affect the probability of movement. The model that included sex had little support (ΔQAIC$_c$ = 2.04; weight = 0.069) and the 95% confidence intervals of the β_{sex} value overlapped zero (β_{sex} = -0.03, SE = 0.36, 95% CI = -0.73, 0.67).

Overall, low annual movement probabilities among the populations reflect high site fidelity (Table 4, Fig. 3). Movement was highest in early summer and lowest in late summer which corresponds with the greatest and least (respectively) number of temporary ponds on the landscape. Only the two closest populations had movement probabilities greater than 0.01 (Table 4, Fig. 3). The highest movements occurred between ponds B and C (80 m apart) with more movement occurring from C to B (0.038, SE = 0.016) then from B to C (0.014, SE = 0.006). Ponds D and E (810 m apart) had more movements between E to D (0.031, SE = 0.022) than D to E (0.018, SE = 0.009) (Fig. 3).

Temporary Emigration Movements (Out of pond complex and back)

Adult

The top model for temporary emigration in adults was random temporary emigration which varied by season (Table 5). Random emigration indicates that the probability of an individual being in the pond is not dependent on its presence in the pond in the preceding trapping session. The seasons were modeled as winter/early summer vs. late summer. This combined winter and early summer reflects when water was abundant in temporary ponds across the landscape.

Two other models were within 2 ΔQAIC$_c$. The second model (ΔQAIC$_c$ = 2.01) was the same as the first, except sex was also included (Table 5). Females had a slightly higher probability of temporary emigration than males; however, the 95% confidence intervals of the β_{sex} value overlapped 0 (β_{sex} = 0.168, SE = 0.222, 95% CI = -0.27, 0.60) indicating probabilities of temporary emigration for males and females overlap and, therefore, the difference may not be biologically significant. The third model had temporary emigration constant across all ponds and seasons. Models that did not include temporary emigration ($\gamma'' = \gamma' = 0$) were not supported by the data (ΔQAIC$_c$ = 31.8). Models that included Markovian temporary emigration were not estimable.

Consequently, the model that included sex was not used in model averaging. Model averaged estimates of the probability of temporary emigration were higher in winter/early summer than in late summer (Table 6).

Juvenile

More temporary emigration (there-and-back again movements to-from a local population) occurred than directional movements between populations which were so rare they could not be modeled. The top model for temporary emigration in juveniles was constant random temporary emigration (Table 7). The other model within 2 $\Delta QAIC_c$ included two seasons (winter and summer). Model averaged estimates indicate that temporary emigration was highest in winter (0.047, SE = 0.042), then in summer (0.025, SE = 0.015) (Table 6).

Models that did not include temporary emigration ($\gamma'' = \gamma' = 0$) were not well supported by the data ($\Delta QAIC_c = 4.56$). Models that included Markovian temporary emigration were not estimable. The top temporary emigration model for adults (i.e., winter combined with early summer as compared to late summer) did not converge.

Population Growth Models

Two complete years of data were used to parameterize demographic models of turtle population growth. Although two years are not sufficient to capture actual dynamics of the population, the modeling provides a way to interpret how relative changes in turtle vital rates due to roads could translate into higher-level effects on population growth.

Under all three scenarios, the population is increasing in “good” years (2003 data) while the population is decreasing under current and no movement scenarios in both “bad” (2004 data) and average years (Table 8).

When the effects of roads are removed (no roads scenario) the amount of increase in λ compared to the current situation ranges from 9.2% to 27.3% depending on which data set is used (Table 8). In average and “bad” years, λ changes from negative in the current scenario to positive in the no roads scenario.

The population growth rate is decreased by <1% to 5.6% when movements are removed (no movement scenario) in all data sets. Lambda remains positive in “good” years and remains negative in average and “bad” years compared with the current scenario.

DISCUSSION

Ours is the first study to examine interpopulation and temporary emigration movement probabilities for freshwater turtle species using statistically rigorous methods. Overall, interpopulation movement probabilities were very low (< 0.04). Temporary emigration rates were slightly higher (a high of 0.069 for adults and 0.047 for juveniles).

Interpopulation Movement

As expected, painted turtle movement estimates indicate a high degree of site fidelity. Although several studies (e.g., Sexton 1959, Taylor and Nol 1989, Gibbons et al. 1990, Rowe 2003) describe long range movements of painted turtle, few directly examine the relationship between distance and movement probabilities (but see Bowne et al. 2006). Movement probabilities were strongly influenced by linear distance, with the probability of movement decreasing as linear distance increased. However, movements within a complex are not included in the interpopulation movement analysis. If these data were included, the distribution may be best approximated by the negative exponential of distance rather than a linear distance distribution.

Increased overland migrations in response to drought have been noted in many aquatic turtle populations (McAuliffe 1978, Gibbons et al. 1983, Christiansen and Bickham 1989, Lindeman and Rabe 1990, Hall and Cuthbert 2000). Water depth in permanent ponds was an important factor in movement probabilities. Turtles moved more frequently from drying ponds to the deeper ponds that still retained water. Bowne et al. (2006) also suggested habitat quality was a factor in movement probabilities.

Interpopulation movement probabilities varied seasonally with the highest rates of movement occurring in early summer and the lowest estimates occurring in late summer. The highest rates coincide with the largest amount of water available on the landscape, which could be the reason for this pattern and may suggest a stepping-stone model of movement. Alternatively, large temperature and humidity differences can occur between these seasons which also could affect seasonal movement patterns.

The presence of the highway had a strong negative effect on movement probabilities. In the CMR framework, we were unable to distinguish whether these negative effects were a result of turtles unable to successfully cross the highway or if a behavioral response (i.e., avoidance of the road) occurred. Recent development of multistate models that allow inclusion of live and dead encounters (Barker et al. 2005) may help separate these issues in future analyses. However, Kendall et al. (2006) combined multistate and tag recovery data to estimate demographic parameters, but they found many concerns still exist (e.g., need for substantial amounts of data and numerical problems such as multimodality), and only a marginal improvement on precision was reached.

Morreale et al. (1984) and Gibbons (1986) suggested that males travel overland greater distances and more frequently than females. We found that males may move slightly more than females during interpopulation movements; however, we are uncertain of this relationship because the confidence intervals overlap zero. Examining all incidental observations of marked turtles that moved (i.e., not just those used in the modeling analysis), we found no sex bias in movements over all distances (> 0 – 2,140 m). However, CMR methods may underestimate female movements in that an individual has to be captured in two different ponds for movement to be observed; therefore, nesting forays by females (i.e., leaving a pond to nest on land and returning to the same pond) cannot be assessed using interpopulation movements which are from pond to pond.

Temporary Emigration

Temporary emigration measures out and back movements [i.e., forays to unknown destinations]. These movements are biologically different than interpopulation movements which are one way movements to other pond complexes. Roughly twice as much temporary emigration occurred than interpopulation movements. This indicates our pond complexes do not incorporate all areas important to this metapopulation.

The complexes were designed to incorporate typical daily and seasonal movements of turtles to temporary ponds. We expected movements to temporary ponds within our complexes in the spring when shallow ponds warm up faster than the deeper permanent ponds and, therefore, may have available food resources earlier. The fact that a considerable amount of temporary emigration occurred indicates that either painted turtles use larger areas on a seasonal basis than previously thought or that refugia habitats (such as Kicking Horse reservoir or Crow Creek) are important during drought conditions. We expect temporary emigration estimates to increase when turtles move back into the ponds that became unsuitable during the drought. Our study was able to capture the return of some turtles that moved off the study area however, subsequent sampling has shown that turtles are continuing to repopulate the previously unsuitable ponds as water levels increase.

We expected a female bias in temporary emigration for adults because of females nesting forays. However, sex did not significantly influence movement probabilities because even though the model that included sex was within 2 $\Delta QAIC_c$ of the top model, the 95% confidence intervals overlapped zero. Our sampling schedule might not have been close enough together to actually observe female absences which usually occur in 1-2 days. Females potentially had sufficient time to nest and return to the pond in-between the secondary sampling sessions which occurred anywhere from 1-5 days apart.

Understanding the extent of movement off the study area can provide insights on the importance of maintaining movement corridors between populations and refugia habitats and play an important role in the development of management strategies that incorporate all habitat requirements of a species (Muths et al. 2006).

Population Growth Models

We were interested in the effects of interpopulation movements on the metapopulation dynamics. Most observational studies of movement make no assessment on how movement affects overall population dynamics (Morreale et al. 1984, Gibbons et al. 1990; but see Sexton 1959).

Population growth rates are sensitive to the proportion of years equal to bad (2003) or good (2004) estimates. The balance of good and bad years is crucial because even thought the good year models indicate the population is increasing at almost 20% annually, when average estimates were modeled the population rate declined slightly. Our study was conducted during drought conditions. The year 2003 was a relatively wet year compared to 2004; however, both years had precipitation and snow levels below the 95 year average, thus, it is likely more water occurs on the landscape on average. For example, the underlying photo of the study area (taken in April 2001) (Fig. 1) indicated much greater water availability on the landscape. Unfortunately, no hydrology data is available for the wetlands in our study area.

Weather extremes and climate conditions strongly influence hydrology such as hydroperiod and water permanence in glaciated wetlands (Winter 2000). Increased drought conditions are predicted to occur in the prairie pothole region of the United States under all global circulation model scenarios (Johnson et al. 2005). Although our study area is outside the prairie pothole region, the structure and type of wetlands are similar (Winter 2000). In the future, if more years are similar to or better than 2003 estimates, the population is likely to grow. If, on the other hand, climate change alters hydroperiod, increasing frequency or duration of drought, there would likely be more years similar to environmental conditions observed in 2004 and the population is likely to decline. The balance of good to bad years can be critical because the population had a negative growth rate using the 2003-2004 average.

Models that incorporated the estimated road-induced morality indicated that population growth would likely be negatively affected. Under good, bad, and average years, removing road mortality increased the population growth rate, especially in bad and average years when rates changed from negative to positive in the absence of roads. If increases in road mortality occur due to increased development, traffic volume, or widening the highway, the negative population growth rate in average and bad years could be exacerbated.

In a scenario where roads prohibited any movement among populations, population growth would be expected to decline. Movement appears to play a greater role in population dynamics in bad and average years because the greatest percent decrease occurred in these years (1.5% and 5.6%, respectively). Only having two years of movement data on a long-lived species is not likely sufficient to capture the amount of variation in movement that could show the importance of movement to population dynamics.

Interpopulation movement occurs at low rates (< 4%) in this ecosystem; however, the movement rates appear to be high enough to be important for recolonization and for "rescue" of diminishing populations, which is the process that drives true metapopulation dynamics (Levins 1969, Hanski and Gilpin 1997). Two ponds (Ponds A and E) went "extinct" shortly after data collection for this study ended and recolonization has been slowly occurring over the last 2 years (2006 and 2007) (K. Griffin, Unpublished data).

Summary

Managers wishing to conserve habitats capable of supporting viable populations of turtles are often hampered by lack of knowledge. Very little interpopulation movement occurs between pond complexes each year; therefore, what little movement does occur is important in providing connectivity to local populations in each pond complex. Movement probabilities and patterns are influenced both by the presence of roads and environmental conditions such as drought. Effective conservation requires attention to all the necessary features of the landscape and how they interact to influence population dynamics. Minimizing the effects of roads and maintaining movement corridors to refugia habitat are both important in allowing for the recolonization of previously unsuitable habitats and maintaining long-term viability.

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Table 1. Apparent survival and road mortality rates for painted turtles used in matrix models. Estimates are based on our capture-mark-recapture study conducted from 2002 – 2005, in northwestern Montana (Chapters 2 and 4).

			Pond				
Vital rate	**Stage**	**Year**	**A**	**B**	**C**	**D**	**E**
Survival	**Adult**	**2003**	0.613	0.925	0.811	0.397	0.295
		2004	0.246	0.757	0.574	0.265	0.118
	Juvenile	**2003**	1.000	0.337	0.390	0.892	0.611
		2004	0.668	0.425	0.480	0.921	0.681
Road mortality	**Adult**	**2003**	0.000	0.040	0.092	0.062	0.132
		2004	0.168	0.050	0.105	0.097	0.329
	Juvenile	**2003**	0	0.110	0.159	0	0.145
		2004	0	0	0.063	0.145	0.046

Table 2. Pond characteristics of the permanent center pond in each complex from fall 2002 to spring 2005 in western Montana.

	Pond				
Characteristic	**A**	**B**	**C**	**D**	**E**
Size[a] (ha)	0.71	1.60	0.64	1.22	1.24
Water depth (m) - Range[b]	0.3-1.4	2.5-4.2	1.5-2.4	0.7-1.7	0.1-0.9
Pond volume (m^3)	6,750	53,475	13,305	13,880	7,466

[a] Size measured from aerial photo at high water using GIS.

[b] The deepest values were recorded in fall 2002 and the shallowest values were recorded in spring 2005.

Table 3. Multistate robust models used to estimate movement probabilities (Ψ) of adult painted turtles among 5 pond complexes in western Montana. Factors affecting apparent survival (ϕ) and detection probabilities (p) held constant at ϕ(pond*season+year) and p(pond*session), respectively. Models are listed in ascending order of QAIC$_c$, with the lowest QAIC$_c$ values indicating the best models. The most parsimonious models are highlighted in bold and were used in model averaging movement estimates.

Apparent survival	Capture Probability	Movement Probability	Temporary Emigration	QAIC$_c$	ΔQAIC$_c$	w_i	K
$\phi_{\text{pond*2season+year}}$	**$p_{\text{pond*session}}$**	**Ψ distance + depth**	**$\gamma'' = \gamma'$ Random$_{\text{spring/late summer}}$**	**7081.33**	**0**	**0.331**	**57**
$\phi_{\text{pond*2season +year}}$	**$p_{\text{pond*session}}$**	**Ψ distance + depth + 2season**	**$\gamma'' = \gamma'$ Random$_{\text{spring/late summer}}$**	**7082.01**	**0.680**	**0.236**	**58**
$\phi_{\text{pond*2season +year}}$	**$p_{\text{pond*session}}$**	**Ψ distance + depth + road**	**$\gamma'' = \gamma'$ Random$_{\text{spring/late summer}}$**	**7082.83**	**1.499**	**0.157**	**58**
$\phi_{\text{pond*2season+year}}$	**$p_{\text{pond*session}}$**	**Ψ distance + depth + 3season**	**$\gamma'' = \gamma'$ Random$_{\text{spring/late summer}}$**	**7082.91**	**1.577**	**0.150**	**59**
$\phi_{\text{pond*2season+year}}$	$p_{\text{pond*session}}$	Ψ distance + depth + sex	$\gamma'' = \gamma'$ Random$_{\text{spring/late summer}}$	7083.38	2.044	0.069	58
$\phi_{\text{pond*2season+year}}$	$p_{\text{pond*session}}$	Ψ volume + distance	$\gamma'' = \gamma'$ Random$_{\text{spring/late summer}}$	7083.80	2.472	0.056	57
$\phi_{\text{pond*2season+year}}$	$p_{\text{pond*session}}$	Ψ distance	$\gamma'' = \gamma'$ Random$_{\text{spring/late summer}}$	7085.40	4.067	0.056	56
$\phi_{\text{pond*2season+year}}$	$p_{\text{pond*session}}$	Ψ distance + road	$\gamma'' = \gamma'$ Random$_{\text{spring/late summer}}$	7085.42	4.092	0.025	57
$\phi_{\text{pond*2season+year}}$	$p_{\text{pond*session}}$	Ψ distance + 2season	$\gamma'' = \gamma'$ Random$_{\text{spring/late summer}}$	7086.46	5.124	0.015	57
$\phi_{\text{pond*2season+year}}$	$p_{\text{pond*session}}$	$\Psi\ e^{-\text{distance}}$	$\gamma'' = \gamma'$ Random$_{\text{spring/late summer}}$	7086.86	5.527	0.015	56
$\phi_{\text{pond*2season+year}}$	$p_{\text{pond*session}}$	Ψ distance + sex	$\gamma'' = \gamma'$ Random$_{\text{spring/late summer}}$	7087.38	6.051	0.009	57
$\phi_{\text{pond*2season+year}}$	$p_{\text{pond*session}}$	Ψ distance + 2season + year	$\gamma'' = \gamma'$ Random$_{\text{spring/late summer}}$	7090.48	9.151	0.002	59

Notes: Akaike's Information Criterion corrected for small sample size and overdispersion (QAIC$_c$), differences in QAIC$_c$ values (ΔQAIC$_c$), QAICc weights (w_i), and number of parameters (K) are given for each model. Subscripts give parameterizations for each variable: constant = constant over space and time variables; "distance" = linear distance between center ponds within each pond complex; “$e^{-distance}$” = negative exponential distance between center ponds within each pond complex; “2season” = variation over winter and summer (combines early summer and late summer); “3season” = variation over 3 seasons (winter, early summer, and late summer); “spring/late summer” = variation over 2 seasons (combines winter and early summer into spring category); “year” = variation by 2003, 2004, and 2005; “sex” = variation between males and females; “depth” = variation by pond volume each session; and “road” = intervening road between straight line distance between the pond complexes; “temporary emigration” = movement out of the complexes and back again. Subscripts joined by “+” indicate an additive model. Models that did not converge or had parameters estimated with singular values are not shown.

Table 4. Annual estimates of interpopulation movement rates of adult painted turtles in western Montana, 2002-2005 based on multistate robust models. Estimates are averaged over the models within 2 ΔQAICc of the top model. Values of 0.00 indicate probability of movement is less than 0.0001 but greater than 0. Pond depth is the range of water depth in the pond of origin from fall 2002 to spring 2005. Note that all ponds lost water.

Transition	**Movement probability**	**SE**	**Distance (km)**	**Intervening Road[1]**	**Pond depth (m)**
A-B	0.008	0.0053	1.30	N	1.40 - 0.31
A-C	0.007	0.0047	1.36	Y	
A-D	0.003	0.0019	1.81	Y	
A-E	0.001	0.0008	2.29	Y	
B-A	0.001	0.0006	1.30	N	4.17 - 2.50
B-C	0.014	0.0058	0.08	Y	
B-D	0.001	0.0007	1.24	Y	
B-E	0.000	0.0002	2.03	Y	
C-A	0.002	0.0011	1.36	Y	2.40 - 1.50
C-B	0.038	0.0161	0.08	Y	
C-D	0.003	0.0014	1.20	N	
C-E	0.001	0.0004	2.00	N	
D-A	0.002	0.0013	1.81	Y	1.70 - 0.66
D-B	0.007	0.0036	1.24	Y	
D-C	0.007	0.0039	1.20	N	
D-E	0.018	0.0091	0.81	N	
E-A	0.001	0.0010	2.29	Y	0.84 - 0.10
E-B	0.002	0.0017	2.03	Y	
E-C	0.002	0.0018	2.00	N	
E-D	0.031	0.0217	0.81	N	

[1] Yes (Y) and no (N) indicated the presence or absence, respectively, of an intervening highway.

Table 5. Multistate robust models used to estimate temporary emigration probabilities (γ) of adult painted turtles among 5 pond complexes in western Montana. Factors affecting apparent survival (ϕ) and detection probabilities (p) held constant at ϕ(pond*season+year) and p(pond*session), respectively. Models are listed in ascending order of QAIC$_c$, with the lowest QAIC$_c$ values indicating the best models. The most parsimonious models are highlighted in bold and were used in model averaging movement estimates.

Apparent survival	Capture Probability	Movement Probability	Temporary Emigration (TE)	QAIC$_c$	ΔQAIC$_c$	w$_i$	K
$\phi_{\text{pond*}\textbf{2season}\text{+year}}$	$p_{\text{pond*session}}$	$\Psi_{\text{distance + depth}}$	$\gamma''=\gamma'$ Random$_{\text{spring/late summer}}$	**7081.332**	**0**	**0.55377**	**57**
$\phi_{\text{pond*}\textbf{2season}\text{+year}}$	$p_{\text{pond*session}}$	$\Psi_{\text{distance + depth}}$	$\gamma''=\gamma'$ Random$_{\text{spring/late summer + sex}}$	**7083.145**	**1.8125**	**0.22374**	**58**
$\phi_{\text{pond*}\textbf{2season}\text{+year}}$	$p_{\text{pond*session}}$	$\Psi_{\text{distance + depth}}$	$\gamma''=\gamma'$ Random$_{\text{constant}}$	**7083.156**	**1.8238**	**0.22248**	**56**
$\phi_{\text{pond*}\textbf{2season}\text{+year}}$	$p_{\text{pond*session}}$	$\Psi_{\text{distance + depth}}$	$\gamma''=\gamma'$ Random$_{\text{3season}}$	7083.37	2.0375	0.05596	58
$\phi_{\text{pond*}\textbf{2season}\text{+year}}$	$p_{\text{pond*session}}$	$\Psi_{\text{distance + depth}}$	$\gamma''=\gamma'$ Random$_{\text{2season}}$	7084.453	3.1205	0.03256	57
$\phi_{\text{pond*}\textbf{2season}\text{+year}}$	$p_{\text{pond*session}}$	$\Psi_{\text{distance + depth}}$	$\gamma''=\gamma'=0$ No TE	7113.16	31.8279	0	55

Notes: Akaike's Information Criterion corrected for small sample size and overdispersion (QAIC$_c$), differences in QAIC$_c$ values (ΔQAIC$_c$), QAICc weights (w$_i$), and number of parameters (K) are given for each model. Subscripts give parameterizations for each variable: constant = constant over space and time variables; "distance" = linear distance between center ponds within each pond complex; "$e^{\text{-distance}}$" = negative exponential distance between center ponds within each pond complex; "2season" = variation over winter and summer (combines early summer and late summer); "3season" = variation over 3 seasons (winter, early summer, and late summer); "spring/late summer" = variation over 2 seasons (combines winter and early summer into spring category); “year” = variation by 2003, 2004, and 2005; “sex” = variation between males and females; “depth” = variation by pond volume each session; and “road” = intervening road between straight line distance between the pond complexes; “temporary emigration” = movement out of the complexes and back again. Subscripts joined by “+” indicate an additive model. Models that did not converge or had parameters estimated with singular values are not shown.

Table 6. Estimates and (standard errors) of temporary emigration rates of adult and juvenile painted turtles in western Montana, 2002-2005 based on capture, mark, recapture.

Temporary Emigration			
	Winter	**Early Summer**	**Late Sumer**
Adult	0.069 (0.013)	0.069 (0.013)	0.020 (0.016)
Juvenile	0.047 (0.042)	0.025 (0.015)	0.025 (0.015)

Table 7. List of candidate set of temporary emigration models of capture-mark-recapture data collected on juvenile painted turtles within 5 pond complexes using robust models in western Montana 2002-2005. Factors affecting survival and capture probabilities were held constant at $\phi_{\text{pond*season2+year}}$ and $p_{\text{pond*session}}$., respectively. Models are listed in ascending order of QAIC_c, with the lowest values indicating the best models. The most parsimonious models are highlighted in bold and were used in model averaging temporary emigration estimates.

Apparent survival	Capture Probability	Temporary Emigration	QAIC_c	ΔQAIC_c	w_i	K
$\phi_{\text{pond*2season+year}}$	**$p_{\text{pond*session}}$**	**$\gamma''=\gamma'$ Random$_{\text{constant}}$**	**3675.75**	**0**	**0.509**	**52**
$\phi_{\text{pond*2season+year}}$	**$p_{\text{pond*session}}$**	**$\gamma''=\gamma'$ Random$_{\text{2season}}$**	**3676.62**	**0.871**	**0.330**	**53**
$\phi_{\text{pond*2season+year}}$	$p_{\text{pond*session}}$	$\gamma''=\gamma'$ Random$_{\text{pond}}$	3678.84	3.090	0.109	55
$\phi_{\text{pond*2season+year}}$	$p_{\text{pond*session}}$	$\gamma''=\gamma'=0$ No TE	3680.31	4.561	0.052	51
ϕ_{constant}	$p_{\text{pond*session}}$	$\gamma'',\ \gamma'$ Markovian$_{\text{constant}}$	3727.48	51.732	0	42

Notes: Akaike's Information Criterion corrected for small sample size and overdispersion (QAIC_c), differences in QAIC_c values (ΔQAIC_c), QAICc weights (w_i), and number of parameters (K) are given for each model. Subscripts give parameterization for the variable: constant = constant over space and time; "pond" = variation over space (i.e., pond complex); "2season" = variation over winter and summer (combines early summer and late summer); "year" = variation by 2003, 2004, and 2005; Subscripts joined by "+" indicate an additive model and "*" indicates a factorial model. Not all models shown. Models that did not converge or had parameters estimated with singular values are not shown.

Table 8. Estimates of population growth rate (λ) under three scenarios for painted turtles in western Montana.

Scenarios	2003 "Good" Year	2004 "Bad" Year	Average
Current Situation[a]	1.19	0.92	0.99
No Roads[b]	1.30	1.13	1.26
No Movement[c]	1.19	0.91	0.94

[a] Current Situation: uses current estimates of survival and movement probabilities.

[b] No Roads: increases survival rates by known road mortality rates and assumes all road mortalities were successful movements.

[c] No Movement: assumes all movements were unsuccessful by setting movement probabilities to zero.

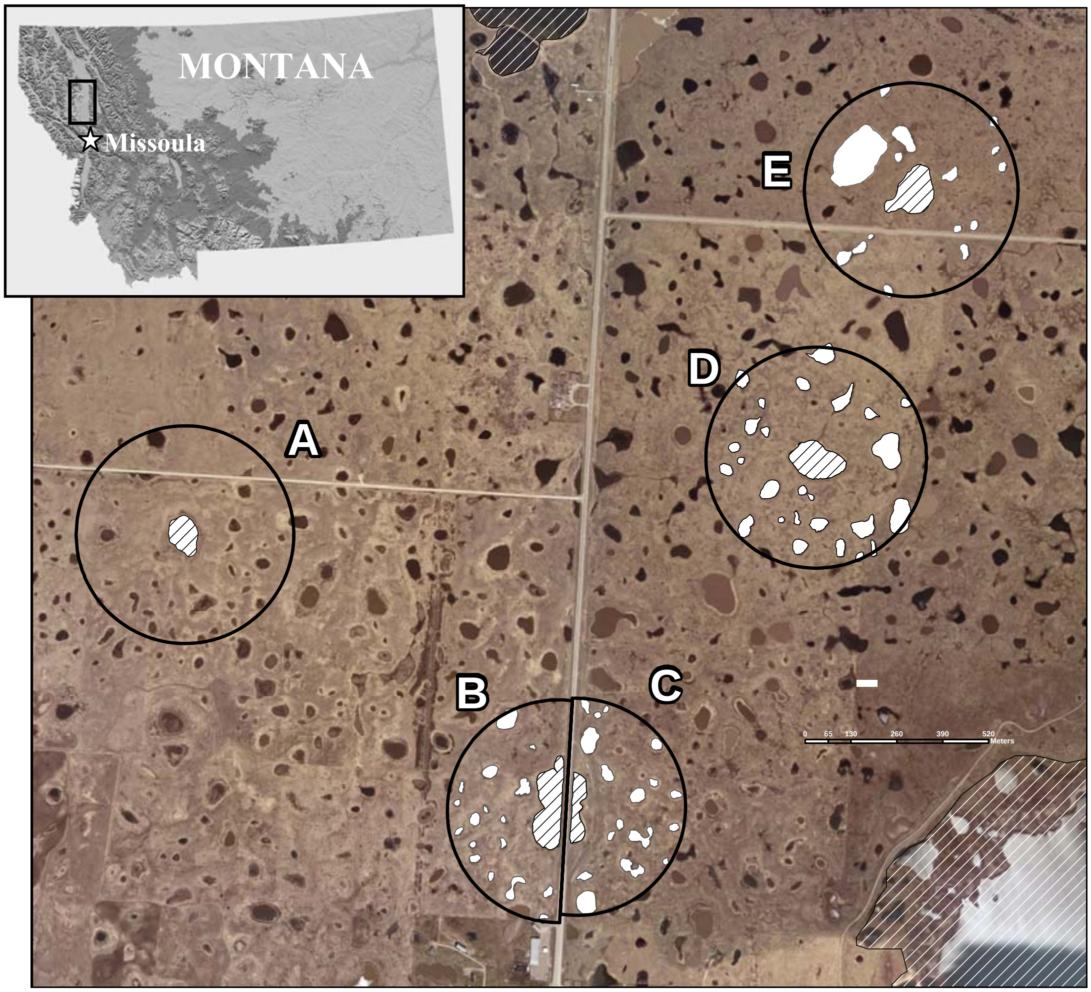

Fig. 1. Aerial photo of study area in the Mission Valley of Montana. Pond complexes are labeled A – E. Pond complexes are centered on “permanent” overwinter ponds (white with black hatch marks). All temporary ponds within complexes (white) were sampled when water was present. Note: temporary ponds in Complex A never held water during the study. The rest of the photo shows temporary ponds outside the complexes. Virtually all temporary ponds were dry by the end of July each year. Two permanent bodies of water occur in the area, Kicking Horse Reservoir and an irrigation pond (white hatched areas, upper center and lower right of photo). Also, note that U.S. Highway 93 runs north – south through the study area.

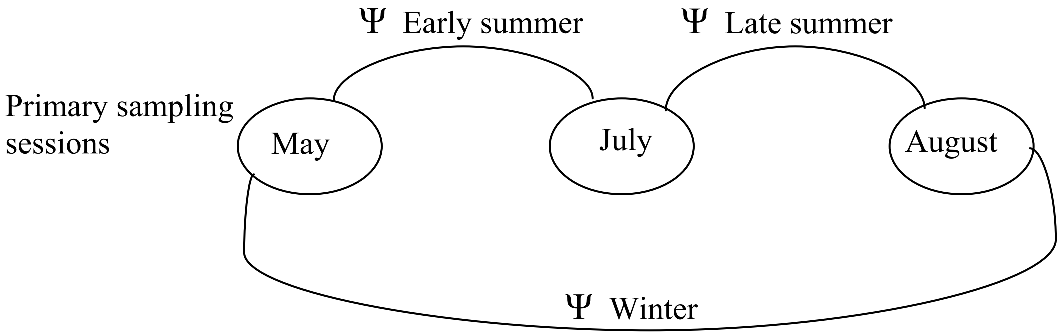

Fig. 2. Schematic of primary sampling session for capture-mark-recapture data in western Montana from August 2002 through May 2005. Primary sessions lasted 12 days each with between two and four secondary sessions within each primary session. Movement probabilities (Ψ) are estimated between primary sampling sessions. Movement in winter is most likely to occur in late fall or early spring just before or after hibernation.

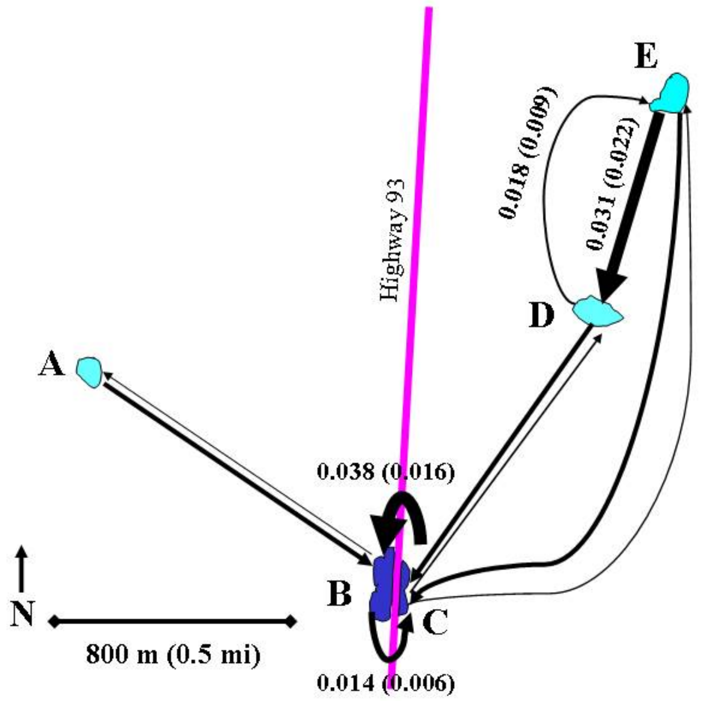

Fig. 3. Annual interpopulation movement probabilities (SE) for adult painted turtles in northwestern Montana, 2002 – 2005. Width of arrow represents relative probability of movement. The highest movement probabilities are shown on the figure; all other estimates are presented in Table 4 and are less than 0.01. If no arrow connects the ponds the probability of movement between those ponds was zero.

CHAPTER 4. THE EFFECTS OF ROAD MORTALITY ON TURTLE POPULATION SIZE AND STRUCTURE IN NORTHWESTERN MONTANA

ABSTRACT

The effects of roads on wildlife have gained attention over the last decade because of the ubiquitous network of roads and the visibility of road mortality. Turtle species may be particularly susceptible to the effects of roads because of life history traits that make it difficult to respond to perturbations in survival rates. Most research on the effects of roads on turtle populations have focused on either the number of turtles killed on roads or the alteration of population structure through disproportionate road mortality by sex. We assessed the potential impacts of highway-based mortality on western painted turtles (*Chrysemys picta bellii*) in the Mission Valley of northwestern Montana from 2002 to 2004. To accomplish this we conducted a capture-mark-recapture study along with concurrent road mortality surveys to estimate the percentage of the population killed on the road and to examine potential alteration in population sex and age structure. Road mortality averaged 186 individuals/year on about 5 km of road. Annual road mortality varied between pond complexes and years. In general, ponds that lost water during the drought had higher percentages of the population killed on the roads (4% - 13%) compared to ponds that retained >1.5 m depth (1.5% - 6.9%). Most ponds had annual mortality rates that equaled or exceeded the 2 - 3% mortality predicted by other studies to likely affect long-term viability in turtle populations. Road mortalities were not biased toward a particular sex and living populations did not vary significantly from an equal sex ratio regardless of distance from the highway. Local drought conditions and landscape structure (i.e., location of nesting habitat) may off-set the potential for female-biased road mortality.

INTRODUCTION

Highways and other road systems can present problems to wildlife populations through a multitude of effects such as changes in quantity and quality of habitat, direct mortality, altered behavior, and reduced landscape connectivity (Evink 2002; Forman et al. 2003). These effects can lead to fragmented populations, reduced population size, and, ultimately, lower population viability for some species (Ruediger 1996; Trombulak & Frissell 2000).

Aquatic and semi-aquatic turtle species may be especially vulnerable to the effects of roads because they use terrestrial landscapes for nesting and seasonal movements, but have limited ability to move effectively across the landscape (Gibbons et al. 1990; Mitchell & Klemens 2000). Road mortality is expected to affect population dynamics of turtles because of their life history traits: low recruitment rates, delayed sexual maturity, and low natural adult mortality (Congdon et al. 1993; 1994). This combination of traits makes turtle populations susceptible to declines and possibly extirpation when road mortality causes increased adult mortality (Heppell 1998).

Research on the effects of roads on turtle populations has focused on two main issues: direct road mortality and alteration of population structure through disproportionate road mortality by sex or stage class. Both outcomes could affect long-term persistence of turtle populations.

Studies on direct road mortality of turtles have mostly been limited to counts of individuals killed (Ashley & Robison 1996; Fowle 1996; Boarman et al. 1997; Haxton 2000; Aresco 2003). Translating such counts into population-level assessments of the consequences of road mortality is not possible without estimates of population size and this step is often missing due to the difficulty in estimating population size adjacent to roads. In response to the lack of population-level assessments using empirical data, Gibbs and Shriver (2002) used computer simulations based on traffic volumes, road density, and movements to predict effects of road mortality on turtle populations. They predicted road mortality would impact populations of land turtles and large-bodied pond turtles in many regions of the U.S. However, the simulations predicted small-bodied pond turtles, such as painted turtles, would not be affected by road mortalities at the regional level, although Gibbs and Shriver (2002) acknowledged substantial uncertainties in their estimates, in part due to lack of information on movement.

Population structure can be altered if road mortality disproportionately affects subgroups within the population. For example, more females than males may be killed, skewing the sex ratio; alternatively, more juveniles than adults could be killed, skewing the age-class ratio. Both types of changes in population structure can have long-term consequences for regional population persistence. Nesting forays may result in increased female mortality by increasing their likelihood of encountering roads (Haxton 2000; Steen & Gibbs 2004; Aresco 2005a). Marchand and Litvaitis (2004), Steen and Gibbs (2004), and Aresco (2005a) attributed male-biased sex ratios in turtles populations to road mortality, and Gibbs and Steen (2005) suggested roads have resulted in a long-term trend towards male sex bias in turtle populations over the last century. Steen et al. (2006) evaluated the hypothesis that females are more vulnerable to road mortality because of differential movements and concluded that females of aquatic and semi-aquatic species are more vulnerable to road mortality.

Age classes in most turtle populations are skewed toward adults; however juvenile-to-adult ratios can vary widely (see Ernst et al. 1994 for review). Adults have the greatest influence on annual population growth rates in freshwater turtles (Heppell 1998). Skewing the age ratio to juveniles through disproportionate road mortality on adults may result in a decrease in population growth. We know of no research that divides road mortality into age classes and examines the potential effects on age class ratio.

Previous studies make important contributions to understanding effects of roads on turtle populations, but none have combined road mortality with estimated population size and data on sex and age structure to assess population-level impacts. The full effects of road mortality may not be completely recognized if only one component (i.e., either population size or structure) is examined at a time. Our study examines the potential impacts of road mortality on both the overall population size and population structure via sex and stage class ratios of a western painted turtle (*Chrysemys picta bellii*) population in northwestern Montana.

METHODS

Study Area

The study area is located in the Mission Valley of northwestern Montana (47° 27' N, 114° 04' W; elevation 920 - 940 m) and contains glaciated, depressional wetlands that resemble the prairie pothole region of the mid-western United States (US Fish and Wildlife Service 2007). The valley has a high density of wetlands with over 2,000 permanent and ephemeral wetlands in an area of approximately 78 km^2 (Fowle 1996). The permanent ponds are characterized by very little emergent or submergent vegetation. The surrounding matrix is ungrazed grassland, although some areas were heavily grazed until 2001. See Chapter 2 for a full description of the study area and pond habitat.

We selected five permanent ponds that were separated from the next nearest permanent pond by a distance that exceeded the average reported movement distance (<200 m) of painted turtles (McAuliffe 1978; Rowe 2003) (Fig. 1). These five ponds were important overwintering ponds for turtles in our study area. Because not all required resources may be contained within the aquatic habitat (Pope et al. 2000), we identified a "complex" around each permanent pond. A complex was defined as the area within a 300 m (985 ft) radius circle centered on each permanent pond (Fig. 1). This distance incorporated typical movements that include most terrestrial activities such as nesting and seasonal use of temporary ponds (Gibbons 1968; McAuliffe 1978; Rowe 2003). All wetlands that held water within each complex were surveyed during each trapping session.

Three roads occur within the study area; U.S. Highway 93, Mollman Pass Trail, and Duck Road (Fig. 1). Road density within our study area was low (0.72 km/km^2). Measured traffic volumes on Highway 93 were considered high with an average of 290 vehicles/lane/hour during the day (Table 1). Traffic volumes increased on all roads during daylight hours when turtles are most likely to move (Rowe 2003).

Field Methods

Pond complexes were sampled intensively in three sessions per year: spring (May 21-June 1), summer (July 2-13), and fall (August 13-24). Every pond was sampled between two and four times during each session.

Temporary ponds outside the complexes but within the overall study area (about 10.2 km^2) and two permanent bodies of water outside the study area (Kicking Horse Reservoir and an irrigation pond; Fig. 1) were sampled opportunistically each year.

Capturing and Marking Turtles

We captured painted turtles using seine nets, basking traps, hoop nets, and dip nets to minimize the potential for sampling bias by sex or stage class (Ream & Ream 1966; Gibbons 1990a; Koper & Brooks 1998). The first time a turtle was captured each year we recorded: location, plastron length (PL) and width (mm), carapace length and width (mm), weight (g), sex, and age, if possible. Shell measurements were all straight-line measurement taken with calipers and weight was measured using spring scales. On subsequent recaptures within a year, we recorded only turtle identification, location, and sex. Sex was determined by examining secondary sexual characteristics (elongated foreclaws and elongated preanal region of the tail, [Frazer et al. 1993]) and age was determined by annuli aging techniques on turtles less than 4 - 5 years old (Graham 1979).

Each turtle was individually marked by drilling the margins of the carapace (Cagle 1939; McAuliffe 1978) as well as injecting a Biomark™ passive integrated transponder (PIT) tag (Camper & Dixon 1988; Buhlmann & Tuberville 1998). Turtles smaller than 50 mm PL (about 30 g) did not receive a PIT tag. Hatchlings and some juveniles were notched using nail clippers rather than drilling because some shells were not yet fully ossified (McAuliffe 1978; Camper & Dixon 1988).

Road Mortality Surveys

Road mortality surveys were conducted on a 3.2 km (2 mi) section of U.S. Highway 93 from Olson Road to Beaverhead Lane, a 1.6 km (1 mi) section of Mollman Pass Trail Road, and a 1.6 km (1 mi) section of Duck Road (Fig. 1).

We walked all roads within the study area approximately once a week from mid-May through late August, with one final survey the first week of October, 2003 and 2004. One or two crew members walked each side of the roadway, scanning the road bed and about 2 m into the grass right-of-way to document road-killed turtles. We estimated carcass locations to the nearest 160 m road marker. All turtle mortalities were examined to determine sex and age class and whether marked. All road mortalities were removed to avoid subsequent recounting.

All road mortality counts were considered minimum counts because we have no information on the probability of recovery of road killed individuals. For example, some turtle carcasses may have been removed from the highway by scavengers or knocked off the survey strip by vehicle impact. However, between road surveys, crew members moved new carcasses to the side of the road to minimize destruction and ensure that the individual was counted during the survey, thus, minimizing the loss of uncounted individuals.

Analytical Methods

Classification of Turtles into Sex and Stage Classes

We grouped turtles into stage classes (juvenile and adult) because reliability of aging decreases with age due to shedding of the scutes (Sexton 1959; Wilbur 1975). Juveniles were turtles with a plastron length (PL) ≤ 104 mm and sex was treated as unknown in all analyses. However, in our study, 79 mm was the smallest PL where male secondary sexual characteristics were observed; therefore, the juvenile category included some (< 1.8%) male turtles that exhibited secondary sexual characteristics. Adults were turtles with a PL ≥ 105 mm. Any individual that was at least 105 mm PL and not showing signs of secondary sexual characteristics was considered female (Mitchell 1985). Based on subsequent recaptures, all male turtles exhibited secondary sexual characteristics by the time they reached 105 mm PL.

Population Structure

Sex Ratios

Sex ratios can be calculated in different ways. Cohort sex ratios (based on size rather than maturity) include immature and mature females but only mature males (Gibbons 1990b). Functional sex ratios (based on sexual maturity) only include mature individuals of both sexes; therefore the sizes (and age) of turtles included vary because males mature at smaller sizes than females. We chose to use a cohort sex ratio because of the potential for differences in sizes at maturity among different populations or ponds within a region (Zweifel 1989; Gibbons 1990b) and because we did not know whether females matured at different rates within the various ponds. Using the conservative size estimates for adults assures that all individuals used in the sex ratio analyses were of known sex.

Sex ratios were determined for live turtles for the entire study area and for each pond complex. Only adult turtles of known sex were used (see above for size categories) to determine the living adult sex ratio. The sex ratio of road mortalities was based only on adults where sex could be positively determined. We assumed a 1:1 sex ratio in the living population for the total number of adult turtles captured. Chi-squared (χ^2 test) analyses were used to test if observed sex ratios of living turtles were biased. Bonferroni corrected *p*-values (Rice 1989) were used to reduce the chance of inflated Type I error due to multiple comparisons of the same hypothesis. We then compared the sex ratio of turtles killed on the road to the sex ratio of the living population to determine if one sex was more susceptible to road mortality.

Stage Class Ratios

We determined the proportion of adults in the living population and in the road mortality counts for 2003 and 2004. The number of adults and juveniles in the living population was based on the number of marked individuals in each category for both years. The proportion of adults in the road mortalities was based on counts of only individuals in the known stage categories. We compared the proportion of adults in the road mortalities to that of the living population using chi-squared (χ^2 test) analysis.

Population Size

Population size was estimated within each pond complex for both stage classes using a capture-mark-recapture framework (multistate robust models for adults and Pollock's robust design models for juveniles) within Program MARK. The modeling is fully discussed in chapter 2.

Percentage of the Population Killed on Roads

We estimated the percentage of the population within each complex killed on roads for each stage class and year using the number of turtle carcasses found on the roads divided by the population size. We used only road mortalities that could be identified to the individual and, thus, the date and location of the last capture was known. Population size within each complex was estimated at the beginning of each year. To incorporate the uncertainty in the population size estimates, upper and lower bounds of the percentage of the population affected by road mortality were estimated using the upper and lower profile likelihood confidence intervals (Williams et al. 2002) of the population size estimates. All estimates of the percentage of the population killed on the roads were conservative because only a portion (16% in 2003 and 36% in 2004) of all dead-on-the-road turtles could be identified to individual.

RESULTS

Population Structure – Sex and Stage Class Ratios

We marked 2,305 individual turtles between 2002 and 2004. Overall, no sex bias was found in the living adult turtle population in the study area (776 male and 793 female) ($\chi^2 = 0.18$, df = 1, p = 0.67). Sex ratios within pond complexes did not differ significantly from a 1:1 sex ratio (Table 2). The living stage classes were skewed toward adults (389 juveniles to 932 adults) with a juvenile-to-adult ratio of 1:2.4.

Population Size Estimates

Overall, population size within the pond complexes decreased from 1,035 in 2003 to 660 in 2004 (Table 3). Abundance of adults decreased within most pond complexes. Ponds that lost significant amounts of water due to drought (Ponds A, D, and E; Fig. 1) had less than half the number of adults in 2004 than in 2003 (Table 3). Only one pond (Pond B, which retained >1.5 m depth) increased in numbers of adults from 2003 to 2004. Numbers of juveniles within all pond complexes remained relatively stable between the two years (Table 3).

Road Mortality

In the 29 road mortality surveys conducted over the two years, we found 373 turtle carcasses: 360 on Highway 93, 12 on Mollman Pass Trail, and one on Duck Road. On Highway 93, this averaged about 56 turtles/km/year. Sex could not be determined on 37% (79) of adult road mortalities. However, of those turtles where sex could be determined (68 males and 65 females; Table 4), no sex bias in road mortalities ($\chi^2 = 0.12$, df = 1, p = 0.73) was found compared to the living population of 51% female and 49% male. Of the identifiable turtles killed on the highway, 212 (79.7%) were adults and 54 (20.3%) were juveniles (Table 4). Stage class could not be determined for 107 (28.7%) individuals. Overall, a significantly greater proportion of adults (0.80) were killed on the road than were found in the overall population (0.71) ($\chi^2 = 10.8$, df = 1, $p < 0.01$). However, this does not hold true in both years. In 2004, no significant difference between stage class ratios of living and road killed populations was found ($\chi^2 = 2.4$, df = 1, p = 0.12).

Our pond complexes ranged from 32 m to 1,130 m from the highway, and known marked individuals found dead on the road included turtles from every pond complex (Table 5). The number of road kills from a specific pond was unrelated to the distance that pond is located from the highway (p = 0.560). Of the marked road-killed individuals we could positively identify, the largest number (26) were last seen alive in complex E which is the second furthest (880 m) from the highway. Road mortalities of turtles associated with the two ponds split by the highway were 15 in Pond B and 24 in Pond C (which lost more depth than Pond B) (Table 5).

Percentage of Population Killed on Roads

Overall, in ponds that lost the most water (Ponds A, D, and E) a higher percentage of the pond complex population was killed in 2004 (range: 4.0% – 13.1%) than in 2003 (range: 0 – 7.6%) (Table 6). In Ponds B and C, which retained depths of over 1.5 m, the percentage of the population killed on the road remained relatively stable between the two years (range: 1.5% - 6.9%).

The percentage of the adult population killed on roads ranged from 0% to 9.3% in 2003 to 2.5% to 24.6% in 2004, depending on pond depth. Similar to the total population pattern, in general, ponds that lost the most water (depth dropped to <0.5 m) had higher percentages of the population killed on the road than ponds that retained <1.5 m water (Table 6).

The percentage of the juvenile population killed on roads ranged from 0% to 9.3% in 2003 to 0% to 15.0% in 2004; however, the pattern was not as clear as in the adult estimates (Table 6). In 2003, the deep ponds close to the highway (Ponds B and C) had higher percentages of the juvenile population affected by road mortality than the shallower ponds that were further from the highway (Ponds A, D, and E). However, in 2004, Pond D (652 m from the highway) had the highest percentage of the juvenile population killed on the road (12.3% to 15.0%).

DISCUSSION

Population Structure

Sex Ratio

Contrary to expectations, road mortality was not female biased and the overall population sex ratio was not affected by roads. The living turtle sex ratio was not significantly different from a 1:1 male to female ratio as many long-term studies have shown (Ernst et al. 1994). Other studies found ponds adjacent to roads were male biased while ponds further from roads, and presumably not affected by road mortality, had sex ratios in parity (Marchand & Litvaitis 2004; Aresco 2005a). Distance from highway did not influence sex ratios in our pond complexes. All pond complexes had sex ratios in parity including ponds immediately adjacent to the highway (ponds B and C) (Table 2). Drying conditions in 2003 and 2004 forced turtles to leave ponds, thus, exposing them to the possibility of road mortality.

Biased sex ratios may result from disproportionate movements by females, due to their nesting forays, which makes them more susceptible to road mortality (Steen & Gibbs 2004; Aresco 2005a; Gibbs & Steen 2005; Steen et al. 2006). However, local conditions (drought) and landscape structure (location of nesting habitat) may off-set the movement differentials between males and females. Turtles may have moved in search of suitable water rather than nesting habitat. In support of this, we found no difference between the sexes in movement rates between the complexes in our capture-mark-recapture modeling (Chapter 3). Also, more road-killed males than females were encountered adjacent to the ponds split by the highway (Ponds B and C; 47 m and 32 m from the road, respectively) (Fig. 1). These distances are well within the average distance females travel to nest (Rowe et al. 2005). Therefore, if females are more susceptible to road mortality due to nesting forays we would expect more female than male road mortalities in this area.

The location of suitable nesting habitat may also affect the rates at which females encounter roads. Nesting females tend to move from pond to nest and back to the original pond (Rowe et al. 2005). In our study, both ponds adjacent to the highway had suitable nesting habitat surrounding the pond; therefore, it was not necessary for a female to cross the highway to find suitable nesting habitat.

Sex ratios are sensitive to how the analysis was conducted and the analysis is complex because of the relationship of size at sexual maturity between males and females. This difference in maturation rate between the sexes may influence the perceived sex ratios (Gibbons 1990b; Lovich 1996). We restricted the analyses of sex ratio to known adult turtles (PL ≥ 105 mm), thus calculating a "cohort" sex ratio. This conservative value of size at maturity minimizes the effect that earlier maturing males would have on the sex ratio. By contract, functional sex ratios are expected to be male biased because males mature at smaller sizes than females (Lovich 1996). Using a functional sex ratio on our study would indicate a male biased sex ratio. However, using the same categories for known individuals killed on the road (therefore, maturity was known before they were found dead) indicated road mortalities reflect the same proportion of mature individuals in the road mortalities. Thus, again, females are not being killed disproportionately on the road and therefore the road is not affecting sex ratio of the population.

Trapping methods may also cause the appearance of biased sex ratios (Ream & Ream 1966). However, we used a variety of trapping methods, including extensive use of seine netting, which unlike other trapping methods does not rely on a specific behavior (i.e., basking or feeding). Our variety of techniques minimized the potential for biased captures.

Stage Class Ratios

High rates of adult mortality in a long-lived species could affect population viability of turtle populations (Crouse et al. 1987; Heppell et al.1999). Our observed juvenile-to-adult ratio in the living population (1:2.4) falls within the lower end of that already documented for painted turtles (Ernst et al. 1994). Overall, (2003 and 2004 combined), a disproportionate number of adults were killed on the road (1:3.9) compared to the living population (1:2.4). In 2003, ponds began drying and adults began moving out of these ponds as evidenced by less adults caught in the drying ponds in 2004, yet juvenile numbers remained similar to previous years. In 2004, adult road mortality was 49% less than in 2003, therefore, adults were moving less than in the previous year.

Because egg and hatchling survival rates are highly stochastic (Congdon et al. 1993), the age ratio in the living painted turtle population could vary greatly from year to year. Although it appears that road mortality is affecting adults disproportionally, longer-term studies are necessary to fully understand if road mortality is affecting age structure in this population.

Percentage of Population Killed on the Roads

Our estimates of the percentage of the population killed on the road are conservative. Numbers of road mortalities were a minimum count because it is unlikely we detected all carcasses. Also, using only carcasses identified to individual is a conservative estimate of road mortalities; we were able to identify to individual just over one-third of the carcasses known to be marked. A minimum count of road mortalities leads to underestimates of the percentage of the population killed on the road.

Even using conservative road mortality values, roads are affecting local populations and ponds affected by drought had the highest percentages of the population killed on roads. The level of annual road mortality estimated in almost every pond complex equals or exceeds the 2 - 3% additive (i.e., not compensatory) mortality that other studies suggest is likely to affect long-term viability in turtle populations (Doroff & Keith 1990; Brooks et al. 1991; Congdon et al. 1993, 1994).

In turtle species, road mortality is not likely compensated for by density-dependent responses such as increases in reproduction, growth rates, and egg or hatchling survival (Brooks 2007). Brookes et al. (1991) found that a population of snapping turtles (*Chelydra serpentina*) did not have the ability to effectively compensate for increases in adult mortality. To maintain a stable population, Congdon et al. (1993) found that increases in already high juvenile survival rates were required to off-set the persistent reduction in adult survival. Increases in juvenile survival rates are not likely to occur in our study area because juveniles are also killed on the road in higher proportions than is thought to be sustainable in the long-term.

High traffic volumes and movement patterns of painted turtles may combine to negatively affect some populations on a local level, even in areas with low road densities such as in our study. This is contrary to Gibbs and Shriver's (2002) prediction that regional road densities and traffic volumes would not affect populations of small-bodied pond turtles such as painted turtles. Road densities in our study area were low (overall < 1 km/km^2), yet traffic volumes were very high (290 veh/lane/hour; 3,480 veh/lane/daylight hours) compared to most other studies (e.g., Gibbs & Shriver 2002; Aresco 2005a). This level of traffic volume greatly exceeds those modeled (≤ 1,000 veh/lane/daylight hours) by Gibbs and Shriver (2002). Movements modeled by Gibbs and Shriver (2002) incorporate only single, annual nesting forays of 100 m in a random direction. Turtles in our study may be moving more frequently, greater distances, and in more directed movements. Based on capture-mark-recapture data, 496 individuals (21%) moved between ponds. About 10% of these individuals made more than one movement a year and the average distance traveled was 410 m (range 30 – 2,400 m) (Griffin & Pletscher 2006). Also, turtles appeared to make directed movements out of drying ponds to specific ponds that where more permanent (K. Griffin, unpublished data).

Conservation and Management Implications

The full impacts of road mortality may not be recognized if only one component of the population (i.e., population size or structure) is examined at a time. Although the highway has not altered the sex ratio in this turtle population, the population is being affected through direct road mortality and potentially through disproportionate mortality of adults. This could have consequences on the long-term viability of this population. Life history traits that include low recruitment rates of juveniles result in very slow recovery from increased adult mortality (Gibbons 1987; Brooks et al. 1991; Congdon et al. 1994; Heppell 1998). Sustained levels of unusually high adult mortality in turtles have long-term consequences in that populations may never be able to recover (Congdon et al. 1994).

Lowering rates of road-related mortalities, particular in adults, is important in maintaining populations. A potential mitigation approach to minimize the impacts of road mortality is to implement crossing structures and barriers that facilitate the use of crossing structures. These measures are most effective for turtles where populations undertake directed movements to specific sites (e.g., hibernacula, suitable habitat during drought conditions, nesting). Turtles will use culverts especially when directed by barrier fencing (Boarman et al. 1997; Guyot & Colbert 1997; Barichivich & Dodd 2002; Dodd et al. 2004; Aresco 2005b). However, barrier fencing must be specifically designed to prevent turtles from climbing the barriers (Aresco 2005b; Griffin 2006).

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Table 1. Description of road types and traffic volumes (vehicles/lane/hour) averaged over summer months (May – August) and years (2003 - 2004) in the study area in northwestern Montana.

Road	# Lanes	Surface	Posted Speed Limit (mph)	Time	Traffic Volume[a] (Ave. # veh/lane/hr)
Highway 93	2	paved	70	Night & Day	171
				Day Only	290
Mollman Pass Trail	2	paved	50	Night & Day	11
				Day Only	27
Duck Road	1 – 2	dirt	35	Night & Day	3
				Day Only	4

[a] Traffic volume was counted using traffic hose counters checked twice daily for at least five consecutive days, three times each summer. U.S. Highway 93 traffic volumes were corrected with monthly axle correction factors for each year (D. Wark, MDT, personal communication).

Table 2. Living sex ratios of painted turtles associated with each pond complex in northwestern Montana. Probabilities reflect Bonferroni corrected chi-squared tests of equal sex ratio.

Pond Complex	**Female**	**Male**	**p**
A	108	91	0.65
B	151	152	0.95
C	136	165	0.38
D	90	95	0.92
E	135	85	0.06
Total	620	588	0.74

Table 3. Population size estimates (± SE) of the turtle population within each pond complex by stage class in 2003 and 2004 in the Mission Valley of northwestern Montana based on capture-mark-recapture models.

	Adult		**Juvenile**		**Total**	
Pond	**2003**	**2004**	**2003**	**2004**	**2003**	**2004**
A	222 (27)	29 (5)	19 (4)	22 (1)	241 (28)	51 (5)
B	168 (51)	228 (24)	39 (10)	38 (9)	207 (54)	266 (24)
C	148 (8)	109 (5)	27 (4)	32 (2)	175 (9)	141 (5)
D	165 (15)	68 (5)	46 (3)	55 (3)	211 (16)	123 (6)
E	154 (16)	35 (5)	47 (5)	44 (3)	201 (17)	79 (6)
Total	857	469	178	191	1035	660

Table 4. Number of road-killed turtles by sex and stage class found by walking surveys on all roads in the study area in northwest Montana in 2003 and 2004.

	Adult					
Year	**Female**	**Male**	**Unknown Sex**	**Juvenile**	**Unknown Age**	**Total**
2003	46	37	44	29	79	235
2004	19	31	35	25	28	138
Total	65	68	79	54	107	373

Table 5. Road mortality[a] of painted turtles associated with each pond complex in northwestern Montana. Distance from highway was measured from the nearest edge of the center pond in each complex to the nearest edge of the highway. Number of turtles marked in each complex is reported in Table 2.

		Adult		**Juvenile**		**Total**	
Pond Complex[b]	**Distance from Highway (m)**	**2003**	**2004**	**2003**	**2004**	**2003**	**2004**
A	1130	0	3	0	0	0	3
B	47	4	7	3	1	7	8
C	32	8	7	3	6	11	13
D	652	6	4	0	8	6	12
E	881	12	7	1	6	13	13
Total		30	28	7	21	37	49

[a] Road mortality values only include marked turtles that were positively identified.

[b] The pond complex associated with the mortality indicates the last known location of the living turtle before it was found dead on the highway.

Table 6. Estimated proportions of adult, juvenile, and total turtle populations within each complex killed on the roads within the study area in northwestern Montana in 2003 and 2004. Lower (LCI) and upper (UCI) estimates are based on profile likelihood confidence intervals for the estimated population size.

	Adult				**Juvenile**				**Total**			
Pond	**2003**		**2004**		**2003**		**2004**		**2003**		**2004**	
Complex	**LCI**	**UCI**	**LCI**	**UCI**	**LCI**	**UCI**	**LCI**	**UCI**	**LCI**	**UCI**	**LCI**	**UCI**
A	0	0	0.064	0.129	0	0	0	0	0	0	0.040	0.067
B	0.012	0.038	0.025	0.037	0.028	0.073	0	0	0.015	0.045	0.020	0.033
C	0.047	0.059	0.057	0.069	0.073	0.132	0.051	0.067	0.053	0.069	0.056	0.069
D	0.030	0.042	0.049	0.067	0	0	0.123	0.155	0.023	0.033	0.082	0.108
E	0.061	0.093	0.139	0.246	0.016	0.024	0.037	0.050	0.051	0.076	0.086	0.131
Overall	0.023	0.043	0.048	0.070	0.023	0.040	0.048	0.071	0.025	0.043	0.048	0.070

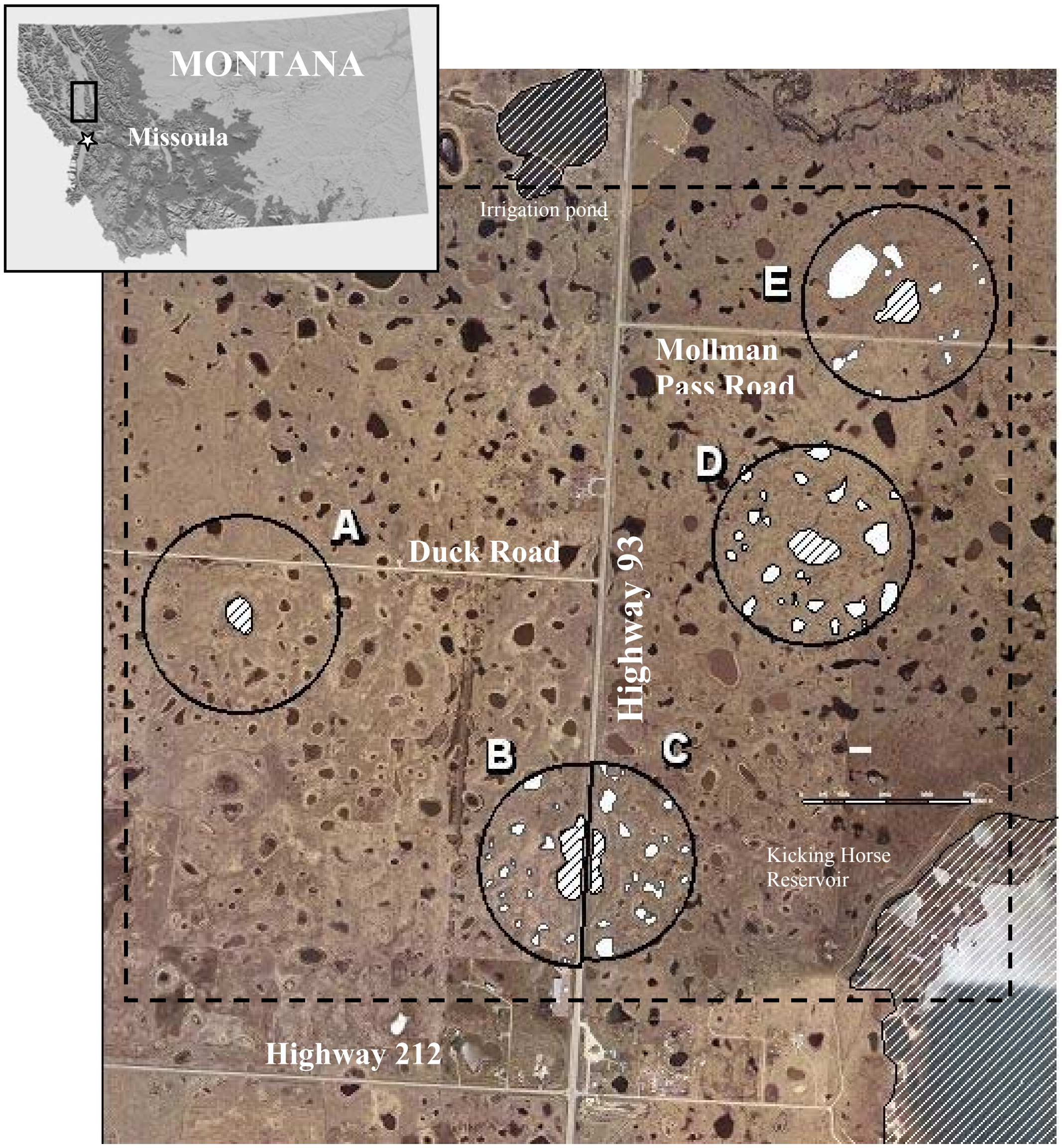


Fig. 1. Aerial photo of study area (dashed line) in the Mission Valley of northwestern Montana. U.S. Highway 93 runs north – south through the study area. The other two roads are secondary, low-use roads. Pond complexes (labeled A – E) are centered on “permanent” overwinter ponds (white with black hatch marks). All temporary ponds within complexes (white) were sampled when water was present. Note that temporary ponds within complex A never held water during my study. The rest of the photo shows temporary ponds outside the complexes. Virtually all of these ponds were dry by August each year. However, two permanent bodies of water occur in the area (white hatched areas, upper center and lower right of photo).

APPENDIX 1. POND HYDROLOGY AND MAPS REFERENCING THE POND NUMBERING SYSTEM.

Table 1. Pond hydrology[a] and depth measurements (m) during various months from 2001 – 2007 in Northwestern Montana.

Pond Number[b]	Turtle[c]	2001[d]	2002		2003			2004			2005	2006		2007	
		April	July	Aug	May	July	Aug	May	July	Aug	May	May	June	May	July
1	Y	W	W	D	D	D	D	D	D	D	W				
2	Y	W	0.58	0.50	W	D	D	D	D	D	0.50				
85	Y	W	0.71	0.60	W	W	D	0.20	0.20	D	0.70				
A1 (A)		W	W	1.40	1.30	1.10	0.80	0.60	0.50	0.03	W	W	0.80	W	0.48
A2	Y	W	D	D	D	D	D	D	D	D	W	W	0.30	W	W
A3		W	D	D	D	D	D	D	D	D	W	W	W		D
A4		W	D	D	D	D	D	D	D	D	D		D		D
A5		W	D	D	D	D	D	D	D	D	D		D		D
A6		W	D	D	D	D	D	D	D	D	D		D		D
A7		W	D	D	D	D	D	D	D	D	D		D		D
A8		W	D	D	D	D	D	D	D	D	W		D		D
A9		W	D	D	D	D	D	D	D	D	D		D		D
A10		W	D	D	D	D	D	D	D	D	D		D		D
A11		W	D	D	D	D	D	D	D	D	D		D		D
A12		W	D	D	D	D	D	D	D	D	W		D		D
A13		W	D	D	D	D	D	D	D	D	W		D		D
A14		W	D	D	D	D	D	D	D	D	W		D		D
A15		W	D	D	D	D	D	D	D	D	trace		D		D
A16		W	D	D	D	D	D	D	D	D	W	W	W		D
A17	Y	W	D	D	D	D	D	D	D	D	W	W	W		D
A18		W	D	D	D	D	D	D	D	D	D	W	W		D
A19	Y	W	D	D	D	D	D	D	D	D	W	W	W	W	trace
A20		W	D	D	D	D	D	D	D	D	D	W	W		D
A21		W	D	D	D	D	D	D	D	D	W	W	W		D
A22	Y	W	D	D	D	D	D	D	D	D	W	W	W		D
A23	Y	W	D	D	D	D	D	D	D	D	W	W	W		D
A24		W	D	D	D	D	D	D	D	D	W	W	W		D
A25		W	D	D	D	D	D	D	D	D	D	W	W		D
A26		W	D	D	D	D	D	D	D	D	D	W	W		D
A27		W	D	D	D	D	D	D	D	D	D		D		D
A28	Y	W	D	D	D	D	D	D	D	D	W	W	W		D

Table 1 Cont. Pond hydrology[a]

Pond Number[b]	Turtle[c]	2001[d]	2002		2003			2004			2005	2006		2007	
		April	July	Aug	May	July	Aug	May	July	Aug	May	May	June	May	July
A29	Y	W	D	D	D	D	D	D	D	D	W	W	W		D
A30		W											D		D
BA	Y	W	W	W	W	W	W	W	W	W		W	W	W	W
BA1	Y	W						W	W						
BA10		W	W					W	W						
BA2	Y	W						W	W						
BA3		W						W	W						
BA4	Y	W						W	W						
BA5		W						W	W						
BA6	Y	W						W	W						
BA7	Y	W						W	W			W	W	W	W
BA8		W						W	W						
BA9	Y	W						W	W						
BC1 (B)	Y	W	3.7	4.2	W	3.7	2.5	3.0	3.4	W	W	W	W	W	2.9
BC2 (C)	Y	W	2.4	W	W	2.1	2.0	1.9	2.0	1.8	2.4	W	W	W	2.1
BC3		W	W	W	D	D	D	D	D	D	W			W	W
BC4	Y	W			0.1	D	D	0.1	D	D	W				D
BC5		W			0.2	D	D	0.2	D	D	W				D
BC6	Y	W			D	D	D	D	D	D	W			W	W
BC7	Y	W	W	W	D	D	D	D	D	D	W			W	W
BC8		W			D	D	D	D	D	D	W			W	W
BC9	Y	W	0.1	D	W	D	D	D	D	D	W			W	W
BC10		W	D	D	D	D	D	D	D	D	W				D
BC11		W	D	D	D	D	D	D	D	D	W				D
BC12		W	W	D	D	D	D	D	D	D	W				D
BC13		W			trace	D	D	0.1	D	D	W				D
BC14	Y	W			D	D	D	0.1	trace	D	W				D
BC15	Y	W	W	W	1.6	1.5	1.2	1.1	0.9	0.8	W	W	W	W	W
BC16		W	D	D	D	D	D	D	D	D	W				D
BC17		W	D	D	D	D	D	0.1	D	D	W				D
BC18		W	D	D	D	D	D	D	D	D	W				D

Table 1 Cont.

Pond Number[b]	Turtle[c]	2001[d]	2002		2003			2004			2005	2006		2007	
		April	July	Aug	May	July	Aug	May	July	Aug	May	May	June	May	July
BC19	Y	W	W	D	D	D	D	D	D	D	W			W	W
BC20		W	D	D	D	D	D	D	D	D	W				D
BC21		W	D	D	D	D	D	D	D	D					D
BC22	Y	W	W	D	D	D	D	D	D	D	W				D
BC23		W	D	D	D	D	D	D	D	D					D
BC24	Y	W	W	W	0.3	0.1	D	D	D	D	W			W	W
BC34		W	W	D	0.1	D	D	0.2	trace	D	W				D
BC35	Y	W	D	D	D	D	D	D	D	D	W				D
BC37	Y	W	D	D	D	D	D	D	D	D	W				D
B25		W	D	D	D	D	D	D	D	D	D				D
B26		W	D	D	D	D	D	D	D	D	W				D
B27		W	D	D	D	D	D	D	D	D	W				D
B28		W	D	D	D	D	D	D	D	D	W				D
B29	Y	W	D	D	D	D	D	W	D	D	W			W	W
B30	Y	W	D	D	D	D	D	D	D	D	W				D
B31	Y	W	W	W	W	0.2	D	D	D	D	W			W	W
B32	Y	W	W	W	0.3	W	D	0.3	trace	D	W			W	W
B33		W	D	D	trace	D	D	0.2	D	D	W				D
C25	Y	W			0.1	D	D	D	D	D	W			W	W
C26		W			D	D	D	D	D	D					D
C27	Y	W			D	D	D	trace	D	D	W				D
C28		W			0.1	D	D	0.1	D	D	W			W	W
C29	Y	W			0.1	D	D	0.1	D	D	W			W	W
BO1	Y	W	W	1.1	1.0	0.8	W	0.5	0.3	0.28				W	W
BO2	Y	W	W	W	0.6	W	trace	0.3	D	D					
BO3	Y	W	W	W	0.5	W	0.5	0.5	0.1	0.1	0.6			W	W
BO5	Y	W	D	D	W	D	D	W	D	D					
CO1	Y	W	W		W	D	D	0.3	D	D					
CO2	Y	W	W	W	W			0.2							
CO3	Y	W	W	W	0.5	W	?	0.1	D	D					
CO4	Y	W			W	W	W	W	D	D					

Table 1 Cont.

Pond Number[b]	Turtle[c]	2001[d]	2002		2003			2004			2005	2006		2007	
		April	July	Aug	May	July	Aug	May	July	Aug	May	May	June	May	July
CO5	Y	W	W	W				W	D	D					
CO6		W	W					W	D	D					
CO7	Y	W	W												
D1 (D)	Y	W	1.7	W	1.4	1.3	0.9	1.0	0.8	0.6	0.9	W	W	W	0.9
D2	Y	W	W	D	W	D	D	0.1	D	D	W			W	W
D3		W	W	?	D	D	D	D	D	D	W			W	W
D4	Y	W	W	?	W	D	D	0.2	trace	D	W			W	W
D5	Y	W			0.1	D	D	trace	D	D	W			W	W
D6	Y	W			D	D	D	D	D	D	W				D
D7	Y	W	W	W	0.15	D	D	0.15	D	D	W			W	W
D8	Y	W			0.15	D	D	0.2	D	D	W				D
D9	Y	W			0.2	D	D	0.5	trace	D	W				D
D10		W			D	D	D	trace	D	D	W			W	W
D11	Y	W			0.2	D	D	0.1	D	D	D				D
D12		W			D	D	D	D	D	D	W				D
D13	Y	W	0.3	0.1	0.2	D	D	0.2	trace	D	W			W	W
D14	Y	W	W	W	0.1	D	D	0.1	D	D	D			W	W
D15	Y	W	W	W	0.1	D	D	0.1	D	D	W			W	W
D16		W			D	D	D	D	D	D	D				D
D17		W			D	D	D	D	D	D	W				D
D18	Y	W			W	D	D	0.2	D	D	W			W	W
D19		W			D	D	D	D	D	D	W				D
D20		W			D	D	D	D	D	D	D				D
D21		W			D	D	D	D	D	D	D				D
D22		W			D	D	D	D	D	D	W				D
D23		W			D	D	D	D	D	D	trace				D
D24		W			D	D	D	D	D	D	W				D
D25		W			D	D	D	trace	D	D	W			W	W
D26	Y	W	W	D	0.1	D	D	0.2	D	D	W			W	W
D27		W			0.2	D	D	0.3	D	D	W			W	W
D28		W	W	D	trace	D	D	0.1	D	D	W			W	W

Table 1 Cont.

Pond Number[b]	Turtle[c]	2001[d]	2002		2003			2004			2005	2006		2007	
		April	July	Aug	May	July	Aug	May	July	Aug	May	May	June	May	July
D29E	Y	W			W	W	W	W	W	W	W			W	W
D29W		W			0.05	D	D	0.05	D	D	W			W	W
D30		W			0.1	D	D	D	D	D					D
DO1E	Y	W			0.2			W	?						
DO1W	Y	W			0.1			W	?						
DO2	Y	W	0.34	0.1	D	D	D	D	D	D					
DO3	Y	W	W	0.2	D	D	D	D	D	D					
DO4	Y	W						W	D	D					
DO5	Y	W						W	trace	trace					
DO6		W													
DO7	Y	W						W	trace						
DO8	Y	W						W	?						
DO9	Y	W						W	?						
DO10		W	W												
DO11		W	W												
DO12	Y	W	W												
E1 (E)	Y	W	0.9	0.8	W	0.7	0.5	0.4	0.4	0.1	0.4	W	0.66	W	0.43
E2	Y	W	0.5	0.4	W	0.4	D	0.2	0.1	D	0.3	W	0.64	W	W
E3		W			D	D	D	trace	D	D	W				D
E4	Y	W			0.1	D	D	trace	D	D	W	W	W	W	trace
E5		W			D	D	D	D	D	D	W				D
E6	Y	W			0.25	0.1	D	W	0.2	D	W	W	W	W	W
E7		W			D	D	D	D	D	D	W				D
E8	Y	W			D	D	D	D	D	D	W				D
E9		W			D	D	D	trace	D	D	W				D
E10	Y	W			0.1	D	D	0.1	D	D	W			W	trace
E11	Y	W			0.2	0.1	D	0.2	0.1	D	W			W	trace
E12		W			D	D	D	trace	D	D	W			W	trace
E13		W			D	D	D	D	D	D	W				D
E14W		W	D	D	trace	D	D	0.1	D	D	W			W	trace
E14E	Y	W	W	0.14	0.22	0.1	D	0.25	0.2	D	W			W	W

Table 1 Cont.

Pond Number[b]	Turtle[c]	2001[d]	2002		2003			2004			2005	2006		2007	
		April	July	Aug	May	July	Aug	May	July	Aug	May	May	June	May	July
E15		W	D	D	D	D	D	trace	D	D	W			W	trace
E16		W	D	D	D	D	D	D	D	D	W				D
E17		W	D	D	D	D	D	D	D	D	W			W	trace
E18		W	D	D	D	D	D	D	D	D	W				D
E19	Y	W	D	D	D	D	D	0.25	D	D	0.25				D
E20		W	D	D	D	D	D	D	D	D	W				D
EO1	Y	W	W	0.3	?	?		W	trace	trace	W				
EO2		W									W				
EO3		W									W				
EO5	Y	W						W							
EO6		W													
EO7	Y	W						W	W						
EO8		W						W							
EO9		W						W							
EO10	Y	W						W							
EO11	Y	W						W							
EO12		W						W							
EO13		W						W							
EO14	Y	W						W							
EO15	Y	W						W							
EO16	Y	W						W							
EO17		W	W	W				W							
EO18		W						W							
EO19	Y	W						W							
EO20	Y	W						W	W						
EO21		W	W					W	W	trace					
EO22		W	W												
EO23		W	W												
KH	Y	W	W	W	W	W	W	W	W	W	W	W	W	W	W
KH1		W						W	W	D					
KH2	Y	W						W	W	D					

Table 1 Cont.

Pond Number[b]	Turtle[c]	2001[d]	2002		2003			2004			2005	2006		2007	
		April	July	Aug	May	July	Aug	May	July	Aug	May	May	June	May	July
KH3		W						W	W	D					
KH4		W						W	W	D					
KH5		W						W	W	D					
KH6		W						W	W	D					
KH7		W	W					W	D	D					
KH8		W						W	W	W					
KH9	Y	W						W	W	W					
KH10	Y	W						W	W						
KH11	Y	W						W	W						
KH12		W						W							
KH13		W						W							
KH14	Y	W						W	D	D					
KH15	Y	W						W	D	D					
KH16	Y	W						W	W	W					
KH17	Y	W						W	D	trace					
KH18		W						W							
KH19	Y	W						W	W						
KH20	Y	W						W	W	W					
KH21	Y	W						W	W						
KH22	Y	W						W	W						
KH23	Y	W						W	W	W					
KH24	Y	W						W	W						
KH25	Y	W						W	W						
KH26		W						W							
KH27	Y	W						W	W						
KH28	Y	W						W	W						
KH29		W						W							
KH30	Y	W						W	W						
KH31	Y	W						W	W	W					
KH32	Y	W						W	W						
KH33		W						W	W						
KH34		W						W	W	W					

Table 1 Cont.

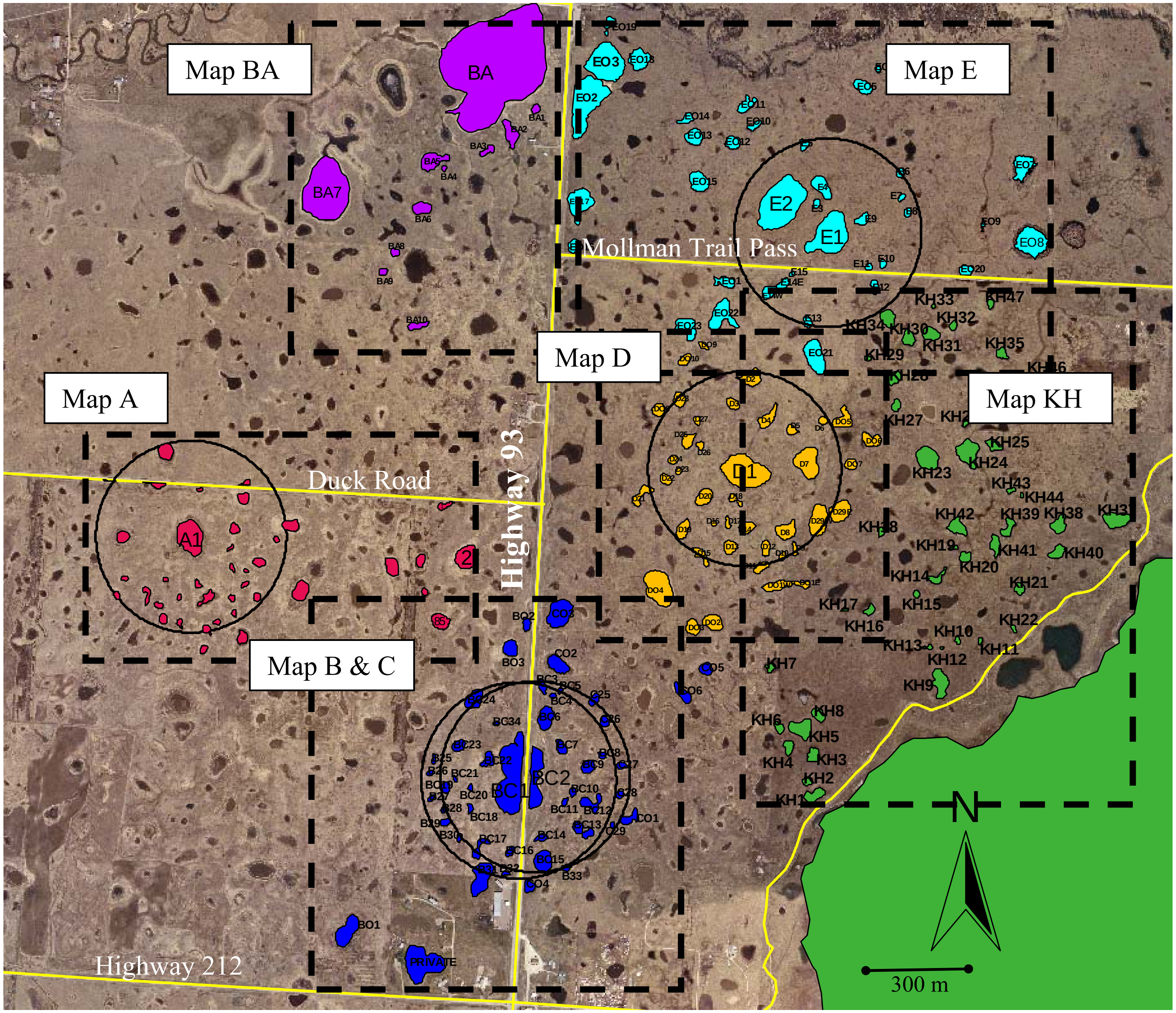
Pond Number[b]	Turtle[c]	2001[d]	2002		2003			2004			2005	2006		2007	
		April	July	Aug	May	July	Aug	May	July	Aug	May	May	June	May	July
KH35	Y	W						W	W						
KH36	Y	W						W	W						
KH37	Y	W						W							
KH38	Y	W						W	W	W					
KH39	Y	W						W	W	W					
KH40	Y	W						W							
KH41	Y	W						W	D	D					
KH42	Y	W						W	W	W					
KH43		W													
KH44		W													
KH46		W													
KH47		W													
Private	Y	W	W	W	W	W	W	W	W	W	W	W	W	W	W

a/ Pond hydrology: W = water available but not measured; D = dry; trace = less than 0.05 m (~2 in.) of water; "blank" = pond was not checked that particular month/year.

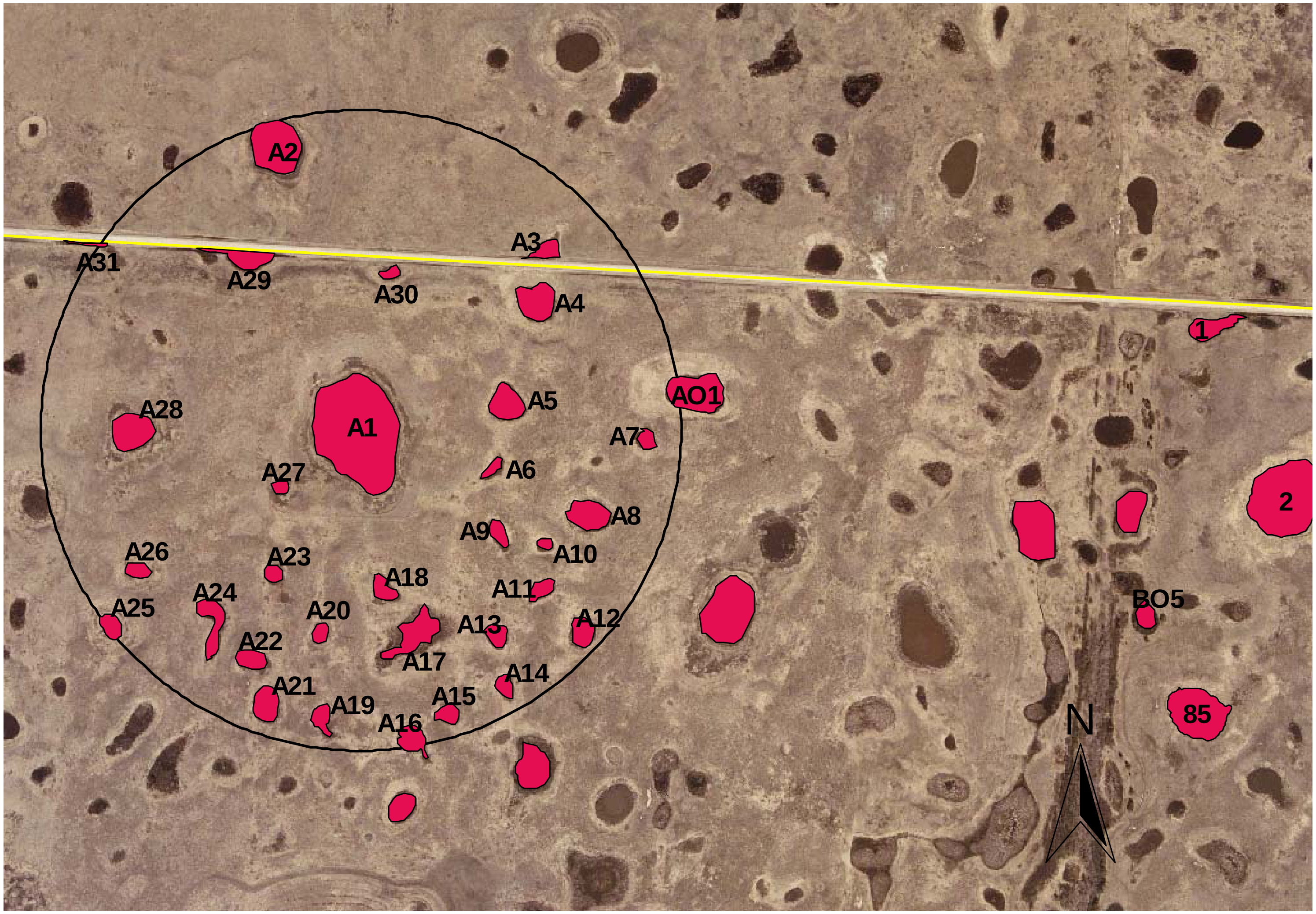
b/ Pond number: Location of ponds are found on the maps following this table.

c/ Turtle: Y = yes turtle present; at least 1 turtle was captured in that pond over all years.

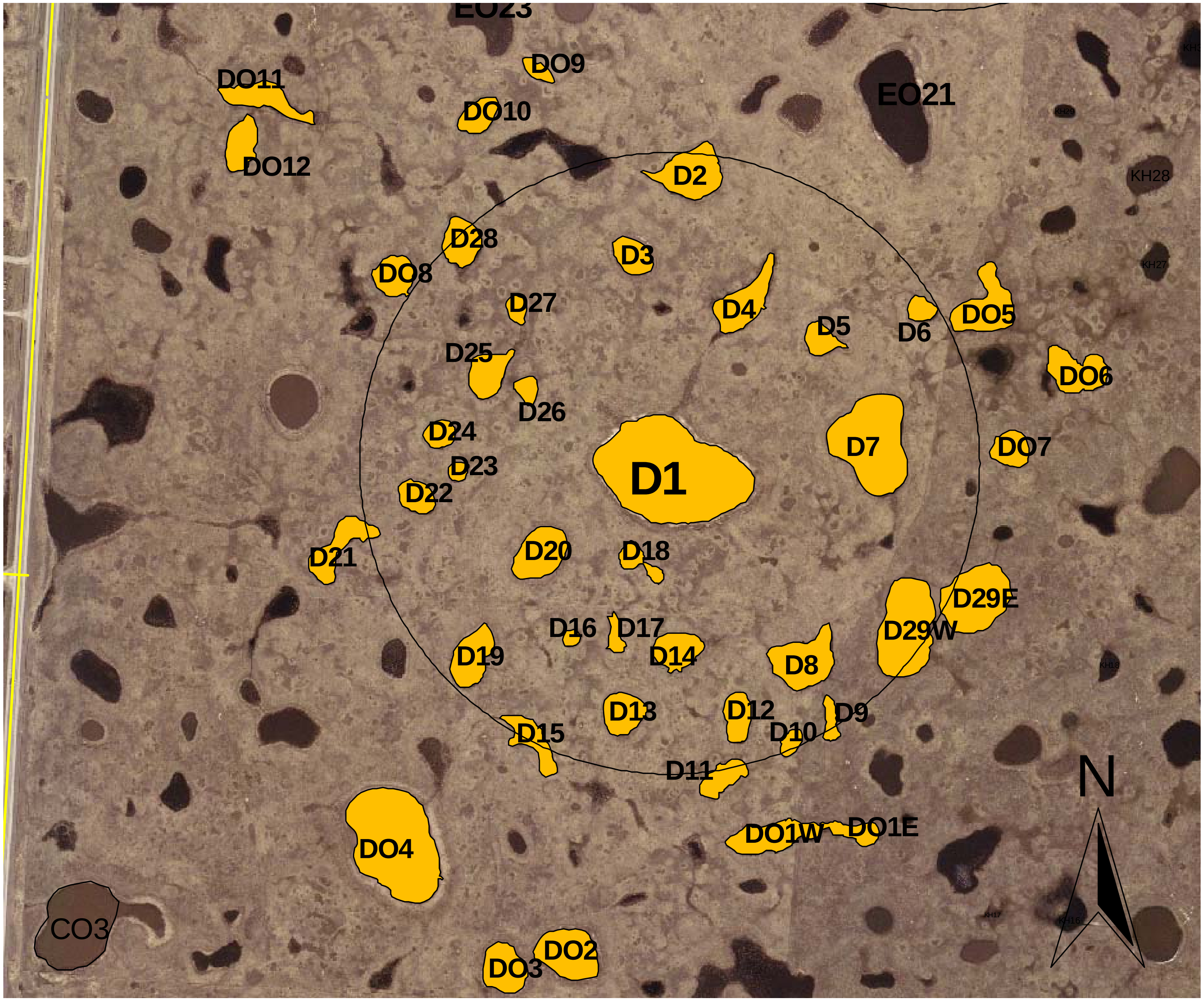
d/ April 2001 data was taken from an aerial photo.



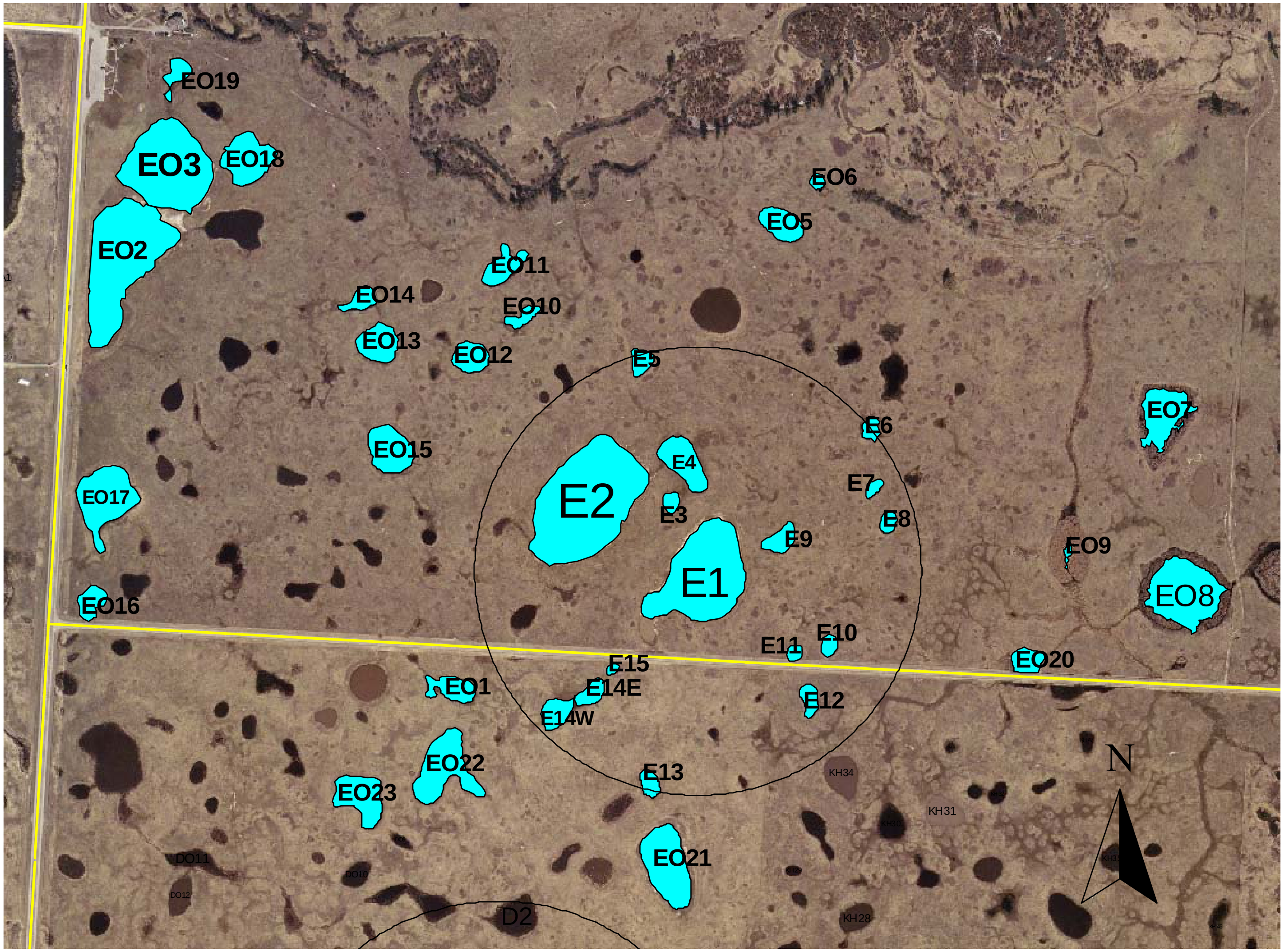
Map 1. Reference map for the pond numbering system maps that follow.



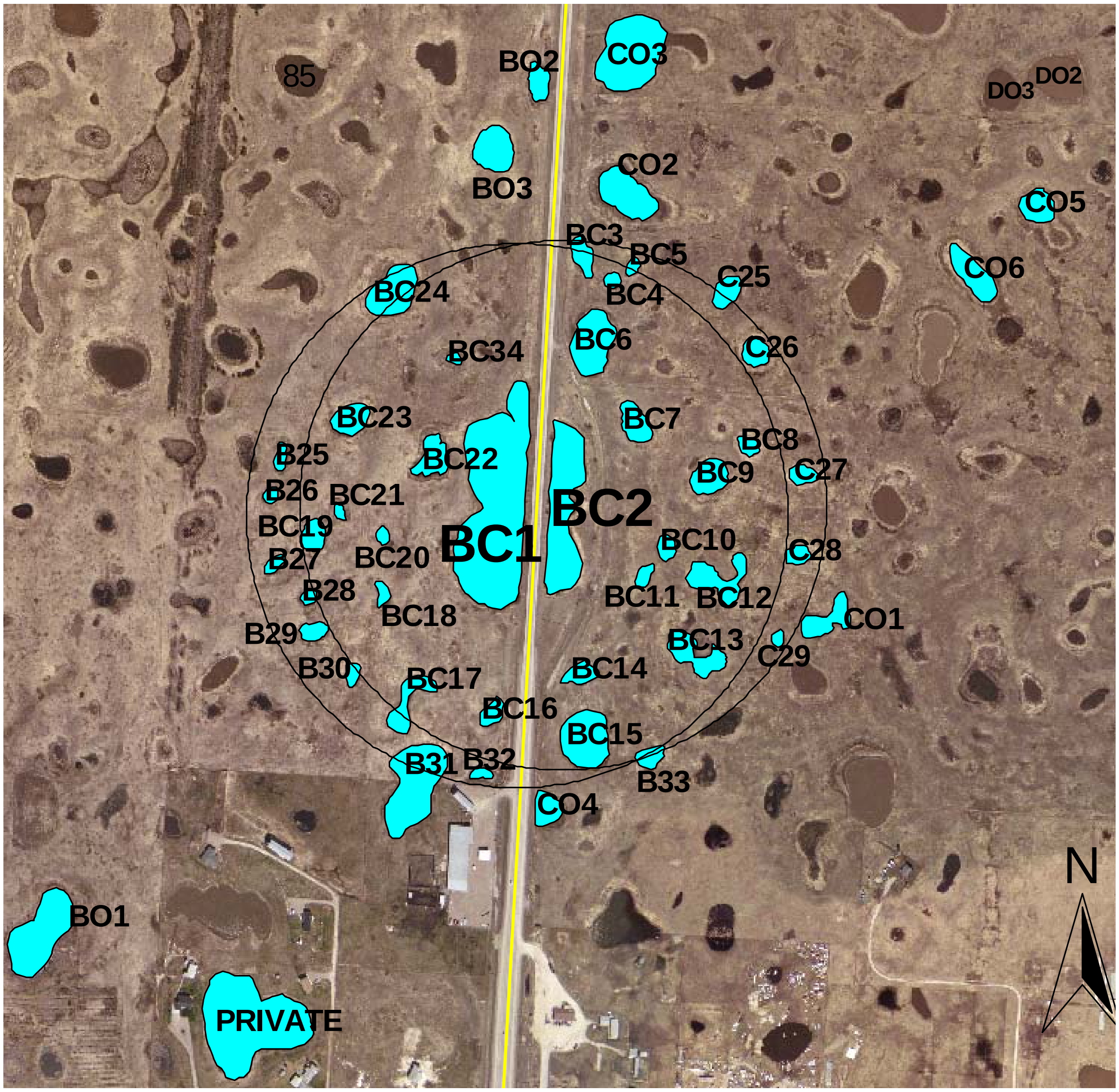
Map A. Ponds located south of Duck Road.



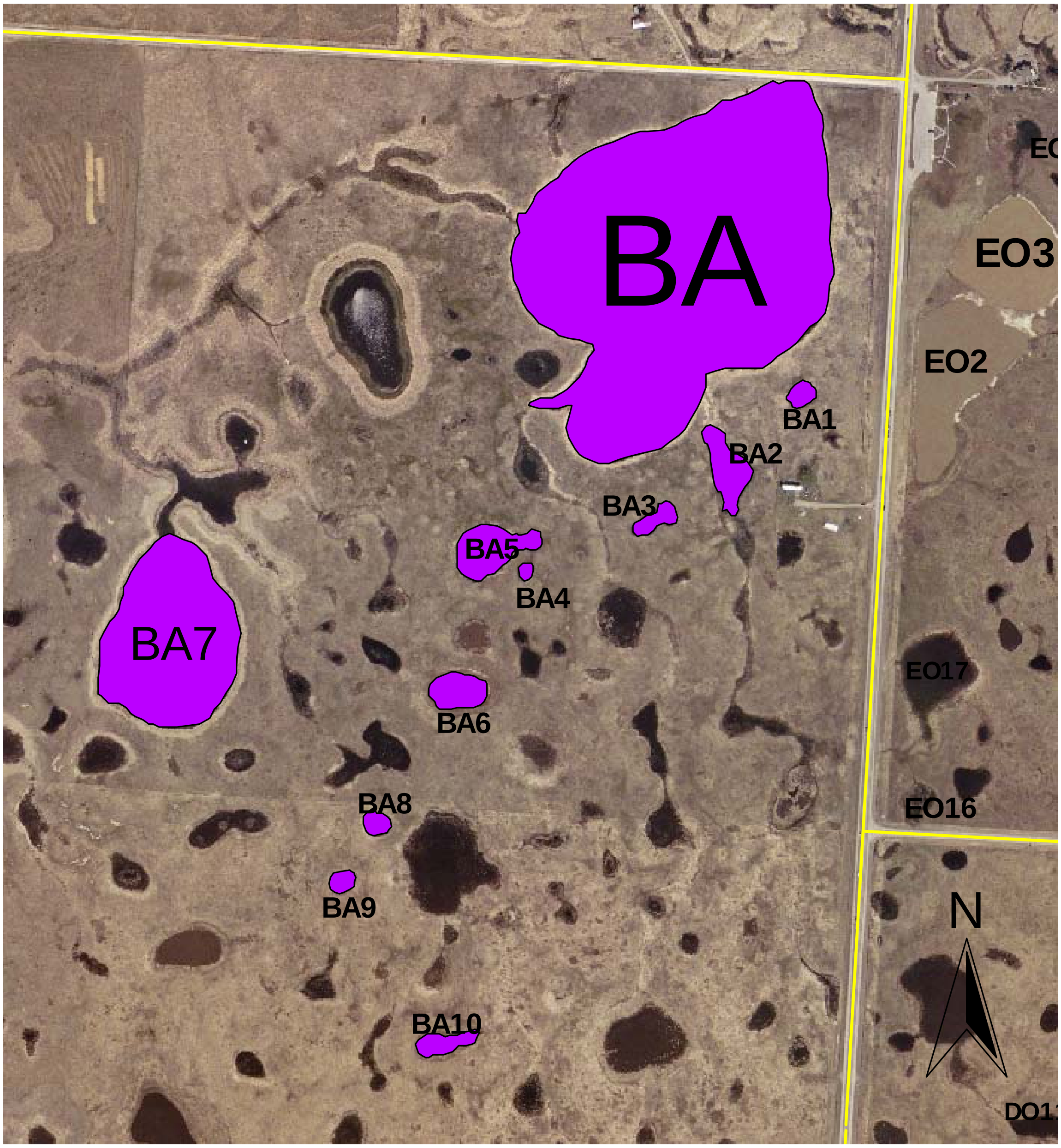
Map D. Ponds located east of Highway 93 and south of Mollman Pass Trail.



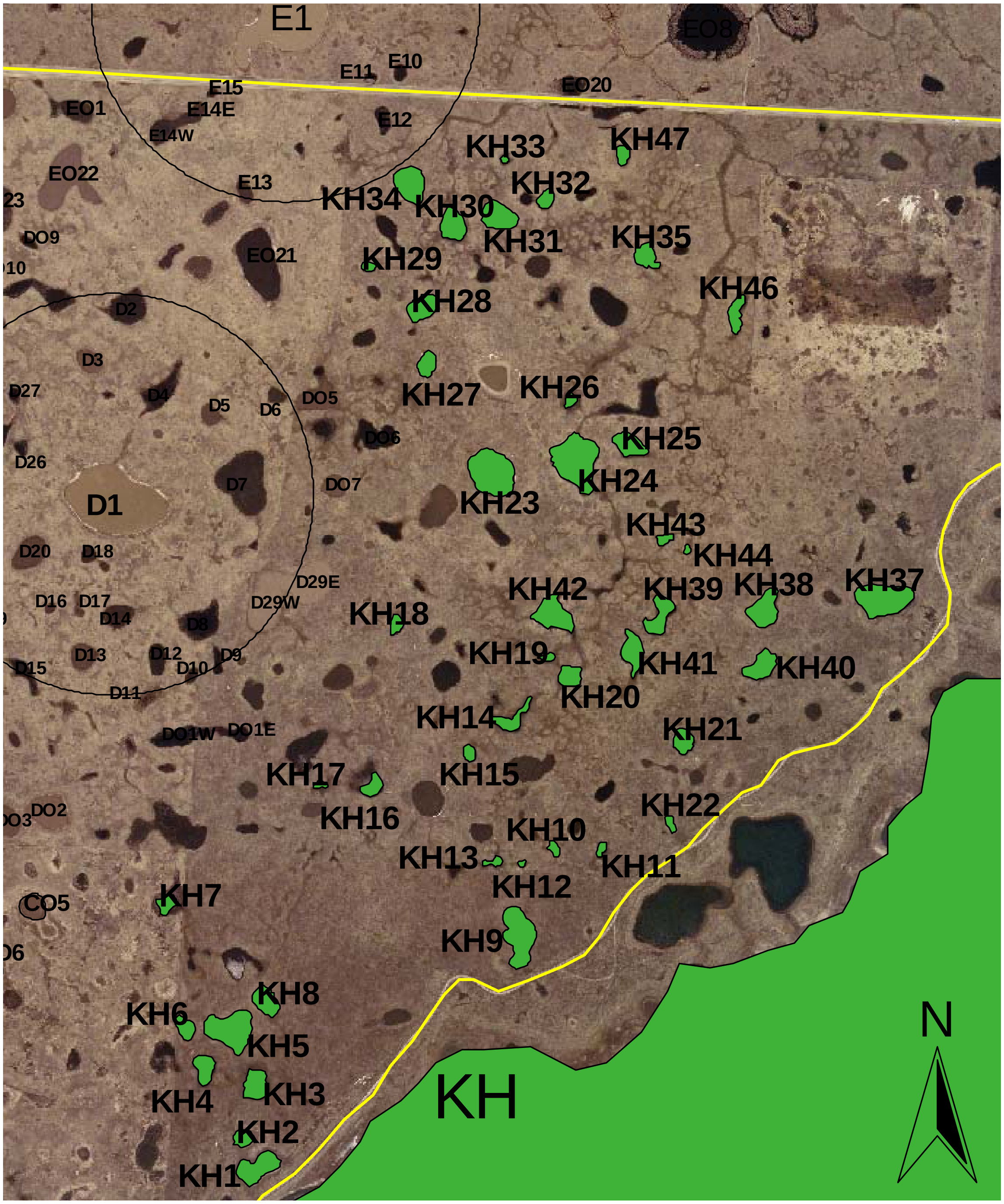
Map E. Ponds located along Mollman Pass Trail and east of Highway 93.



Map B & C. Ponds located along Highway 93, north of Highway 212.



Map BA. Ponds located west of Highway 93 and south of Beaverhead Lane.



Map KH. Ponds located adjacent to Kicking Horse Reservoir , east of Highway 93, and south of Mollman Pass Trail.

APPENDIX 2. FINAL REPORT TO THE MONTANA DEPARTMENT OF TRANSPORTATION: POTENTIAL EFFECTS OF HIGHWAY MORTALITY AND HABITAT FRAGMENTATION ON A POPULATION OF PAINTED TURTLES IN MONTANA.

Potential effects of highway mortality and habitat fragmentation on a population of painted turtles in Montana

Final Report

by

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16. Abstract

Highways and other road systems can present problems to wildlife populations though direct mortality and indirectly by reducing landscape connectivity by creating significant barriers to movement. These impacts can lead to fragmented populations, alteration of animal behavior, lowered population sizes and, thus, lowered population viability for some species. This research examined the potential effects of human-caused fragmentation on a population of western painted turtles (*Chrysemys picta bellii*) in northwestern Montana. Two studies were conducted: 1) a Capture-Mark-Recapture (CMR) study to examine survival and movement rates and 2) road mortality surveys to examine the number of road kills and the potential affect on the population. Together these studies help to determine the overall affect of the highway on the population and on the landscape level connectivity of the population.

In a 6.4-km (4-mile) stretch of Highway 93 in the Ninepipe/Ronan area, a total of 1,040 turtles were killed from 2002 to 2004. Three priority areas were identified where road mortality levels were very high; the 2 kettle ponds split by the highway and the area near the scenic turnout at Beaverhead Lane.

Typically, overwinter survival rates were very high (0.8 - 0.9) and summer survival rates were lower (0.8 – 0.4) when turtles were more likely to be moving and encountering the highway. Annual apparent survival rates were between 0.85 and 0.13 and would not be sustainable in a closed population. These survival rates are confounded with permanent emigration. During the drought, turtles moved off the study site to refugia habitats indicating a larger regional population (i.e., not a closed population), thus, maintaining connectivity across the landscape is essential in order to sustain viable populations in the future.

A review of available fencing methods used in herpetofauna-highway interaction projects is provided in Appendix A. An experiment to examine the effectiveness of flashing material as a barricade on low fencing was conducted (Appendix B). Turtles were able to climb fencing material that did not have a flashing barrier. Therefore, incorporating fencing as a barricade or to direct turtles to crossing structures needs to take into account the climbing ability of the turtles.

Ultimately, the information in this report can be used to guide design and placement of wildlife crossing structures during the Highway 93 reconstruction project.

17. Key Words Population dynamics, survival, habitat connectivity, road mortality, road-kill, western painted turtle, *Chrysemys picta bellii*, capture-mark-recapture, wildlife crossing structures, wildlife fencing, Wildlife		18. Distribution Statement Unrestricted. This document is available through the National Technical Information Service. Springfield, VA 21161	
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CONVERSION CHART	
Metric	**English**
1 millimeter (mm)	0.039 inches (in)
1 centimeter (cm)	0.394 in
1 meter (m)	39.4 in
	3.3 feet (ft)
1 kilometer (km)	0.62 miles (mi)
1 gram (g)	0.035 ounces (oz)
1 hectare (ha)_	2.5 acres (ac)

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INTRODUCTION

Highways and other road systems can present problems to wildlife populations though direct mortality and indirectly by reducing landscape connectivity by creating significant barriers to movement. These impacts can lead to fragmented populations, alteration of animal behavior, lowered population sizes and, thus, lowered population viability for some species (Ruediger 1996, Trombulak and Frissell 2000). Both wildlife managers and government agencies responsible for transportation have expressed concern over wildlife-highway interactions. Much attention has been paid to highway-wildlife interactions during the past decade via international conferences on ecology and transportation (Evink et al. 1996, 1999, ICOET 2003, 2005). The degree to which roads affect wildlife depends on many factors including road densities, road widths, traffic volumes, and the physical ability and behavior of each species.

Sheer numbers of individuals killed on the road can affect local population size which, in turn, can impact the regional population size and, ultimately the long-term population persistence (Figure 1). Direct road mortality is expected to have negative impacts on turtle population dynamics because of their life history traits. Most turtle species have low recruitment rates, delayed sexual maturity, and low natural adult mortality. This combination of traits makes turtle populations susceptible to declines and possibly extirpations when road mortality or other anthropogenic causes increase adult mortality. Low recruitment rates of juveniles result in very slow recovery from increased adult mortality (Gibbons 1987, Brooks et al. 1991, Congdon et al. 1994, Heppell 1998). Sustained levels of unusually high adult mortality have long-term consequences in that populations may never be able to recover.

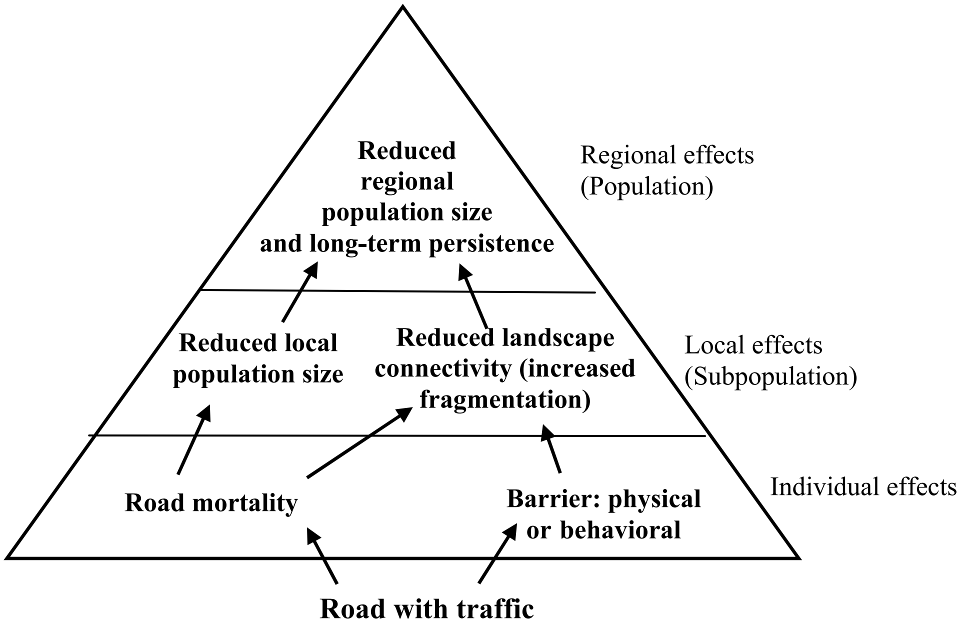

Figure 1. Road system effects on animals at various levels from individuals to populations.
(Adapted from Forman et al 2003).

Direct road mortality has the potential to not only directly affect turtle populations through sheer numbers of deaths but also may affect the population structure by disproportionately affecting subgroups within the populations. For example, more females than males may be killed, skewing the sex ratio; alternatively, more juveniles than adults could be killed, skewing the age structure. Both these changes to population structure can have long-term consequences on regional population persistence. Females may be more susceptible to road mortality due to nesting forays which make them more likely to encounter roads (Haxton 2000; Steen & Gibbs 2004; Aresco 2005a). Steen and Gibbs (2004) suggested that the number of females killed on roads in high road density areas significantly altered turtle sex ratios favoring males. Gibbs and Steen (2005) suggested that a long-term trend towards male sex bias in turtle populations across the U.S. over the last century is most consistent with a hypothesis of increased road mortality of females. Aresco (2005a) suggested male biased sex ratios in Florida are caused by females being disproportionately killed on roads. These studies attempted to address the relationship of roads to population dynamics, though they did not include empirical road mortality data. Prior to these more recent studies, only a few studies have examined the effects of roads on amphibians and reptiles (Boarman and Sazaki 1996, Fowle 1996a, Rudolf et al. 1998, Means 1999) and none have been able to document the effects of mortality on population dynamics.

Human created barriers such as roads can fragment wildlife populations. This fragmentation – the reduction and isolation of patches of natural habitat – is a major threat to species conservation (Gilpin and Soule 1986, Morrison et al. 1992, Fahrig and Merriam 1994, Harrison 1994). Barriers reduce the amount of movement on the landscape by direct mortality and avoidance which fragments the population by creating smaller, more isolated local populations that are at greater risk of extinction from catastrophes, demographic stochasticity, and genetic deterioration (Morrison et al. 1992) (Figure 1).

One of the major consequences of fragmentation caused by roads is the change in landscape connectivity among remnant habitat patches (Morrison et al. 1992, Fahrig and Merriam 1994, Mills et al. 2003). Landscape connectivity is important for 2 main reasons. First, many animals regularly move across the landscape to obtain their daily or life time needs. Second, landscape connectivity allows for movements to recolonize (or repopulate) areas that have undergone population declines or extinctions. In the case of turtles, many make regular seasonal movements for reproduction (nesting or mate seeking), locating hibernation sites, and/or to depart from unsuitable habitat, such as when ponds begin to dry up and repopulate ponds when water returns (Gibbons 1990). Ultimately, reduced connectivity results in lower regional population sizes and lower long-term persistence (Figure 1).

Movement between habitat patches creates connectivity across the landscape and is the process that allows local populations to be interconnected into a functional demographic unit on a regional scale (Merriam 1984). Semi-aquatic pond turtles, such as painted turtles, are especially vulnerable to barriers to movement and fragmentation because, although these turtles use terrestrial landscapes for nesting and seasonal movements, they have limited abilities to move effectively across the landscape (Mitchell and Klemens 2000).

This research was designed to examine the potential effects of human-caused fragmentation on a population of western painted turtles (*Chrysemys picta bellii*) in northwest Montana. Although this pothole region has a high level of natural fragmentation, fragmentation due to anthropogenic factors is likely to increase given anticipated growth in development and traffic volumes (FHWA and MDT 2000). Currently, an 18 km section of roadway in the

Ninepipe/Ronan section of the existing U.S. Highway 93 is proposed for improvements (FHWA et al. 2005). The highway project may increase the width of the highway which could exacerbate the current issue of turtle mortality along roads in this area. However, planned mitigation measures (e.g., wildlife crossing structures/culverts) could positively affect the population in terms of both reduced road mortality and maintaining landscape connectivity.

Objectives

The primary goal of this research was to build on existing knowledge of the painted turtle, its demography, and patterns of movement to gain a landscape-level understanding of connectivity and the potential effects of a highway on the population. Two main studies were conducted, 1) a Capture-Mark-Recapture (CMR) study, and 2) a road mortality study. More specifically, there were 5 objectives:

1. To determine the demographic rates of survival in and movements between ponds;
2. To determine the extent to which the highway acts as a barrier to movements;
3. To examine the potential affects of road mortality on the population;
4. To compare available fencing methods used in herpetofauna-highway interaction projects and assess their effectiveness at minimizing turtle road kill as well as directing turtles to wildlife crossing structures (Appendix A);
5. To test flashing material as a barricade on fences to keep turtles from breaching barriers or directional fencing (Appendix B).

METHODS

Study Area

Study Area

The study area is located in the Mission Valley of northwestern Montana (47° 27' N, 114° 04' W) at an elevation of about 940 m. Historically, the Mission Valley was Palouse prairie but over time it has been extensively modified by agriculture and development. The study site is an area of high-density wetlands with over 2,000 permanent and ephemeral wetlands in an area of approximately 78 km^2 (Fowle 1996b). The wetlands are primarily palustrine emergent basins with various water regimes ranging from permanent to seasonally flooded (Cowardin et al. 1979). The permanent ponds are characterized by very little emergent vegetation although some cattails (*Typha* spp.), rushes (*Juncus* spp.), and duckweed (*Lemna* spp.) occur along the edges of some ponds. Submergent vegetation in the permanent ponds is sparse and consists mostly of milfoil (*Myriophyllum* spp.). The ponds are surrounded by grasslands, some of which were heavily grazed until 2001. Currently, the grasslands are ungrazed and dominated by western wheatgrass (*Agropyron smithii*), Kentucky bluegrass (*Poa pratensis*), fescue (*Festuca* spp.) and invasive species such as spotted knapweed (*Centaures maculosa*), erect cinquefoil (*Potentilla recta*), whitetop (*Cardaria draba*), mustard (*Brassica* spp.), and thistle (*Cirsium* spp.) (Anderson 2003).

Many land ownerships cover this pothole region including federal (Waterfowl Production Areas), Tribal (Ninepipe National Wildlife Refuge and trust lands of the Confederated Salish and Kootenai Tribes), state (Ninepipe Wildlife Management Area), and private lands. The Montana Department of Transportation has management responsibility for the right-of-way along Highway 93.

Study Sites

Two different areas were used for the 2 different studies: road mortality surveys and the Capture-Mark-Recapture (CMR) study. The road mortality survey area consisted of a 6.4 km section of Highway 93 from Olson Road, north to Beaverhead Lane; Mollman Pass Trail Road from Highway 93 east 2.4 km; and Duck Road from Highway 93 west 1.6 km (Figure 2).

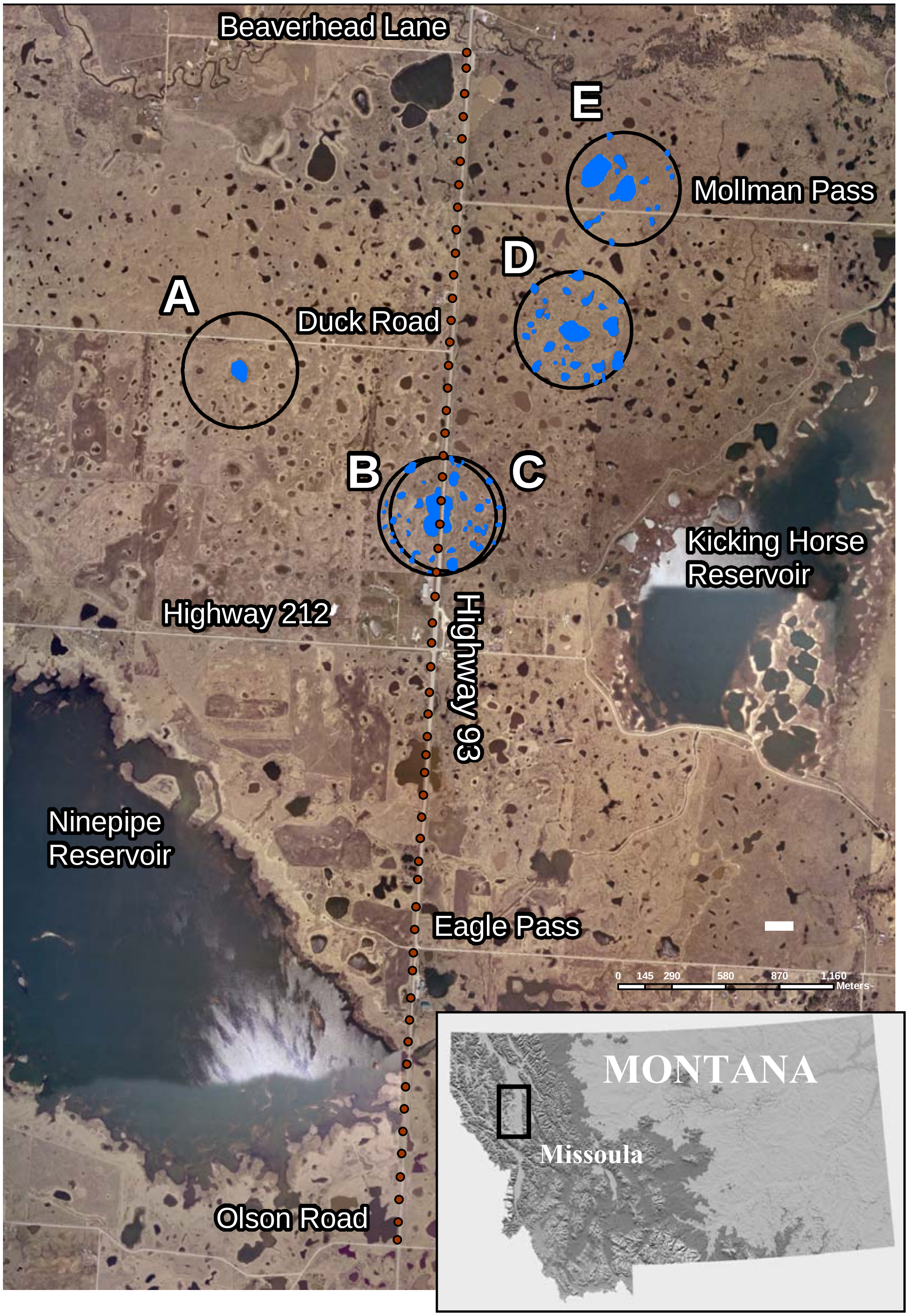

Figure 2. Aerial view map of study area. Road Mortality survey area along Highway 93 is from Olson Road to Beaverhead Lane (dots indicate survey road markers). Capture-mark-recapture survey area is indicated by pond complex circles (labeled A through E).

The CMR study site consisted of 5 pond complexes adjacent to Highway 93 between Highway 212 and Beaverhead Lane (Figure 2). A pond complex was identified as a 300 m radius circle centered on a permanent pond. All wetlands that held water within the circle were surveyed during the trapping sessions (described below). The 5 permanent ponds at the center of the complexes are important overwintering ponds for turtles.

Field Methods

Road Mortality Surveys

Roads within the study area were walked approximately once a week from mid-May through late August, 2003-2005. In 2002, surveys were conducted between mid-July and mid-September. In 2003 and 2004, surveys began in mid-May and continued through mid-September with 1 final survey the first week of October. Crews walked each side of the roadways simultaneously and documented road-killed turtles as well as all other dead vertebrates.

Animal locations were referenced to approximately evenly spaced (160 m) numbered reflector posts along the highway and numbered telephone poles along the secondary roads. Although this report focuses on road morality of turtles, road mortality counts and road locations for all vertebrate species encountered during surveys were summarized (Appendix C). Dead turtle locations were estimated to the nearest marker or the nearest mid-way point between markers (e.g., approximately to the nearest 45 m). All turtle mortalities were examined in an attempt to identify marked turtles and to determine sex and age class (when possible).

All road mortality counts are considered minimum counts because there is no information on the probability of recovery of road killed individuals. For example, some turtle carcasses may have been removed from the highway by scavengers or thrown off the survey strip by large vehicles. Road kills were recovered as quickly as possible to minimize the loss of uncounted individuals.

Traffic volume on Highway 93, Mollman Pass Trail Road, and Duck Road were counted using Montana Department of Transportation (MDT) traffic counters. Traffic volumes were measured at various times throughout the summer.

Capture – Mark – Recapture Study

Capturing and Marking Turtles

Painted turtles were captured using seine nets, basking traps, and dip nets to minimize the potential for sampling bias by sex or age class (Ream and Ream 1966, Gibbons 1990, Koper & Brooks 1998). The following measurements were taken the first time a turtle was captured each year: plastron length and width, straight carapace length and width, body height, and weight. On subsequent recaptures within a year, only turtle identification, location, and sex were recorded. Gender was determined by examining secondary sexual characteristics and age by using an annuli aging technique for turtles about 4 - 5 years old (Graham 1979). Reliability of this method decreases with age due to shedding of the scutes (Sexton 1959, Wilbur 1975); therefore, turtles are grouped into stage classes (see below).

Size is more important in determining maturity in turtles than age (Ernst et al. 1994). Seventy-nine mm was the smallest plastron length (PL) where male secondary sexual characteristics (elongated foreclaws and elongated preanal region of the tail, [Frazer et al. 1993]) were observed. By 105 mm PL virtually all males exhibited secondary sexual characteristics. Stage classes were broken into 2 categories: juveniles and adults. Juveniles were turtles with a PL ≤ 104 mm (≤ approximately 4 years old) and sex is considered unknown; however, this category does include some male turtles that exhibited secondary sexual characteristics. Sex determination for most turtles in this size category cannot be determined; therefore sex is considered unknown in the analysis. Males that exhibited secondary sexual characteristics made up less than 1.8% of the turtles in this category. Adults were considered sexually mature individuals with a PL ≥ 105 mm (greater than 4 years old). Any individual that was at least 105 mm PL and not showing signs of secondary sexual characteristics was considered female (Mitchell 1985). Based on subsequent recaptures, all male turtles exhibited secondary sexual characteristics by 105 mm PL.

Each turtle was individually marked by drilling the margins of the carapace (Cagle 1939) as well as injected with a Biomark™ passive integrated transponder (PIT) tag (Buhlmann and Tuberville 1998). Each PIT tag had a unique 10 digit alpha-numeric code that was activated by a hand-held recorder, allowing recaptured turtles to be quickly identified with little to no error.

Turtles smaller than 50 mm PL (about 30 grams) did not receive a PIT tag because of their size. Hatchlings and some juveniles were notched using nail clippers rather than drilling because some of these shells were not yet fully calcified.

Pond Measurements

Pond depth was measured during each trapping session using a graduated pole. Measurements were taken in the center of small, uniformly-shaped ponds. In larger, irregular shaped ponds, 3 depth measurements were taken across the pond and averaged. Pond volume was calculated using pond depth from measurements taken in the field and pond circumference, determined from Geographic Information System (GIS) data layers at a high-water period (April 2001); therefore, calculated volumes represent a relative measure of volume based on the high water mark.

Sampling Sessions

Following the Multistate Robust Design capture-recapture model (described below), there were 7 primary periods (trapping sessions) between 2002 and 2004. In 2002, only the fall trapping session (August 13-24) was conducted. In 2003 and 2004, there were 3 primary periods a year: spring (May 21-June 1), summer (July 2-13) and fall (August 13-24). Primary periods lasted 12 – 13 days during which all ponds in all complexes were sampled between 2 and 4 times (secondary periods). In spring, ponds were generally only sampled twice because of the large number of temporary ponds within the complexes due to spring rains and snow melt. By summer and fall trapping sessions, virtually all temporary ponds dried up, consequently all remaining ponds were sampled 4 times. The spring session was timed to capture turtles before they moved out of their overwinter ponds. The fall session was timed to occur when presumably turtles had moved back to overwinter ponds.

Analytical Methods

An information-theoretic approach (Burnham and Anderson 2002) was used to simultaneously evaluate relative support of multiple models describing relationships between survival and movement and variables of interest. *A priori* models were developed to address biological questions regarding survival and movement and were implemented in Program MARK Version 4.3 (White and Burnham 1999, Cooch and White 2002).

A Multistate Robust design module within Program MARK was used to generate point estimates of survival (S), movement probabilities (Psi), and capture probabilities (p) and their precision to evaluate relative support for candidate models given observed data. Program MARK uses generalized linear models to generate maximum likelihood estimates of regression coefficients and their associated sampling variances and covariances.

The Multistate Robust design combines a Pollock's Robust design and Multistate designs (Arnason 1973, Pollock 1982, Hestbeck et al. 1991, Brownie and Robson 1993, Nichols et al. 2000, Williams et al. 2002). Pollock's Robust Design (Pollock 1982) requires sampling at 2 temporal scales. Primary periods are those between which the population is considered open (allows births, deaths, and movements). Populations are assumed to be closed during the secondary periods, within primary periods. The Robust Design models also allow for modeling temporary emigration which increases the precision on the survival parameter (Kendall and Nichols 1995, Kendall et al. 1995, Kendall et al. 1997). Apparent survival rates estimate the product of survival and fidelity to the study area (i.e., that the individual stayed on the study area). There are 2 situations in which an individual may be off the study site; 1) temporary emigration and 2) permanent emigration. Emigration lowers the true survival rate but can not be separated out from mortality; hence, apparent survival is estimated. The Robust Design (which is able to estimate temporary emigration) allows for an apparent survival rate that is closer to the true survival because an individual only temporarily off the study site is accounted for and therefore not counted as a mortality.

Multistate Designs (Arnason 1973, Hestbeck et al. 1991, Brownie and Robson 1993) require sampling at multiple locations during each sampling period and allows for movements between locations. In this study, the locations are the 5 pond complexes (Ponds A – E; Figure 2). The multistate models allowed examination of the amount of movement occurring between pond complexes and whether the movement was affected by variables of interest such as the presence of an intervening road.

Only 1 juvenile turtle moved between pond complexes, therefore, the analysis was restricted to adults. All adults were considered mature; all males had developed secondary sexual characteristics by 105 mm PL and Mitchell (1985) found all females greater than 105 mm PL were mature.

Model Selection

Hypotheses were evaluated using model selection based on Akaike's Information Criteria (AIC) (Akaike 1973) specifically, AIC_c was used which includes a small sample-size, second-order bias adjustment and is recommended when the number of estimated parameters is large relative to the sample size (Burnham and Anderson 2002). Models within 2 AIC values of the best approximating model were considered in the discussion (Burnham and Anderson 2002). Model selection uncertainty in the parameter estimates was incorporated by model averaging.

Goodness of Fit

Goodness-of-fit (GOF) is a diagnostic procedure for testing the assumptions underlying the models. The assumptions for this model include those for the respective closed (Seber 1982, Pollock et al. 1990) and the open models. When there is a lack of fit or overdispersion in the data, this reflects either a lack of independence or heterogeneity among individuals (Pollock et al. 1990). The overdispersion factor ($\hat{c}$) was estimated from the Pearson goodness-of-fit (GOF) chi-square statistic of the most general model and its degrees of freedom ($\hat{c} = \chi^2/df$) (Lebreton et al. 1992) using MSSRVRD (Multi-stratum Survival and Robust Design; available on-line at www.mbr-pwrc.usgs.gov/software.html). Individual covariates cannot be included in the MSSRVRD program; therefore, $\hat{c}$ was estimated using the most highly parameterized model possible without including covariates. When overdispersion was detected (i.e., $\hat{c} > 1$), the quasi-likelihood AIC (QAIC) was used which inflates the sampling variance by multiplying those values by $\hat{c}$ (Burnham and Anderson 2002).

Population Level Effects

Data from both the road mortality and the CMR surveys were needed to determine the percentage of the regional turtle population killed on the roads. Both the upper and lower boundaries of the percentage of the population affected by road mortality were estimated to incorporate the uncertainty in both the abundance and road mortality estimates. For the lower boundary, the population abundance was estimated via modeling which only included adult turtles within the pond complexes and the road mortality estimate used only adult mortalities known to be marked from within the CMR study area (from Highway 212 to Beaverhead Lane). This road mortality estimate is a conservative estimate because any turtle not positively identifiable to age class or whether marked was not included. Using this conservative estimate of road mortality allowed the lower boundary of the affect of the highway on the adult population to be estimated.

For the upper boundary, the minimum number of all turtles (adults and juveniles), caught each year throughout the entire study area (i.e., not only within pond complexes) was used. This value does not take into account the probability of detection that the modeling value used above does and, therefore, under represents the total population size. All road mortalities (adult, juveniles, and unknown) were included in this estimation. This combination of a conservative population estimate and all road mortalities provides the upper boundary of the effect of the highway on the population.

In general, both of these estimates are conservative because the road mortality surveys did not include a probability of detecting dead-on-the-road turtles. It is likely that the actual number of road kill is higher than reported because some carcasses may have been removed (e.g., by scavengers) or thrown off the road before being counted. Therefore, all road mortality estimates are considered minimum values.

RESULTS

Road Mortality Surveys

Road Mortality Surveys

Overall

In the 33 road mortality surveys that were conducted in the project area over the 3 years, a total of 1,059 individual turtles were killed in the study area roads: 1,040 on Highway 93, 18 on Mollman Pass Trail, and 1 on Duck Road. Of those turtles killed on the highway, 451 (43.3%) were adults and 221 (21.3%) were juveniles (Tables 1a and 1b). Age class could not be determined for the remaining 368 individuals. Sex could not be identified on most (639, 61%) road mortalities. However, of those turtles where sex could be determined, roughly equal numbers of males and females (99 and 81, respectively) were found (Table 1a). No sex bias in road mortalities ($\chi^2 = 1.8$, df = 1, P = 0.18) was found.

Table 1a. The number of road-killed turtles by year, sex, and age class found along a 6.4 km section of Highway 93 in the Ninepipe/Ronan area.

Year	Adult			Juvenile	Unknown	Total
	Male	Female	Sex Unknown			
2002		3	101	87	166	357
2003	50	49	92	86	137	414
2004	49	29	78	48	65	269
Total	99	81	271	221	368	1040

Table 1b. The number of road killed turtles by year, sex, and age class found within the Capture – Mark – Recapture study area, 3.2 km section of Highway 93 from Highway 212 north to Beaverhead Lane in the Ninepipe/Ronan area.

Year	Adult			Juvenile	Unknown	Total
	Male	Female	Sex Unknown			
2002	3		50	57	77	187
2003	46	37	44	29	79	235
2004	19	31	35	25	28	138
Total	68	68	129	111	184	560

The highest numbers of both male and female mortalities occurred in June, subsequently mortalities for both sexes declined over the summer. Females exhibited less mortality in late summer than males (Figure 3). Adults were killed more often in early summer than late summer while juveniles experienced more consistent numbers of road kills throughout the summer (Figure 4). A spike of juvenile road mortalities occurred in late August. Overall, more individuals were killed in the early summer months (up to mid-July) than late in the summer.

The highest numbers of road mortalities occur where there are large ponds adjacent to both sides of the highway (Figure 5). Road locations 22 and 33 – 34 occur where the highway divides 2 kettle ponds. Road locations 49-52 occur in the vicinity of the scenic turnout at Beaverhead Lane where a large permanent pond is located on the west side and 2 semi-permanent ponds are on the east side of the highway.

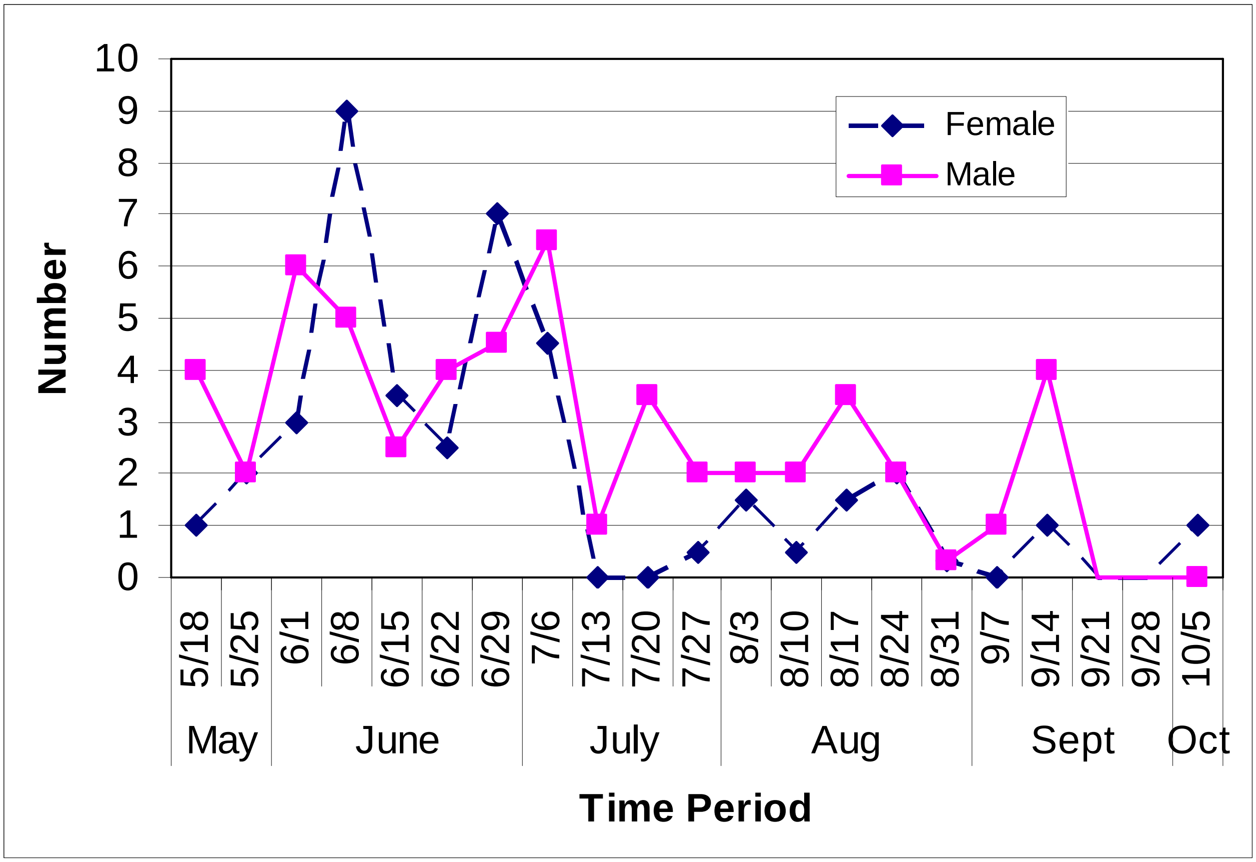

Figure 3. Average road mortality (2002-2005) on a 6.4 km section of Highway 93 separated out by weekly time periods and sex. Zero values indicate no individuals were found during that survey period, except on 9/21 and 9/28 no surveys were conducted.

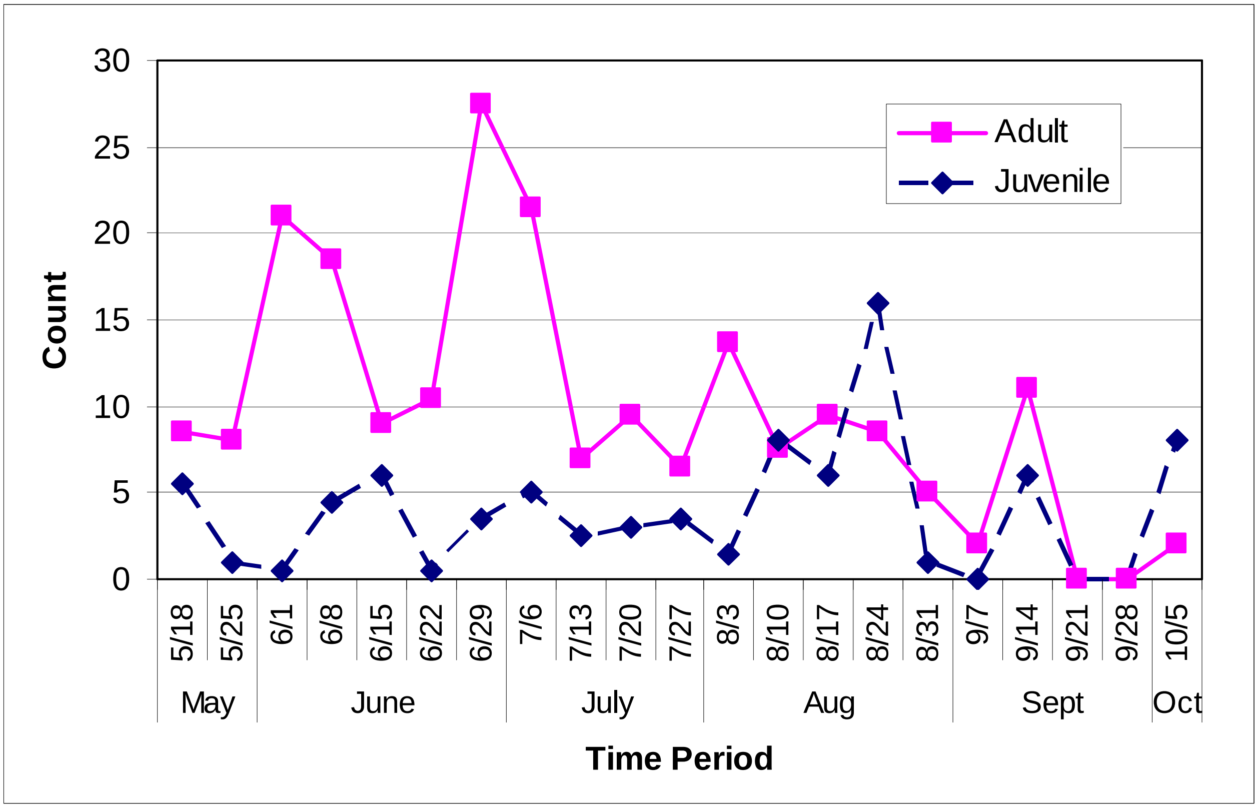

Figure 4. Average road mortality (2002 – 2005) on a 6.4 km section of Highway 93 separated out by weekly time periods and age class. Zero values indicate no individuals were found during that survey period, except on 9/21 and 9/28 no surveys were conducted.

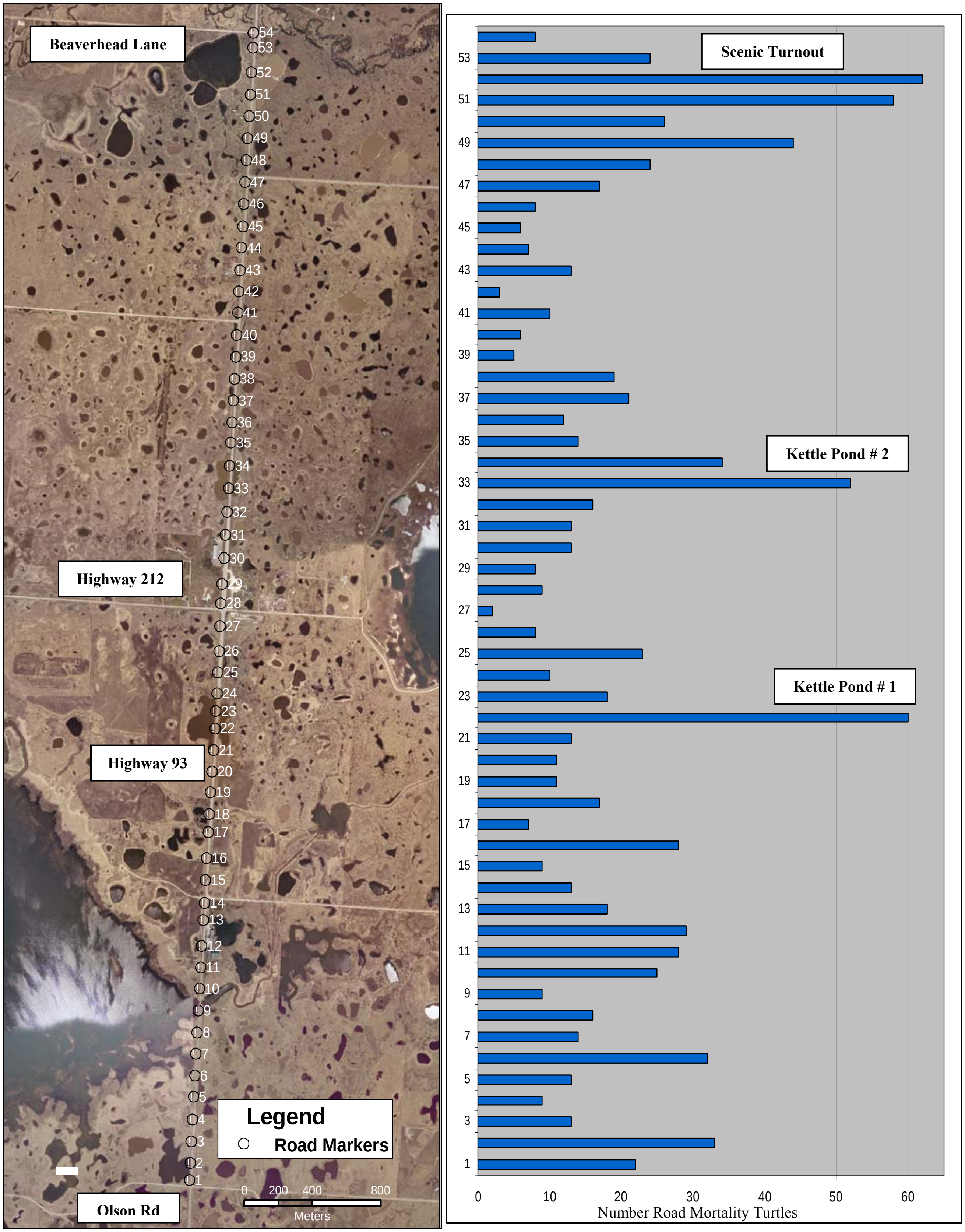

Figure 5. On the left, road marker locations along Highway 93. On the right, the total number (2002-2004) of turtle road mortalities corresponding to mapped road markers. Road marker 1 occurs at Olson Road and Marker 54 occurs at Beaverhead Lane. The markers are approximately every 160 m.

Overall, road mortality was a more important mortality factor than overwinter kill (Table 2). Most dead-on-the-road turtles that could be identified came from ponds E and C (881 m and 32 m from the highway, respectively). Only 3 turtles identified as road mortalities came from pond A, the furthest (1,130 m) pond from the highway.

Table 2. Number of marked[1/] adult and juvenile turtles found dead from overwinter and road mortality in each pond complex[2/] between 2002 and 2004.

Mortality Type	**Pond**	**2002**	**2003**	**2004**	**Total**
Overwinter	**A**	0	0	34	34
	B	0	0	14	14
	C	0	0	4	4
	D	0	1	4	5
	E	0	1	7	8
	Total	0	2	63	65
Road	**A**	0	0	3	3
	B	0	6	8	14
	C	3	11	13	27
	D	0	6	13	19
	E	2	14	13	29
	Total	5	37	50	92
Total All Mortalities		5	39	113	157

1/ Only those turtles that were marked and positively identified were included.
2/ The “pond” associated with road mortality indicates the last known location of the living turtle before it was found dead on the highway

Within the Capture – Mark – Recapture Study Area

Because the Capture – Mark – Recapture study overlapped only the northern half of the road mortality survey area, in order to be able to compare population estimates from modeling with road mortalities within the same area, road mortalities were also summarized within the CMR study area (Highway 212 north to Beaverhead Lane [Figure 1]). A total of 560 dead-on-the-road turtles were encountered (Table 1b). An equal number of males and female (68) and 111 juveniles were identified in the road mortalities and 313 (56%) could not be determined to sex or age.

Traffic Volumes

Traffic volumes on Highway 93 were roughly constant over the 3 years of study ranging between 500 to 620 vehicles per hour (both directions were recorded) (Table 3). These values were consistent with Montana's Automatic Traffic counts for 2002 – 2004 located at RP 22.7, Arlee (MDT 2002, 2003, 2004). Secondary roads, Mollman Pass Trail and Duck Road, showed considerably lower traffic volumes (Table 3). All 3 roads showed increased traffic during daylight hours when turtles are more likely to be moving.

Table 3. Description of road types within the project area and traffic volumes (vehicles per hour) averaged over summer months (May – August). Highway 93 values were corrected with monthly axle correction factors for each year. N/A = data not available.

Road	# Lanes	Surface	Posted Speed Limit (mph)	Volumes (average # vehicles/hour) Time	2002	2003	2004
Highway 93	2 – 3	paved	70	Night/Day	459	336	348
				Day Only	615	566	594
Mollman Pass Trail	2	paved	50	Night/Day	32	22	22
				Day Only	54	67	38
Duck Road	1 – 2	dirt	35	Night/Day	N/A	3	2
				Day Only	N/A	4	4

Capture – Mark – Recapture (CMR) Study

Descriptive Demographics

From 2002-2004, 8,520 captures of 2,335 individual turtles were recorded. Overall, there was no sex bias in the living adult turtle population (873 males and 803 female) ($\chi^2 = 2.92$, df = 1, P = 0.09). Two pond complexes (C and E) had sex ratios significantly different from a 50:50 sex ratio (Table 4). Pond C favored males over females (153 to 113, respectively) while females were favored over males (114 to 78, respectively) in pond E. The sex ratios in the remaining ponds did not differ significantly from a 50:50 sex ratio. Marked juveniles totaled 659 individuals.

Table 4. Number of female and male adult turtles in each pond complex encountered during the Capture – Mark – Recapture study from 2002 to 2004. P-values reflect a chi-square test of equal sex ratio.

Pond Complex	Female	Male	P-value
A	105	89	0.25
B	110	115	0.74
C	118	160	* 0.01
D	85	93	0.55
E	117	80	* 0.01
Total	535	537	0.95

* values indicate significant differences between the sexes.

The capture process also netted a total of 65 marked turtles that were found dead in the ponds (Table 2). The winter of 2003/2004 had particularly low temperatures (< – 28º C, [– 20º F]) for about 1 week which may have caused shallower area within ponds to freeze to the bottom potentially causing the death of hibernating turtles.

Observed Movements

Most movements occurred within complexes (less than 300 m) between permanent and temporary ponds (Figure 6). The longest movement observed was 2,400 m made by a juvenile. There was no significant difference between the number of pond to pond movements made by males and females (317 to 265, respectively) ($\chi^2 = 1.35$, df = 1, P = 0.24). These values incorporate all observed movements including between ponds within as well as between complexes and some individuals moved more than once. With CMR techniques, an individual would have to be captured in 2 different ponds for movement to be observed, therefore, female nesting forays (leaving to nest on land and returning to the same pond) cannot be assessed using these movement data.

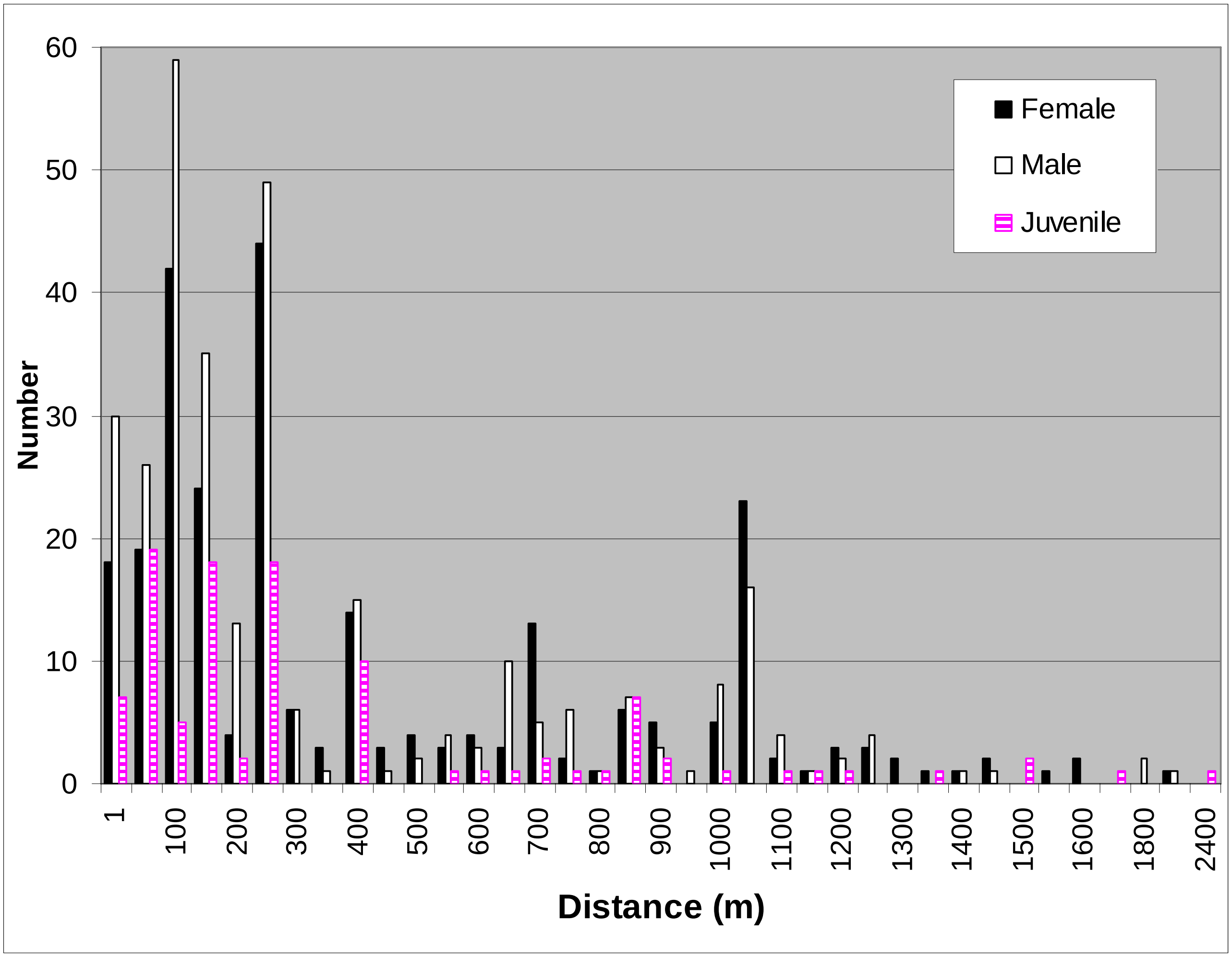

Figure 6. The number of adult and juvenile turtles that moved separated out by sex and distance (m) categories. Some individuals moved more than once. Approximately 95% of the marked turtles remained in their original pond with no recorded movements.

Fine-Scale Movement and the Highway (Ponds B and C)

Movements and road mortality data between pond complexes B and C (the 2 kettle ponds split by the highway) were investigated to examine fine-scale movements. Turtles made 106 movements away from pond B without crossing the highway. In pond C, 78 turtles moved away from the pond without crossing the highway. Forty adult individuals from these ponds successfully crossed the highway. However, 150 road mortalities were recorded between the complexes (between road markers 30 – 36), of which 69 were known to be adult and of these 36 (52%) were known to be marked. Therefore, about half (47%) of the turtles that attempted to cross the road were killed (40 crossed successfully while 36 known marked were killed). This percentage of successful crossings (53%) is a high estimate because it could not be determined if some dead-on-the-road turtles were marked (19 were unknown).

Modeling

Only adult turtles captured within pond complexes were included in the CMR modeling analyses. A total of 1,032 individuals were used with 4,652 recaptures. The most parameterized model was

$$S(_{\text{Pond * Season}})\ Psi(_{\text{Distance Category * Season + Temporary Emigration}})\ p(_{\text{Pond * Session}}).$$

Where S = survival probability is a function of the interaction between pond and season; Psi = movement probability is a function of an interaction between distance category and season and temporary emigration; and p = capture probability is a function of the interaction between pond and trapping session. This model was used to test goodness of fit. The variance inflation factor was estimated as $\hat{c} = 2.61$ ($\chi^2 = 1174.9$, df with pooling = 450). The most parsimonious model was

$$S(_{\text{Pond + Season + Drought}})\ Psi(_{\text{Distance + Volume + Season + Temporary Emigration}})\ p(_{\text{Pond * Session}}).$$

Where S = survival probability was a function of pond and season and drought in 2004; Psi = movement probability was a function of distance between ponds, volume, season, and temporary emigration; and p = capture probability was a function of the interaction between pond and trapping session. A sequential modeling process in which parsimonious models for capture probabilities were sought first and then the resulting parameterizations were used as the basis for developing models of survival and movement probabilities separately.

Probability of Movement

Within the candidate set of models, 6 models with alternative movement variables were within 2 $QAIC_c$ of the best approximating model (Table 5). The best models were a function of distance between ponds, season (winter, early summer, late summer), occurrence of temporary emigration, presence of an intervening road, and/or sex. The use of $QAIC_c$ weights to assess model support indicates that these 6 best-fit models have 95% of the support of the data. Consequently, inferences were based on these 6 models and model averaging was used to calculate weighted estimates and standard errors that reflect model uncertainty for all parameters (Burnham and Anderson 2002). Overall, the probability of movement between pond complexes was very low ranging from a high of approximately 0.026 (SE = 0.001) a year for the 2 closest ponds (B and C) to less than 0.01 for all remaining pond complexes (Figure 7). Three of the 6 best-fitting models included the presence of an intervening road and/or sex as factors influencing movement probabilities and were supported by the data (Table 5). The effect size of an intervening road was fairly large and negative ($\beta = -0.82$, SE = 0.87) but the 95% confidence intervals included 0 (95% CI = – 1.8 to 0.27). Females had a slightly higher movement probability than males ($\beta = 0.31$; SE = 0.29) but also had a 95% confidence interval that included 0 (95% CI = – 0.27 to 0.90). Although the inclusion of these variables in the model was supported by data, both had confidence intervals that overlap 0 so there is a lack of information to definitely determine the degree of the relationship with movement. Models that included temporary emigration were more supported than the model without temporary emigration ($\Delta QAIC_c = 20.7$) (Table 5). Temporary emigration rates were high in winter/early spring and early summer (0.07 -0.09, SE = 0.03) compared to movement rates between pond complexes (Figure 7).

Table 5. Mark-recapture models of adult painted turtles used to estimate movement probabilities between pond complexes. Factors affecting probability of survival and capture were held constant. Models ranked from best (lowest delta QAICc value) to worst. Shaded models were used for model averaging movement estimates.

Models							
Survival (S)	Movement (Psi)	Capture (p)	QAICc	Delta QAICc	QAICc Weights	K	Q Deviance
Pond + Season + Drought	Distance + Volume + Season + Temporary Emigration	Pond * Session	6115.91	0	0.2677	50	6016.84
	Distance + Season + Temporary Emigration		6116.67	0.764	0.1827	49	6019.65
	Distance + Volume + Season + Temporary Emigration + Sex		6116.84	0.932	0.1680	51	6015.73
	Distance + Volume + Season + Temporary Emigration + Road		6117.10	1.19	0.1480	51	6015.99
	Distance + Volume + Season + Temporary Emigration + Road + Sex		6117.98	2.07	0.0950	52	6014.83
	Distance Categories + Season + Temporary Emigration		6118.22	2.31	0.0842	49	6021.20
Pond + Season + Drought	Distance + Season + Temporary Emigration Categories + Road	Pond * Session	6119.09	3.18	0.0545	51	6017.98
	Distance + Season + No Temporary Emigration		6136.59	20.69	0.00001	48	6041.61
	Constant		6141.11	25.20	0	45	6052.25

K = Number of parameters

Distance = Actual distance between ponds used as a covariate

Distance Categories = Long (>1000 m), Medium (80 - 1000 m), and Short (< 80 m).

Temporary Emigration = Temporary movements out of the pond complexes and, therefore, off the study-site.

Temporary Emigration Categories = Temporary movements out of the pond complexes grouped into 2 categories dependent on pond densities outside complex.

Drought = Drought conditions in 2004.

Pond*Session = Interaction term between pond and trapping session.

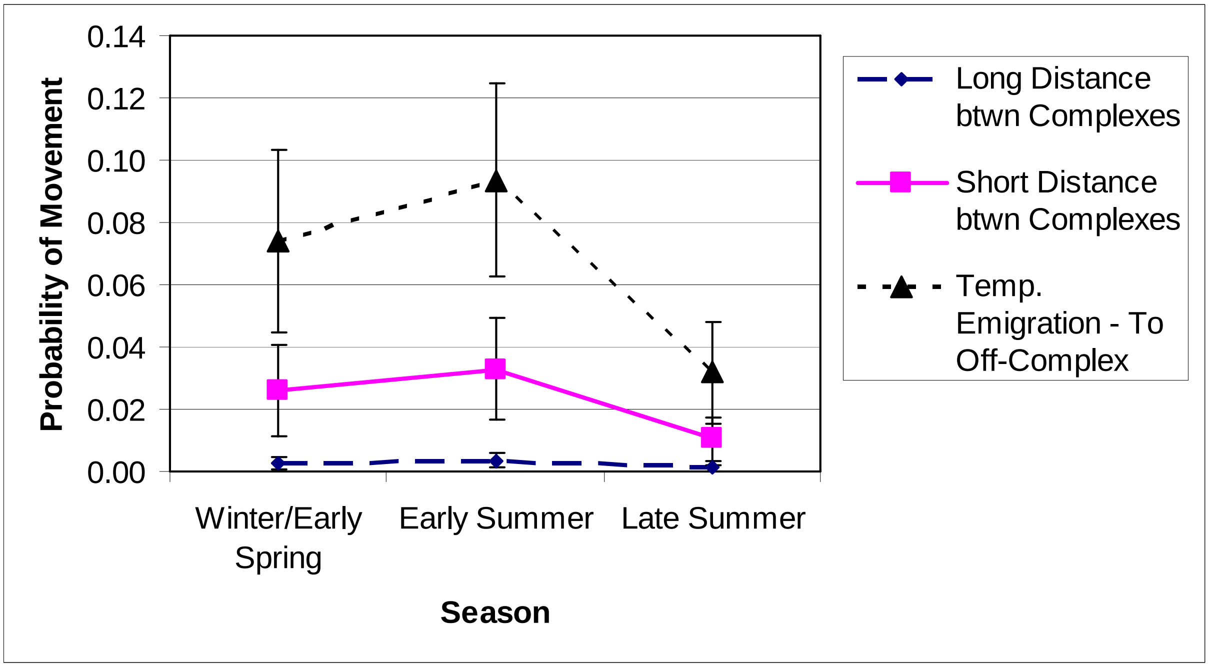

Figure 7. Movement estimates for adult turtles by season for various types of movements. Bars represent standard errors.

Probability of Survival

To assess variation in survival probabilities within pond complexes, factors affecting probability of movement and capture were held constant. Within the candidate set of models, 2 models with alternative survival variables were within 2 $QAIC_c$ of the best approximating model (Table 6). These best approximating models indicated that pond, season, and time (either drought or time over the study) were important factors affecting the probability of survival (Table 6). Survival was not influenced by distance to road ($\Delta QAIC_c = 16.0$) or by specific pond ($\Delta QAIC_c = 99.7$). Season consists of the intervals between trapping sessions: “winter” is 9 months from September to May; “early summer” is 1.5 months from about late May to July; and “late summer” is 1.9 months from about mid-July to late August. Weighted average apparent seasonal survival rates ranged from a high of 0.998 (SE = 0.003) in ponds B and C which retained water during the drought to a low of 0.475 (SE = 0.70) in pond E which virtually dried up (Table 7). Survival rates in all pond complexes were higher overwinter than during summer seasons and 2003 rates were higher than 2004 rates for all seasons (Table 7 and Figure 8). Ponds that retained water over the course of the study (B and C) had higher survival rates than ponds that did not (A, D, and E).

Apparent annual survival rates were higher in 2003 then in 2004 in all pond complexes (Table 7). Apparent annual survival rates ranged from a high of 0.86 in pond C in 2003 to a low of 0.131 in 2004 in pond E (Table 7).

Table 6. Mark-recapture models of adult painted turtles used to estimate survival probabilities within pond complexes. Factors affecting probability of movement and capture held constant. Models ranked from best (lowest delta QAICc value) to worst. Shaded models were used for model averaging survival estimates. See Table 5 for more detailed description of variables.

Models							
Survival (S)	**Movement (Psi)**	**Capture (p)**	**QAICc**	**Delta QAICc**	**QAICc Weights**	**K**	**Q Deviance**
Pond + Season + Drought	Distance between Ponds + Volume + Season + Temporary Emigration .	Pond*Session	6116.7	0	0.6839	49	6019.65
Pond + Time			6118.2	1.57	0.3120	51	6017.13
Pond + Season + Drought + Sex	Distance between Ponds + Volume + Season + Temporary Emigration	Pond*Session	6127.0	10.33	0.0039	50	6032.03
Distance to Highway + Season + Drought			6132.6	15.97	0.0002	46	6041.75
Pond			6216.3	99.65	0	46	6125.42
Volume			6219.8	103.16	0	43	6135.05
Distance to Highway			6220.3	103.60	0	43	6135.49
Constant			6234.2	117.51	0	42	6151.43

Table 7. Estimates of adult turtle apparent survival probabilities by season and annually for each pond complex.

		2003				2004			
Pond Complex	**Season[1/]**	**Seasonal Survival**	**SE**	**Annual Survival**	**SE**	**Seasonal Survival**	**SE**	**Annual Survival**	**SE**
A	Winter	0.989	0.03	0.788	0.06	0.823	0.09	0.539	0.34
	Early Summer	0.893	0.08			0.841	0.10		
	Late Summer	0.892	0.05			0.778	0.10		
B	Winter	0.998	0.00	0.845	0.20	0.981	0.03	0.676	0.16
	Early Summer	0.911	0.04			0.874	0.06		
	Late Summer	0.930	0.07			0.788	0.06		
C	Winter	0.998	0.00	0.864	0.24	0.993	0.01	0.728	0.12
	Early Summer	0.934	0.04			0.907	0.06		
	Late Summer	0.927	0.04			0.809	0.04		
D	Winter	0.963	0.04	0.579	0.11	0.814	0.08	0.309	0.07
	Early Summer	0.703	0.05			0.661	0.05		
	Late Summer	0.855	0.05			0.592	0.06		
E	Winter	0.835	0.08	0.377	0.13	0.503	0.09	0.131	0.05
	Early Summer	0.584	0.06			0.547	0.07		
	Late Summer	0.673	0.06			0.475	0.07		

[1/] Winter (9 months) is September through May; Early summer (1.5 months) is June through mid-July; and Late Summer (1.5 months) is mid-July through August.

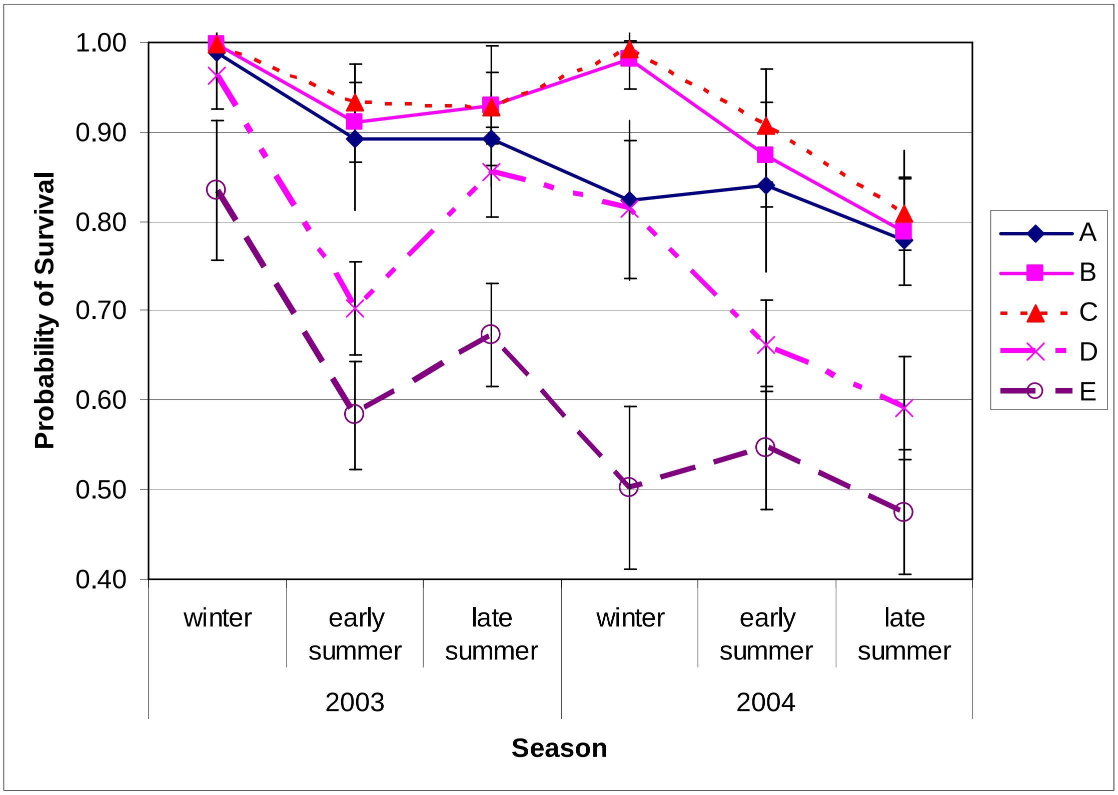

Figure 8. Estimates of adult turtles apparent survival rates by pond over the course of the study. Bars represent standard errors.

Probability of Capture

Capture probability was a function of pond and trapping session but not sex. Animal behavior (i.e., trap happy or trap shy individuals) did not affect capture probability (K. Griffin, unpublished data). Capture probability ranged widely within and between ponds, with a low of 0.009 (SE = 0.009) when pond A was drying to a high of 0.771 (SE = 0.073) in pond D (Figure 9).

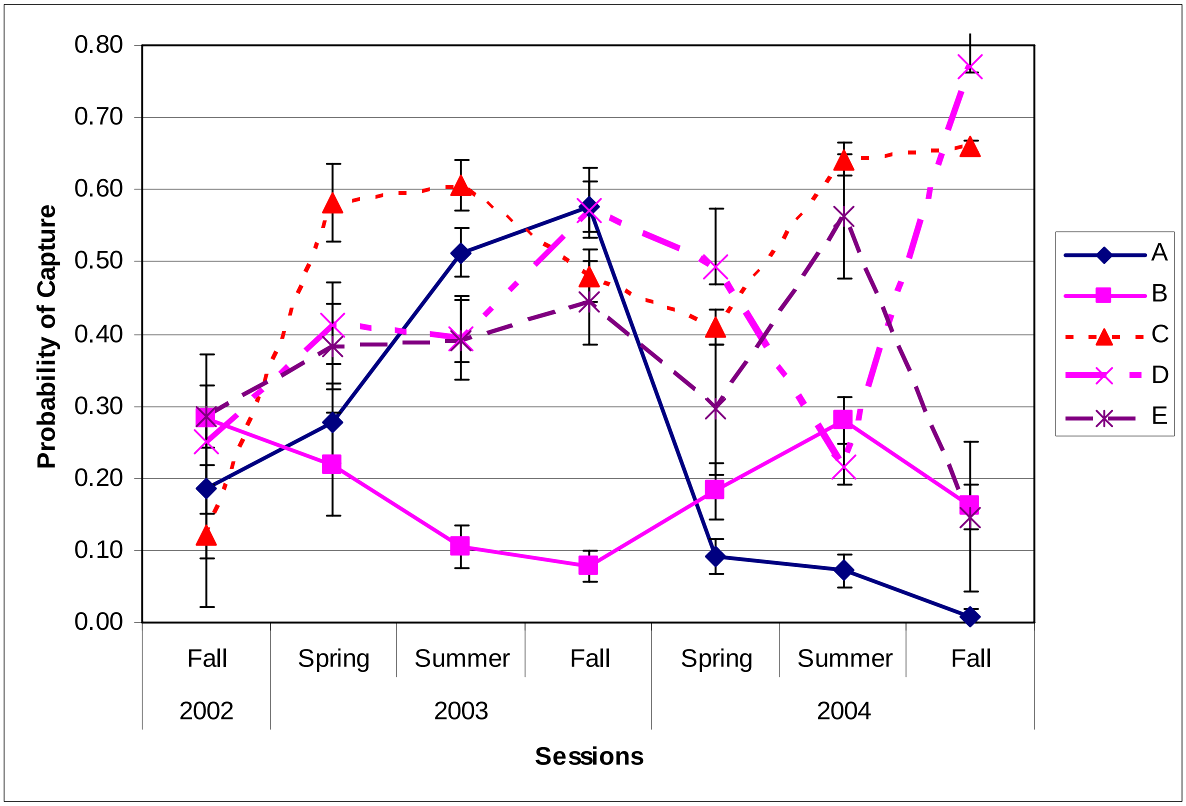

Figure 9. Probability of capture (p) for adult turtles within the pond complexes for each trapping session from 2002 - 2004. Bars represent standard errors.

Abundance Estimates

The Multistate Robust Design model allows for the derived estimation of abundance. Abundances within pond complexes varied over the seasons of the study. The 2 deepest ponds (B and C) had the most consistent abundance values (Figure 10). Abundances in ponds A, D, and E changed dramatically over the study (from highs in the high 100's to the low 200's to dropping to less than 9 in pond E). Depth in all ponds decreased over the study but these 3 ponds were particularly affected by the drought because they were originally not deep ponds. Pond A decreased from 1.4 m to 0.03 m, Pond D decreased from 1.7 m to 0.7 m, and Pond E went from 0.9 m to 0.1 m. Virtually all adult turtles left these ponds by the end of the study.

The regional adult population abundance also declined over the course of the study (Figure 11). The population peaked in spring 2003 at 854 (SE = 117) individuals and fell to 372 (SE = 67) in fall 2004.

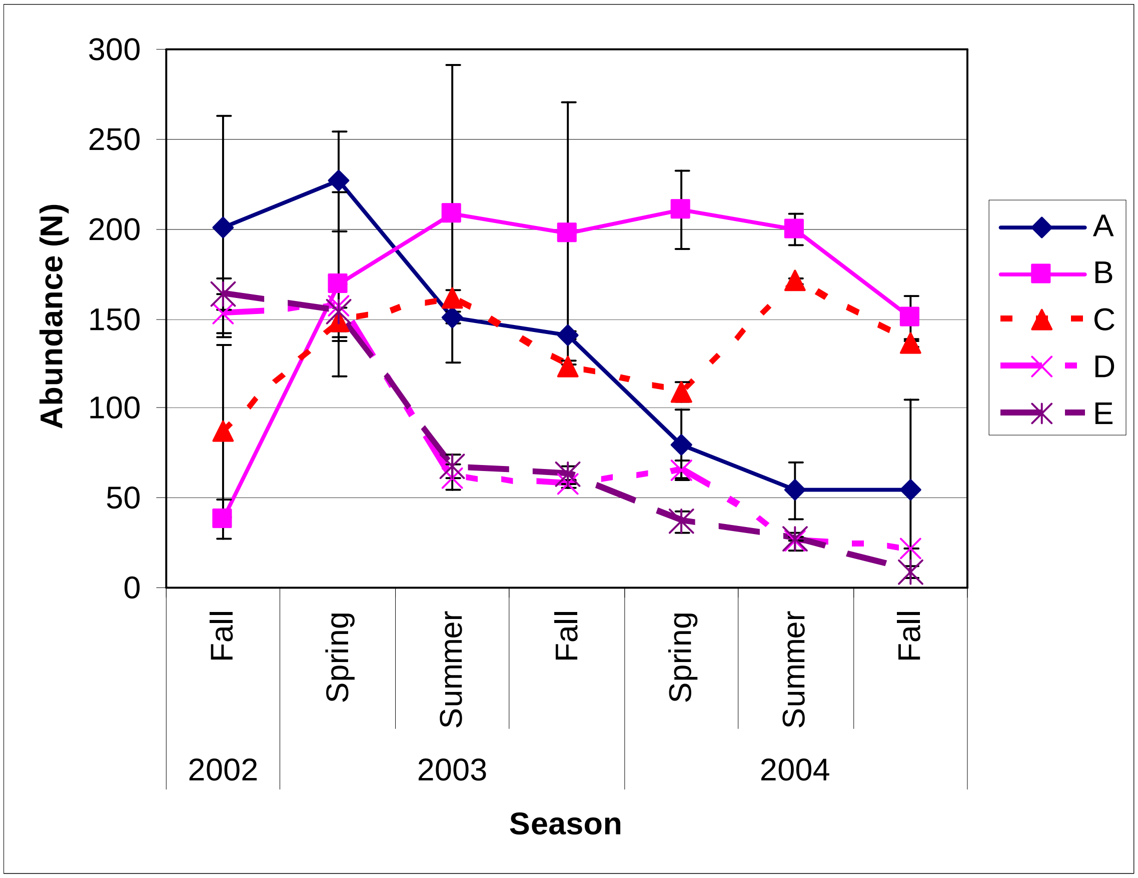

Figure 10. Adult turtle abundance estimates for pond complexes over the seasons. Bars represent standard errors.

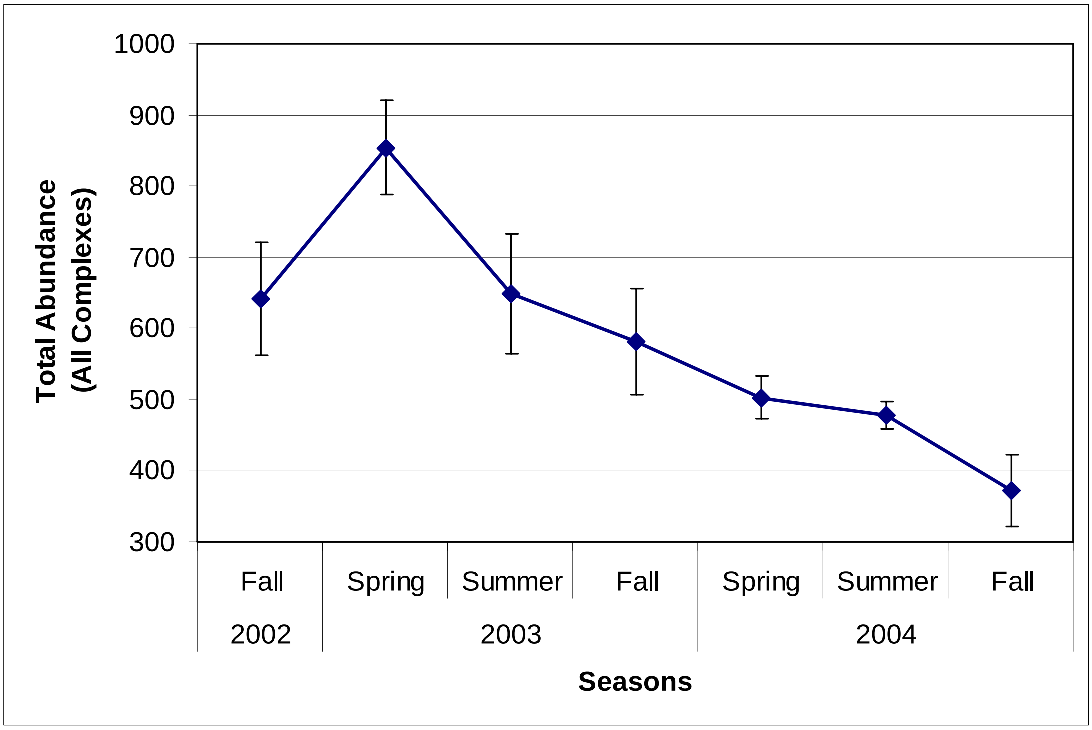

Figure 11. Total adult turtle abundance estimates for all pond complexes combined for each season. Bars represent standard errors.

Population Level Mortality

Both ways of estimating the percentage of the population killed by the highway are considered conservative because road mortality counts are considered a minimum count due to the possibility of not locating all mortalities. The percentage of the population killed on the highway ranged from a lower estimate of 6.0% in 2003 (7.9% in 2004) to a less conservative estimate of 16.9% in 2003 (13.0% in 2004).

DISCUSSION

The main ways that a highway may affect turtle populations are by 1) affecting the survival rate through direct road mortality; 2) changing the population structure through disproportionate road mortality of either sex causing biased sex ratios; and 3) changing movement rates or patterns which ultimately affects population connectivity. The first potential affect, direct road mortality, can have immediate consequences on population viability, while the second 2 potential effects, changing population structure and level of connectivity, may have long-term consequences on population viability.

Survival

This is the first study to allow for survival estimates of painted turtles partitioned seasonally. Modeling showed the most important factor in probability of surviving was the individual pond complex in combination with time (either season or time over the course of study). The model with the most weight (0.68) indicates that season and drought were the most important factors affecting survival rates. Drought conditions appear to have had a strong influence on survival; this study was conducted during a period when the Mission Valley experienced lower than average rain and snowfall in 7 out of the previous 10 years.

'Distance to road' was expected to be an important predictor of survival rate, however this variable was not supported by the data largely due to the fact that ponds far from the highway were still affected by road mortality. Hydrology of the ponds was more important than distance to the highway. Interestingly, pond E, the second furthest (881 m) pond from the highway and greatly affected by the drought, had the highest number of turtles encountered dead-on-the-road. Once the pond began to dry, road mortality data indicate that many turtles attempted to move to the large pond on the west side of the highway at Beaverhead Lane (across from the scenic turnout). This pond is hydrologically connected to Crow Creek and retained water during the drought.

Adult turtles are expected to have high survival rates. Turtles that reach adult size have few predators and, typically, there is little risk of death during winter when turtles hibernate. Apparent annual survival rates in this study range from 0.86 to 0.13. Other studies on painted turtles have estimated annual survival rates between 0.76 and 0.96

(Wilbur 1975, Tinkle et al. 1981, Mitchell 1988). High survival rates are expected in species that have low recruitment rates and hatchling survival (Brooks et al. 1991, Heppell 1998). Annual survival rates are lower 2004 than in 2003. Apparent survival rates are affected by both road mortality and permanent emigration as turtles left ponds for refugia habitats off the study site. The 2 ponds that retained water (ponds B and C) experienced higher survival rates than the other ponds. It is likely these ponds experienced less permanent emigration than ponds that lost significant water. Therefore, these survival rates are less confounded with permanent emigration. This is also indicated by the fact that the percentage of the population killed on the road matches the survival rates in these ponds, particularly in 2003 when the area was less affected by the drought (about 0.17 to 0.15, respectively).

Ponds that lost significant water over the course of the study had extremely low survival rates. For example, survival rates in ponds D and E drop from 0.60 to 0.31 and 0.38 to 0.13, respectively. These survival estimates are confounded with permanent emigration. As these ponds began to lose water, turtles moved off the study site in search of suitable habitat. It is not possible to determine if the turtles survived off the site or died. Many turtles that were last seen alive in these ponds were encountered dead on the highway. The fact that the turtles are moving makes them more susceptible to road mortality. In the area of the split kettle ponds, roughly only half the turtles that attempted to cross the highway succeeded.

Seasonal survival rates varied widely. As expected, winter survival rates were higher than summer survival rates. However, winter survival was higher in winter 2002-2003 then in 2003-2004, likely due to a combination of drought lowering water levels and severe winter temperatures. Dead turtles were recovered in all ponds in early spring 2004. These carcasses were completely intact; therefore, mortality was not due to predation. Hibernating turtles may have gotten caught in shallow areas of ponds that froze to the bottom killing the turtles, thus decreasing winter survival rates in 2004.

Road mortality is expected to reduce summer survival rates. The probability of survival dropped in both the early summer and late summer seasons when turtles were expected to move. The drop in survival rates corresponds to when known turtle road mortalities occurred. In 2003, when the landscape was less affected by the drought, in general survival rates decreased in early summer and increased again in late summer. This corresponds to the road mortality and the movement data, both of which were highest in the same early summer period.

Population Structure

Overall, the population structure does not appear to be affected by the highway. The living turtle sex ratio was not significantly different than 50:50 males to females. Recent studies have stated that there is disproportionate road mortality of females due to higher chances of encountering roads during nesting forays (Steen & Gibbs 2004; Aresco 2005a; Gibbs & Steen 2005). Females were only slightly more likely to make long distance (between pond complex) movements than males, according to the CMR modeling. Examining all movement data (i.e., not only between complexes), no difference in pond to pond movement between the males and females was found. However, this may be misleading because if a female turtle made a nesting foray and returned to the same pond this type of movement would not be detected. Males are not expected to make similar types of there-and-back-again movements for breeding because breeding takes place in the ponds. Therefore, female movements may be underrepresented in the data.

There does not appear to be disproportionate road mortality on females as no sex bias in road mortalities was found. Although most road mortalities could not be identified to sex due to degradation, there is no reason to expect a bias in sex ratio of identifiable and unidentifiable turtles.

Although the overall population sex ratio does not appear to be altered, Pond C, which is adjacent to the highway, did have a significantly male biased sex ratio. It is interesting to note that pond B directly across the highway from pond C did not. Road mortality may be affecting the sex ratio of this particular pond (C). Pond C may be an important pond for reproduction as it had the highest number of hatchling and juveniles caught each year. If more females in pond C than in other ponds were conducting nesting forays and encountering the road, then road mortality could be affecting this local population. However, road mortality data indicates more males than females were encountered dead on the road between ponds B and C. This may indicate factors other than disproportionate road mortality of females may be affecting the sex ratio of this pond.

Movements

Very little movement (between 1% and 2%) a year occurs between pond complexes; therefore, what movement does occur is important in providing connectivity to the local populations in each pond complex. Modeling indicates there is a considerable amount (7-10%) of temporary movement out of the complexes. The complexes were designed as an attempt to incorporate typical daily and seasonal movements of turtles out to temporary ponds in which they may find suitable habitat especially in the spring when temporary ponds warm up faster than the deeper permanent ponds and, therefore, may have more available food resources. The 300 m radius of the complexes was used based on values in the literature as to the distance of typical movements. The fact that there was a considerable amount of temporary emigration outside of the complexes indicates that painted turtles may regularly use larger areas on a seasonal basis than previously thought.

Over the course of the study, the drought caused all permanent ponds to lose water and there were also considerably fewer temporary ponds on the landscape. It appears many turtles moved off the study site and did not return (i.e., permanent emigration) in order to find favorable habitats. The study area has 2 permanent reservoirs (Kicking Horse and Ninepipe) and Crow Creek between approximately 1.5 km and 2.0 km from the closest pond complexes. As the complex ponds became unsuitable, turtles may have moved to these more permanent water bodies, thus lowering the apparent survival rate within the complexes in year 2004. This suggests that turtles are moving outside the complexes but not to other studied complexes. This indicates that other large permanent bodies of water such as Crow Creek and Kicking Horse and Ninepipe reservoirs are important refugia habitats when the smaller permanent ponds become affected by drought.

Movements appear to be hindered by the presence of the highway. The model most supported by the data showed that roads decreased turtle movement rates. Individuals were less likely to move long distances in the presence of an intervening road. As expected, turtles were more likely to move short rather than long distances in the presence of an intervening road. Unfortunately, a situation with 2 permanent ponds relatively close together (30 m) without an intervening road was not available in the vicinity of the study area. This would have allowed examination of short distance movement rates with and without an intervening road. Though the modeling indicates roads decrease turtle movements, it is not possible to determine if turtles are avoiding the highway or if they are simply unsuccessful at crossing the road. Road mortality data can help examine these possibilities.

Focusing at a fine-scale, where 2 ponds are separated by the highway (ponds B and C), CMR data indicate that more movements were made away from the highway from ponds B and C (106 and 78, respectively) than across it (40). However, the fact that there were 150 road mortalities on the highway that falls within these pond complexes suggests that turtles were not avoiding the highway but rather killed attempting to cross it.

Population Dynamics and Connectivity

Highway 93 in the Ninepipe/Ronan area appears to be affecting the turtle population both through direct mortality and reduced landscape connectivity. Conservative estimates of the percentage of the population killed by the highway range from 6.0% to 17.0%. Turtles are long-lived, slow growing animals with delayed sexual maturity and low juvenile survival rates. This combination of life history traits is poorly adapted to high rates of adult mortality (Gibbons et al. 1990, Heppell 1998). Such species often can not replace adult losses quickly and are susceptible to local extinctions (Brooks et al. 1991). Population effects of road mortalities may be exacerbated for wetland species such as turtles when periodic drying results in increased migrations and thus an increased probability of encountering a road (Gibbons et al. 1983, Aresco 2005a). Drought conditions coupled with severe winters can have an even greater affect, lowering survival rates even further because hibernating turtles are at increased risk of freezing in shallow waters. Lowered survival rates for even a short period can cause severe population declines that take years to recover (Fonnesbeck and Dodd 2003). The level of observed mortality during this study would not be sustainable if this were a closed population. Due to the amount of both temporary and permanent emigration it is evident that the regional population likely includes Crow Creek, Kicking Horse Reservoir, and Ninepipe Reservoir. Given this, maintaining connectivity across this landscape is extremely important for this species.

Currently, the highway appears to be a semi-permeable barrier to movements, reducing landscape connectivity for turtles. Although some turtles successfully crossed the highway, road mortality data indicate that most did not; e.g., 40 successful crossings observed in an area where 150 mortalities were recorded. It is important to maintain connectivity for long-term population viability and to maintain the possibility of recolonization of ponds that may lose their local populations such as occurred in ponds A, D, and E during these drought conditions. This study conducted during drought conditions shows the importance of maintaining connectivity to suitable refugia habitat such as Ninepipe and Kicking Horse reservoirs so that recolonization is possible when conditions permit.

RECOMMENDATIONS

Three areas of high priority based on road mortality data were found: the 2 kettle ponds at road locations 22 and 33 (1 just south, the other just north of Highway 212 junction) and the area immediately south of the scenic turnout at Beaverhead Lane. This last area has a permanent pond on the west side and 2 semi-permanent ponds on the east side of the road. All 3 of these areas also appear to have important nesting areas on and adjacent to the road banks.

Culverts and fencing systems have been shown to be effective in reducing turtle road mortality (Dodd et al. 2004, Aresco 2005b). In Florida, turtle mortality declined dramatically with the construction of the barrier wall-culvert system; from 374 mortalities preconstruction to 7 post-construction (Dodd et al. 2004). Turtles used 2.7 m x 2.7 m, inundated, partially submerged box culverts; 0.9 m cylindrical culverts when wet with earthen substrates; and 1.8 m x 1.8 m dry box culverts. All of these culverts were 44 m in length and the smaller ones (the 1.8 m x 1.8 m box culvert and the 0.9 m diameter cylindrical culverts) had light boxes. If light boxes are not used, we recommend over-sizing the culverts to allow light to be seen through the culvert. Painted turtles do not burrow and may show reluctance to enter dark areas.

The Supplemental Draft Environmental Impact Statement (FHWA et al. 2005) for the Ninepipe/Ronan area is considered a "30% design" document. This means that many construction details have yet to be determined. As more design considerations become known more detailed and area specific recommendations can be provided. Current recommendations for reducing the effects of Highway 93 on turtle populations in the Ninepipe/Ronan area of the Mission Valley are below. Note: all recommended culverts would also be beneficial to other wildlife in the area.

1. Construct bridges or over-sized cement box or over-sized metal culverts in the high priority areas that naturally would be water crossings. In particular, these should be placed in the 2 kettle ponds.
2. Construct over-sized cement box culverts in dry crossing areas such as near the scenic turn-out at Beaverhead Lane and just north of Olson Road. Dry land culverts should be flat bottom with an earthen substrate to facilitate turtle terrestrial movements through them.

3. Construction time frame. Movements are highest from mid-May to mid-July. Minimizing construction in the 3 high priority areas during these months would minimize disturbance and mortality.
4. Monitor construction in the kettle ponds due to their importance in overwinter, reproduction, and refugia habitat. The kettle ponds are likely to have detours that could possibly hinder turtle movements as they attempt to avoid construction activities. Providing safe passage under the detours will be important. The placement and timing of the detour is important in minimizing the effects of construction activities on the turtles (see Recommendation #3). As design considerations become known for the area, other recommendations may be warranted such as having on-site inspectors to monitor turtle movements during construction. Monitoring of construction projects has been accomplished on other projects in coordination with the Confederated Salish Kootenai Tribes and contractors (Pers. Comm. Pat Bastings, MDT - Environmental).
5. Install wing or directional fencing to funnel turtles to the culverts (see Appendices A and B). The fencing would be necessary only in the vicinity of the crossing structures and nesting areas. Install low fencing that can not be breached regardless of whether bridges or culverts are implemented because of the nesting that occurs on and adjacent to the road bank in the high priority areas. Even though passages are provided, females may still be drawn to the road edge to nest and consequently be at risk of road mortality and risking human safety.
6. Install 'Turtle Crossing' warning signs to increase awareness of motorists. More general "Wildlife Crossing" signs may not be sufficient to warn motorists to the presence of turtles because most motorists expect large game animals when they see "Wildlife Crossing" signs. Standard warning signs do not appear to affect motorists therefore; signs should be enhanced, and location and time specific. These types of modifications to standard signage have been useful in modifying human behavior (Messmer et al. 2000, Sullivan and Messmer 2003, Al-Ghamdi and AlGadhi 2004, Hardy et al. in press). Signs could be enhanced by using a larger size, reflective color (i.e. neon yellow/green), or additional flagging. Signs should only be visible from June – September when turtles are likely to be

encountered on the road. Sign location should be limited to the Ninepipe/Ronan area of Highway 93. A north bound sign could be placed near Gunlock Road and a south bound sign could be placed near Beaverhead Lane. Limiting the time frame and location may also minimize motorists' habituation to the signs.

7. Post-construction study. It will be possible to identify turtles marked in this study for many years. A post-construction study will provide valuable data on turtle use and efficacy of the wildlife crossing structures in providing landscape connectivity. Currently only 2 studies (Dodd et al. 2004, Aresco 2005b) exist that includes pre- and post-construction effects on connectivity and these do not include pre-construction population data population data as this study does. This study combined with a post-construction study provides a unique opportunity to determine the long-term effects of the highway on connectivity and population dynamics.

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APPENDIX A. Fencing Methods and Efficacy for Minimizing Turtle Road Kill and Directing Turtles to Crossing Structures.

The following report was submitted to the Montana Department of Transportation in 2004. Based on MDT reviewer comments, revisions have been incorporated into the document.

FENCING METHODS AND EFFICACY FOR MINIMIZING TURTLE ROAD KILL AND DIRECTING TURTLES TO CROSSING STRUCTURES

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INTRODUCTION

This report documents a variety of barrier and fencing designs that have been used in wildlife-highway interaction projects and their effectiveness in keeping herpetofauna off roadways and directing them towards wildlife crossing structures.

The National Cooperative Highway Research Program has produced the most extensive synthesis of wildlife and highway issues in the Interaction Between Roadways and Wildlife Ecology: A Synthesis of Highway Practices report (Evink 2002). A survey conducted for that report indicates that many states are attempting to address wildlife-highway issues. Out of the 34 states that responded to the survey, 28 are using fencing to protect wildlife with the most frequent use being to keep deer off the roads.

Because fences are likely to increase the fragmentation effects of highways, the use of culverts and other crossing structures are important in maintaining connectivity (Boarman and Sazaki 1996, Evink 2002). Drainage culverts are one means of providing connectivity. These types of culverts are typically used where highways cross wetlands with fluctuating water levels. Theses culverts then become dual purpose; water transport or hydrological leveling as well as wildlife corridors. The current design proposal for the expansion of Highway 93 in the area of Ninepipe Wildlife Refuge includes the use of culverts as wildlife crossing corridors (Federal Highway Administration and Montana Department of Transportation 2000). The proposed wildlife crossing structures will be at least 1.2 x 1.8 m concrete culverts and will likely be larger in many areas. In addition to the wildlife crossing structures, numerous smaller culverts will be used for hydrological leveling.

In an unpublished report to the Minnesota Department of Natural Resources, Lang (2000) conducted a culvert size and shape experiment with 400 Blanding's turtles (*Emydoidea blandingii*). He used corrugated metal culverts ranging in size from 0.9 – 1.2 m in diameter and varying in shape from round to arched. Although not mentioned specifically in the report, the length of the culverts appears to be that of a paved 2-lane road (approximately 18 - 25 m). Lang found that Blanding's turtles moved through each of the culverts presented. Turtles did not demonstrate a clear preference for culvert size or shape, or light intensity at the far end, given the available choices.

In Europe, culverts for mammals with widths from 5 to 12 m are common and, in general, heights of 3 to 5 m have been successful (Bank et al. 2002).

Jackson conducted experiments on eastern painted turtles' use of "culverts"(S. Jackson, Extension Service Program Director for Natural Resources, Massachusetts, Pers. Comm.). He observed turtles using a 0.6 x 0.6 x 6 m wooden box "culvert". Females used the box readily whether it was lighted or not. The unhesitant use by females however may indicate a drive to reach breeding sites.

Given the information above on the culvert sizes used on other projects, it is likely that the smaller culverts used for hydrological leveling will be dual purpose, that is, serving as wildlife crossing structures as well.

TYPE OF BARRIERS

Fencing

Typical fencing is rectangular mesh or chain link fence from 2.6 – 3.0 m in height. Specific measurements depend on the target species. For small mammals and herpetofauna often smaller mesh (2 x 2 cm to 4 x 4 cm) is attached to the existing chain link or larger mesh fence (Evink 2002) (Figures A-1 and A-2). This mesh is often buried 20 – 40 cm into the ground and then extending to a height of 0.5 to 1 m. To keep reptiles and amphibians from climbing the fence, the upper edge of the finer mesh is often bent out at a 90-degree angle to create a lip.

Figure A-1. Wire fence with plastic fabric mesh (France). Photo: Bank et al. 2002.

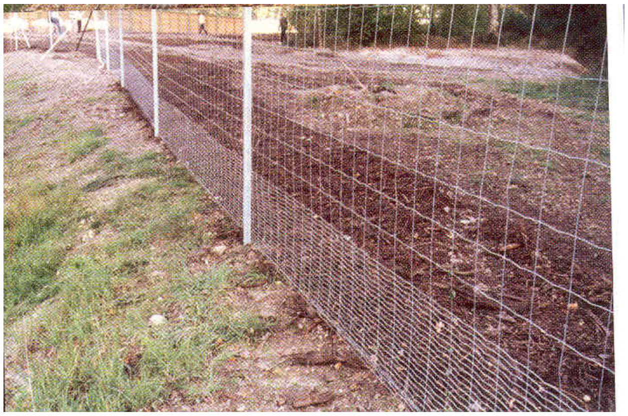

Figure A-2. Wire fence with smaller mesh at the bottom. Photo: Bank et al. 2002.

In 1990, a 24 km desert tortoise (*Gopherus agassizii*) barrier fence was erected by the California Department of Transportation. The fence consists of 60-cm wide, 1.3 cm mesh of galvanized steel hardware cloth buried to 15 cm and extending 45 cm in height (Boarman and Sazaki 1996, Boarman et al. 1997). The fence is supported by a six-strand wire fence; the top 3 are barbed and the bottom 3 are unbarbed to allow easy installation of the hardware cloth. Boarman and Sazaki (1996) found 88% fewer vertebrate roadkill and 93% fewer tortoise roadkill along the fenced section of highway, therefore, the fence was highly successful at reducing road mortality. Later, gaps due to poor maintenance allowed tortoises to access the highway suggesting the need for proper maintenance.

The Iowa Department of Transportation considered many types of fencing to keep ornate box turtles (*Terrapene ornate*), snakes, and small mammals off the highway including half pipes and solid concrete walls. After taking cost and maintenance issues into consideration they are installing 0.6 cm steel mesh attached to regular Type-47 field fence (woven wire livestock fence). The mesh will be buried 20 cm and extend 1 m above ground. This project is currently under construction with completion expected summer 2004, therefore no indications of the effectiveness of this fence type are available (R. Ridnour, Iowa Department of Transportation, Pers. Comm.). The mesh could be bent outward at the top to create a lip, however, it may be time consuming to actually accomplish this, as it is not prefabricated.

In Nebraska, a 0.9 m high chain link fence, buried 15.2 cm, was used to direct Blanding's turtles towards corrugated metal culverts with sizes varying from 0.6 to 0.91 m diameters with flared end sections and lengths from 18 to 36.5 m. The fence was about 1.6 km in length and it appeared to work well in that section, however, road mortality continued near the ends of the fence (L. Rowe, District Engineer, Nebraska Department of Roads, Pers. Comm.).

Problems with Fencing

There are many problems associated with fencing. Overall, depending on the fence type, fencing can be expensive to build, maintenance costs are high, and some people do not like the aesthetics of wire fencing (Figure A-3).

More specifically, if the mesh sizes are too large turtles, especially hatchlings and juveniles, can pass through or get stuck in the openings. Therefore, smaller mesh attached to the bottom of larger mesh fences is necessary. Some turtle species, including painted turtles, are good climbers (M. Aresco, Florida State University, Pers. Comm.; S. Jackson Extension Service, Program Director for Natural Resources, University of Massachusetts, Pers. Comm.). Creating a lip at the top of the smaller mesh is important to prevent climbing over the top (M. Aresco, Wildlife Biologist, Florida State University, Pers. Comm.) (Figure A-4). Another problem is storm water run-off which can cause erosion and often undermines the fence. Burying the mesh can minimize this problem however, proper installation and regular inspection/maintenance is required.

Figure A-3. Smaller mesh fence. Note potential problem with litter build up and fence not connected to outer edge of culvert. Photo: Bank et al. 2002.

Silt fencing which is made either of cloth or fabric should only be used as a temporary solution because of its short life span. Silt fencing can be climbed, can be overgrown quickly, and can rip and tear easily, especially when weathered. All of these compromise the effectiveness of this type of barrier.

Figure A-4. Florida softshell turtle climbing over fabric silt fence. Photo: M. Aresco

Rails and Curved Pipes

Europeans have used a PVC barrier with an angled lip or fabricated galvanized steel rails with a lip along the upper edge as a barrier for amphibians and reptiles (Bank et al. 2002, Frey and Niederstraßer 2000) (Figures A-5 and A-6). A 30 cm diameter PVC pipe, sliced down the middle and half buried has been used in Massachusetts to keep box, wood, and spotted turtles off the roadway (S. Smyers, Wildlife Biologist, Oxbow Associates, Pers. Comm.). Although these barriers are cheap and fairly easy to install, keeping vegetation from growing over them is a constant maintenance problem and they only work for small mammals, reptiles, and amphibians. Also, any vegetation (even short vegetation) growing near-by can drastically reduce their effectiveness. This creates a virtually constant maintenance problem. However, if the rail were built into an asphalt strip or pad these problems could be minimized.

Figure A-5. Galvanized steel rail with lip for amphibians and reptiles (Germany). Photo: Bank et al. 2002.

Figure A-6. Metal rails with lip for amphibians and reptiles (Germany). Photo: Bank et al. 2002.

Concrete Walls

The Payne's Prairie Ecopassage project near Gainesville, Florida has incorporated the dual-use (hydrological leveling and wildlife crossing) culverts and barriers which have been successful in providing connectivity for a wide range of terrestrial and aquatic wildlife. This project has the most pre- and post-construction data available of any wildlife crossing culverts and directional barrier project (Barichivich and Dodd 2002).

A suite of structures including lipped concrete walls, concrete square box culverts, precast concrete bottomless culverts, round concrete pipes, open median drains, and reverse mount guardrail barriers (Type A fencing, see next section below) combine to reduce mortality and allow animals to cross under the highway. The 1.1-m concrete wall with a 15.2-cm lip keeps small mammals, reptiles, and amphibians off the highway (Figures A-7 and A-8).

The concept of a lipped wall can be used in any area where barrier fence for small animals (reptiles, amphibians, small mammals, or even flightless stages of birds such as ducklings) is desired. The height of the wall can be based on whatever species are in the area of concern. Because the Paynes Prairie project had species that were able to climb high walls, it is likely that most situations would need shorter walls.

Figure A-7. Paynes Prairie Ecopassage (Florida) – Artist rendition. Concrete wall with lip. Photo: D. Forsyth. www.fhwa.dot.gov/environment/wildlifecrossings/amphibian.htm

Figure A-8. Paynes Prairie Ecopassage – Artist rendition. Concrete wall with lip. (Florida). Photo: D. Forsyth.

The height of the lipped wall was determined by herpetologists based on the characteristics of several species known to be in the area (alligators were a primary concern). That height was 1 m, but an extra 0.15 m was added to ensure containment of the majority of potential species (P. Southall, Florida Department of Transportation, Pers. Comm.). The 0.15 m lipped extension at the top of the wall was designed to stop an animal before it scaled the top of the wall.

Motorist safety was a big consideration in the design. The lipped wall was placed at the edge of an 11 m clear zone, from which all palm trees had been removed. Stormwater is removed through median and clear zone drains, which also allows light to enter the culverts (Figure A-9).

Concrete was selected because of reduced maintenance costs, long-life span, and the potential effectiveness as a barrier. Other materials for the barrier were considered, including hardware cloth and wire (expensive, short life span, the surface allows some species to climb over), and plastic (short life span). The concrete wall was also simple to construct because it was precast; the 2.9 km of road (therefore, 5.8 km of lipped wall) took about 210 days to construct. Precast structures (wall segments and culverts) saved installation time, and therefore cost. The 'flowable fill' over the culverts allows for the maximum size opening in the road because it is part of the roadway rather than requiring additional fill over it (USDA Forest Service website http://www.wildlifecrossings.info). The cost was listed at greater than $200,000 but there is no indication of what this value includes. The total project cost was listed as $3.5 million. This cost included many aspects

Figure A-9. Paynes Prairie Ecopassage – Artist rendition. (Florida). Photo: http://www.fhwa.dot.gov/environment/wildlifecrossings/amphibian.htm

of the project not related to wildlife mitigation, including shoulder reconstruction, slope and drainage modifications, and a boardwalk for people stopping to view the Preserve's wildlife was included.

A concern in the placement of the barrier was that vehicles might go over the lipped wall, making emergency response more difficult as well as making vehicles more difficult to see from the road. In-sloped and wide clear zones reduced this concern (USDA Forest Service website http://www.wildlifecrossings.info).

Vegetation growing along the wall has allowed some small mammals to breach the lipped wall. Therefore, vegetation maintenance is required. A slope arm mower is used at Paynes Prairie.

The effectiveness of this culvert/barrier system has been well monitored. A 41% reduction in wildlife road mortality was recorded between the pre- and post-construction periods (Barichivich and Dodd 2002). If birds and hylids (climbing treefrogs) which cannot be prevented from access to the highway by the barriers, are eliminated from analysis there was a 93.5% reduction in road mortality. Also, an increase in culvert use for many species was observed. A reduced number of road mortality and an increased use of culverts are considered the best indication of a successful passage design.

Guardrail (Type-A Fence)

As part of the Paynes Prairie Ecopassage project, a reverse mount guardrail barrier made of metal with wood posts facing the traffic was installed at both ends of the wetland to reduce animals traveling around the ends of the lipped wall (Figure A-10). These were buried with hardware cloth to prevent animals from digging under the guardrail. The guardrails were placed in reverse to prevent snakes from climbing the posts and crossing (USDA Forest Service website http://www.wildlifecrossings.info).

Some problems with drainage have occurred in the reverse guardrail barrier. Animals have been able to enter the roadway where water run-off from the road has created gaps under the barrier. Pete Southall (Florida Department of Transportation, Pers. Comm.) believes that if the guardrail were constructed with an asphalt footprint base this would eliminate the drainage and vegetation concerns. In this situation the guardrail may be very effective and have lower maintenance costs. A slope mower arm would be able to mow over the top of the guardrail easily. The reverse mount guardrail was considered effective for smaller animals (P. Southall, Florida Department of Transportation, Pers. Comm.).

Figure A-10. Type-A fence (Paynes Prairie, Florida) Photo: Barichivich and Dodd 2002.

Rock Walls

Rock walls have also been used, usually in association with fencing, to keep small animals off the road. Gabion ™ is a type of wire cage that can be filled with rocks and wired shut. There are 2 examples of the use of Gabion baskets by the New Jersey Department of Transportation. In both cases, Gabion was used as a means to minimize erosion and to keep turtles off a roadway (J. Campy, New Jersey Department of Transportation, Pers. Comm.). The rock wall was about 1 m^2 wide and 91 m long. There was no monitoring of the sites post-construction but the belief is that there was no longer a problem with road mortality. In the approximately 2 years since the rock wall has been in place there has been no maintenance issues (J. Campy, New Jersey Department of Transportation, Pers. Comm.). In the Ninepipe area of Highway 93 this system may not be effective because of the climbing ability of painted turtles.

POTENTIAL ISSUES

In general, amphibians and reptiles are potentially less amenable to mitigation using crossing structures and barriers than mammal species. This is a consequence of the limited movements by many species and the low potential for learning compared with large animals (Rudolph 2000). However, movements through the culverts by at least a few individuals should be sufficient to maintain genetic exchange while at the same time significantly decreasing wildlife road mortality (Barichivich and Dodd 2002).

Animals on the wrong side

One problem associated with fencing is that animals can get trapped on the wrong side of the fence. Bissonette and Hammer (2000) found that deer used earthen ramps about 10 times more often than one-way gates. Scott Jackson (Extension Service, Program Director for Natural Resources, University of Massachusetts, Pers. Comm.) used earthen ramps with flaps cut into silt fencing as "jump outs" for turtles. Two turtles were observed using these.

Erosion

Sheet erosion and other drainage issues can cause problems and breaching of most types of barriers. Burying galvanized metal or aluminum flashing to a depth of 20 cm could significantly decrease access to the road by small animals such as turtles and snakes (Barichivich and Dodd 2002). Also, using asphalt "pads" may also minimize this problem (see discussion under "Guardrail" section). Regular inspection of the barrier should be required.

Vegetation

During the Paynes Prairie Ecopassage project, small mammals, snakes, and treefrogs were observed climbing vegetation adjacent to the concrete wall (Barichivich and Dodd 2002) (Figure A-11). Vegetation generally needs mechanical mowing once a year. Approved aquatic pesticides are used about twice a year on the Paynes Prairie project (P. Southall, Florida Department of Transportation, Pers. Comm.).

Figure A-11. Vegetation growing along concrete wall with lip (Paynes Prairie, Florida) Photo: Barichivich and Dodd 2002.

Maintenance

Because of the above issues, regular inspection and maintenance needs to be incorporated into highway plans. On the Paynes Prairie Ecopassage project mowing occurs about once a year and approved aquatic pesticides are used about twice a year.

RECOMMENDATIONS

There are many different types of barriers that have proven to be effective in minimizing wildlife-highway interactions. The type, dimensions, and materials used are often dictated by the needs of the species of most concern on the project. Given that the Highway 93 Reconstruction through the Ninepipe area is likely to encounter many different types of construction needs, no one type of wildlife barrier can be recommended. Like the Paynes Prairie Ecopassage project, a combination of methods mentioned above is likely to be needed to accommodate the various situations encountered along this stretch of highway (Figure A-12). Where wildlife crossing culverts are located, concrete walls or the galvanized steel railings might easily be incorporated into the design because mechanically stabilized earth will be needed (G. Smith, Senior Project Manager, Skillings Connolly, Pers. Comm.).

Figure A-12. Example of a combination of barrier methods. Arched culvert with large fence along highway and metal rail for amphibians and reptiles (Germany). Photo: Bank et al. 2002.

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If you go to “simple search” and type in “Paynes Prairie”, then click on the name “Paynes Prairie” detailed information on design dimensions and engineering drawings can be found.

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APPENDIX B. Use of Low Fencing with Aluminum Flashing as a Barrier for Turtles.

The following paper was presented at and appears in the Proceedings the 2005 International Conference on Ecology and Transportation (ICOET) which occurred from August 29 through September 2, 2005 in San Diego, California.

Griffin, K.A. 2005. Use of low fencing with aluminum flashing as a barrier for turtles. *In* Proceedings of the 2005 International Conference on Ecology and Transportation, edited by C. Leroy Irwin, Paul Garrett, and K.P. McDermott. Raleigh, NC: Center for Transportation and the Environment, North Carolina State University.

USE OF LOW FENCING WITH ALUMINUM FLASHING AS A BARRIER FOR TURTLES.

Abstract

I examined the effects of road mortality on a population of western painted turtles (*Chrysemys picta bellii*) in west-central Montana; these turtles make up the majority of road mortalities in a section of highway that bisects the Ninepipe National Wildlife Refuge. The objective of the barrier fencing experiment was to determine whether turtles were able to breach fencing designed to direct turtles towards crossing structures and thereby keep them off the road.

I constructed 45.7 cm high turtle enclosures out of 2 by 5 cm fencing with and without 10 or 15 cm high flashing attached at the top. Turtles were placed in the enclosures and behavior was observed for 1 hour. Of 124 turtles, only 4 (3.2%) were able to climb to the flashing. No turtles climbed over the flashing within the time allowed. In enclosures without flashing, 2 (3.8%) were able to breach the fencing. The results of this experiment will help in the design of appropriate barriers to keep turtles off the road and direct them towards crossing structures.

Introduction

In northwestern Montana, U.S. Highway 93 has been slated for capacity and reconstruction improvements along a 90 km (56 mile) section. An approximately 7 km (4.3 miles) portion of this highway bisects a prairie pothole ecosystem that currently supports a variety and abundance of wildlife. One species, the western painted turtle (*Chrysemys picta bellii*), comprises the majority of wildlife road mortalities in this area. Through a cooperative agreement involving the Montana Department of Transportation (MDT), the Federal Highway Administration (FHWA), and the Confederated Salish and Kootenai tribes (CSKT), a series of wildlife mitigation measures involving wildlife crossing structures and other design features will be implemented to decease the amount of road mortality and fragmentation that currently exists (FHWA, MDT, and CSKT 2000).

A variety of barrier and fencing designs have been used in wildlife-highway interaction projects to keep wildlife off roadways and direct them towards wildlife crossing structures. Because barriers and fencing are likely to increase the fragmentation effects of highways, the use of culverts and other crossing structures are important in maintaining connectivity (Dodd et al. 2004, Aresco 2005). Amphibians and reptiles are potentially less amenable to mitigation using crossing structures and barriers. This is a consequence of the limited movements by many species and the low potential for learning compared with large animals (Yanes et al. 1995). However, movements through the culverts by at least a few individuals should be sufficient to maintain genetic exchange while at the same time significantly decreasing wildlife road mortality (Rudolf 2000). Various turtle species are known to use culverts as crossing structures (Foresman 2004, Pelletier 2005, Walsh 2005).

Rails and curved pipes have been used as barriers for amphibians and reptiles (Barichivich and Dodd 2002), (Frey and Niederstraßer 2000), (Bank et al. 2002), as have concrete walls (Barichivich and Dodd 2002), guardrails (Barichivich and Dodd 2002), and fencing (Banks et al. 2002, Evink 2002). Herpetofauna can be directed by drift fences, which have been very effective in directing movements especially during capture sessions (Gibbons et al. 1990, Morreale et al. 1984.). Ruby et al. (1994) compared behavioral responses of captive desert tortoises to various barriers and fences. They found tortoises responded differently to the different barrier types. Tortoises were also observed attempting to climb those barriers constructed of wood (Puky and Vogel 2003). While anecdotal evidence exists that some turtle species (including painted turtles) are good climbers, no one has examined barrier fencing can be breached.

My objective was to determine if aluminum flashing at the top of a wire fence would be sufficient to stop western painted turtles from climbing over barrier fencing. The particular fencing type in combination with aluminum flashing was used to represent a potentially low-cost alternative for use as barrier and directional fencing at crossing structures.

Methods:

The enclosure trials were conducted at various ponds within the Mission Valley, Montana (T20N, R20W, Sections 24-26). All trials were conducted during activity periods of turtles (1335 – 1800 Mountain Daylight Time), between July 4 and 11, 2004 and May 26 and 30, 2005.

Eight circular enclosures were built of 2.5 x 5 cm welded wire. The enclosures were 61 cm in diameter and 45.7 cm high with an open top and bottom. On the inside top of each enclosure either 10 cm or 15 cm of aluminum flashing (#68-010) was attached flush with the top of the enclosure (Figures B-1 and B-2). Four enclosures of each type were made for a total of 8 enclosures. Because of the different flashing widths the distance from the ground to the bottom of the flashing was different for the 2 types of enclosures. Therefore, the enclosures with 10 cm of flashing had 35.6 cm of exposed wire and the enclosures with 15 cm of flashing had 30.5 cm of exposed wire. For the 2005 trials, the flashing was removed making the enclosures 45.7 cm of fencing.

Figure B-1. Wire enclosures with aluminum flashing used to test turtle's climbing ability.

Figure B-2. Turtles in fencing enclosure with aluminum flashing.

The enclosures were placed at the edge of a pond so that the substrate was always dried mud. Enclosures were placed such that the interior was bare or had little vegetation and no food, water, or shelter was provided. Trials were conducted with wild-caught, naïve animals that had no known previous experience with enclosures. Each trial began by randomly assigning 2 turtles to each enclosure and placing the turtles in the center of the enclosure.

A total of 177 turtles were used for the trials. Each trial lasted 1 hour during which turtle behavior was noted. Each time a turtle attempted to climb the fencing the highest level it reached was recorded. A turtle was considered to have reached that level if at least 1 claw held onto that rung of wire. If a turtle fell onto its back it was left alone to see if it could right itself. If after 1 minute the turtle was unable to right itself it was turned over by the observer.

Trials were run simultaneously in all 8 enclosures and observational data were collected during the entire hour period. Crewmembers were responsible for observations in 2 enclosures at a time. Enclosures were placed within 0.5 meter of each other to aid in observations.

Data were analyzed using chi-square analysis to test for differences in distribution of the highest height reached by sex.

Results:
Turtles spent a majority of the time walking the perimeter of the enclosures. Only one turtle, an adult, settled down and made no further explorations after one initial attempt at climbing the fence. Some turtles attempted to extend their head and feet through the wire but none continued to push for periods greater than 3 minutes. No turtles became stuck in the fencing. The presence of another turtle in the enclosure did not appear to alter behavior. Occasionally, turtles crawled over each other while exploring the enclosure and occasionally stood on the back of another in an attempt to climb. Heights reached while aided by another turtle were not recorded because under natural conditions it is unlikely that turtles will be at the same place along the fence.

Males and females climbed to similar heights in the enclosures with 10 cm flashing ($\chi^2 = 7.527$, $P > 0.05$) and in enclosures with 15 cm flashing ($\chi^2 = 4.944$, $P > 0.05$); therefore, sex was pooled in subsequent analyses.

All (N = 177) turtles reached at least the 10 cm level. This could have been obtained by some turtles while keeping one hind foot on the ground. In enclosures without flashing, 75% (N = 53) of the turtles attempted to climb and 3.8% were able to breach the fencing (Figure B-3).

Figure B-3. Turtle about to breach fencing enclosure without aluminum flashing.

In enclosures with flashing, 82% (N = 124) attempted to climb the fencing (climbing was defined as reaching 15 cm [6 in.] which meant that at least both front feet were off the ground). No turtles were able to breach the flashing in any enclosure, however, 2 adult turtles in both the 10 cm and 15 cm flashing enclosures reached the flashing (3.6% and 3.8%, respectively). All turtles that were able to touch the flashing fell to the ground. All turtles, except 1, were able to right themselves within a matter of a minute.

Digging behavior was only observed 3 times during the trials and in no instance was the turtle able to breach the fence.

Discussion

Turtles are known to make seasonal movements (Sexton 1959, Gibbons et al. 1990) and given urban development today they are likely to encounter roadways during these movements. Turtles are susceptible to road mortality due to their slow movements; therefore, fencing is an important issue. With the increase in the use of barrier fencing to direct wildlife towards crossing structures, it is important to determine what methods or designs are most effective. One commonly held belief is that turtles are good climbers and, thus, potentially able to breach fencing that is designed to keep them off the roadway.

I found that although turtles were able to climb wire fencing, it is unlikely that many, if any, turtles are able to breach even relatively low fencing if aluminum flashing is attached at the top. Digging behavior may not have been an issue during this experiment however; longer confinement may have been needed in order for digging behavior to begin. This information can be helpful for agencies, such as transportation departments, in deciding what types of barrier fencing to use.

There are some potential problems associated with fencing. Overall, depending on the fence type, fencing can be expensive to build, maintenance costs can be high, and aesthetics of wire fencing may be an issue. For turtles, if the mesh sizes are too large, hatchlings and juveniles can pass through or get stuck in the openings. Therefore, smaller mesh attached to the bottom of larger mesh fences is necessary (Evink 2002). Fencing should be buried to minimize the chance of turtles breaching the fencing by digging. The type, dimensions, and materials used for barrier fencing should be dictated by the needs of the species of most concern in the project area.

In general, more studies are needed to find the most effective and low cost fencing so that a system of crossing structures and barriers will likely be successfully implemented and maintained. Some specific questions that need to be addressed include whether and how far turtles will follow fencing and if there are specific conditions that cause turtles to turn away from fencing rather than travel along them.

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Biographical Sketch: Kathleen Griffin is currently a Ph.D. candidate in the Wildlife Biology Program, College of Forestry and Conservation, University of Montana in Missoula, MT. Her current research focuses on population dynamics and movements of freshwater turtles in Montana.

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APPENDIX C. Road Mortality Data for All Species.

The following table and graphs depict all road mortalities encountered during road mortality surveys along Highway 93 from 2002 to 2004. Surveys were conducted along a (6.4-km [4-mile] stretch between Gunlock-Olson Road and Beaverhead Lane.

Roads within the study area were walked approximately once a week from mid-May through late August, 2003-2005. In 2002, surveys were conducted between mid-July and mid-September. In 2003 and 2004, surveys began in mid-May and continued through mid-September with 1 final survey the first week of October. Crews walked each side of the roadways simultaneously and documented all dead vertebrates. Animal locations were referenced to approximately evenly spaced (0.16 km) numbered reflector posts along the highway. These road markers start at 1.0 at Gunlock-Olson Road and are approximately 160 m apart. See Figure 5 in the main document for details on marker locations.

All road mortality counts are considered minimum counts because there is no information on the probability of recovery of road killed individuals. For example, some animal carcasses may have been removed from the highway by scavengers or blown off before being counted.

Table C-1. The number of individual animals (not including turtles) found during road mortality surveys along a 6.4 km section of Highway 93 in the Ninepipe/Ronan area from 2002 through 2004.

Road Location	Reptiles-Amphibians[1/]			Birds[2/]			Small Mammals			Medium Mammals[3/]			Large Mammals[4/]	Grand Total
	2002	2003	2004	2002	2003	2004	2002	2003	2004	2002	2003	2004	2003	
1	0	0	0	1	2	2	0	2	3	0	1	0	0	11
2	0	0	0	2	2	0	0	2	1	0	2	1	0	10
3	0	0	0	7	5	1	0	0	1	0	1	1	0	16
4	0	1	0	0	3	1	3	1	0	0	0	0	0	9
5	1	0	0	7	4	0	0	1	0	0	2	0	0	15
6	0	1	1	9	7	2	0	2	2	1	2	1	0	28
7	1	2	0	9	5	0	0	0	0	0	0	0	0	17
8	0	0	0	15	6	4	1	0	1	2	1	0	0	30
9	0	0	0	22	18	11	1	1	2	0	0	1	0	56
10	2	0	1	8	11	2	0	1	0	0	1	0	0	26
11	0	0	1	3	6	1	0	1	0	2	1	1	0	16
12	2	0	0	1	2	2	2	0	2	2	2	1	0	16
13	0	0	0	1	4	0	0	0	0	0	1	0	0	6
14	0	1	0	3	0	2	0	0	1	2	5	0	0	14
15	0	1	0	0	2	0	0	0	0	0	1	1	0	5
16	0	0	0	4	1	1	0	0	0	1	4	1	0	12
17	0	3	0	0	9	2	0	1	0	3	1	0	0	19
18	0	6	0	1	5	1	0	0	0	1	3	1	0	18
19	0	5	1	1	1	0	1	0	2	1	2	1	1	16
20	0	4	0	0	1	1	1	0	0	0	2	0	0	9
21	0	1	0	1	0	0	0	0	0	0	0	0	0	2
22	0	0	0	3	0	2	0	0	0	1	3	1	0	10
23	0	1	0	4	1	0	0	0	1	1	2	0	0	10
24	0	0	0	3	1	0	0	0	3	0	2	0	0	9
25	0	0	4	1	2	3	0	0	0	0	0	1	0	11
26	0	1	0	2	1	1	0	0	0	2	6	0	0	13
27	0	0	0	4	3	2	0	0	0	0	5	0	0	14
28	0	2	1	2	3	0	1	0	0	0	0	0	0	9
29	1	1	0	8	1	0	1	0	1	0	4	0	0	17
30	0	1	1	7	0	0	1	0	0	3	1	0	0	14
31	0	0	0	9	2	1	0	0	0	2	2	0	0	16
32	0	0	1	1	2	1	0	0	0	1	3	0	0	9
33	0	0	0	1	4	0	0	1	1	1	1	1	0	10
34	1	1	0	3	5	0	0	0	0	1	0	0	0	11
35	0	0	0	0	3	0	0	0	0	2	0	0	0	5
36	0	0	0	0	1	1	0	1	0	0	1	0	0	4
37	1	3	0	4	1	0	0	0	0	1	0	0	2	12
38	0	0	0	4	1	0	0	1	0	1	0	0	0	7
39	1	1	0	2	2	0	0	0	0	0	1	0	0	7
40	0	10	0	5	0	1	2	0	0	0	0	0	0	18
41	0	6	0	8	5	1	0	1	0	2	1	0	0	24
42	0	0	0	2	1	1	0	0	0	1	0	0	0	5
43	0	1	1	0	1	1	0	0	0	0	0	0	0	4
44	0	2	1	0	0	0	1	0	0	2	0	0	0	6
45	0	0	0	1	0	2	0	0	0	0	1	0	0	4
46	0	1	0	1	0	0	0	1	0	0	0	0	0	3
47	0	0	0	2	2	2	0	1	0	0	0	0	0	7
48	0	0	0	1	1	0	0	0	0	0	0	0	0	2
49	0	0	0	2	1	0	0	3	0	0	0	0	0	6
50	0	0	0	0	0	0	0	0	1	0	0	0	0	1
51	0	2	0	1	1	1	0	0	0	0	0	0	0	5
52	0	1	0	1	6	1	1	1	0	0	0	0	0	11
53	0	0	0	0	3	2	0	0	0	0	2	0	0	7
54	0	1	0	1	0	0	0	0	0	0	0	0	0	2
Subtotal	10	60	13	178	148	56	16	22	22	36	67	13	3	644
Total Across Years	83			382			60			116			3	644

1/ Reptiles/Amphibians does not include turtles (see main report for details on turtles). All mortalities but 1 (amphibian) were snakes.

2/ Birds. Swallows made up the greatest number (57) while blackbirds (41) and pheasants (30) were next abundant in mortality.

3/ Medium mammals includes badgers, skunks, canines, cats, weasels, muskrats. The majority of road mortalities in this category were muskrats which accounted for 93 out of the 116 total.

4/ Large mammals consisted solely of deer species. This value may be low because deer could have been cleared from the road by transportation or safety agencies before being counted.

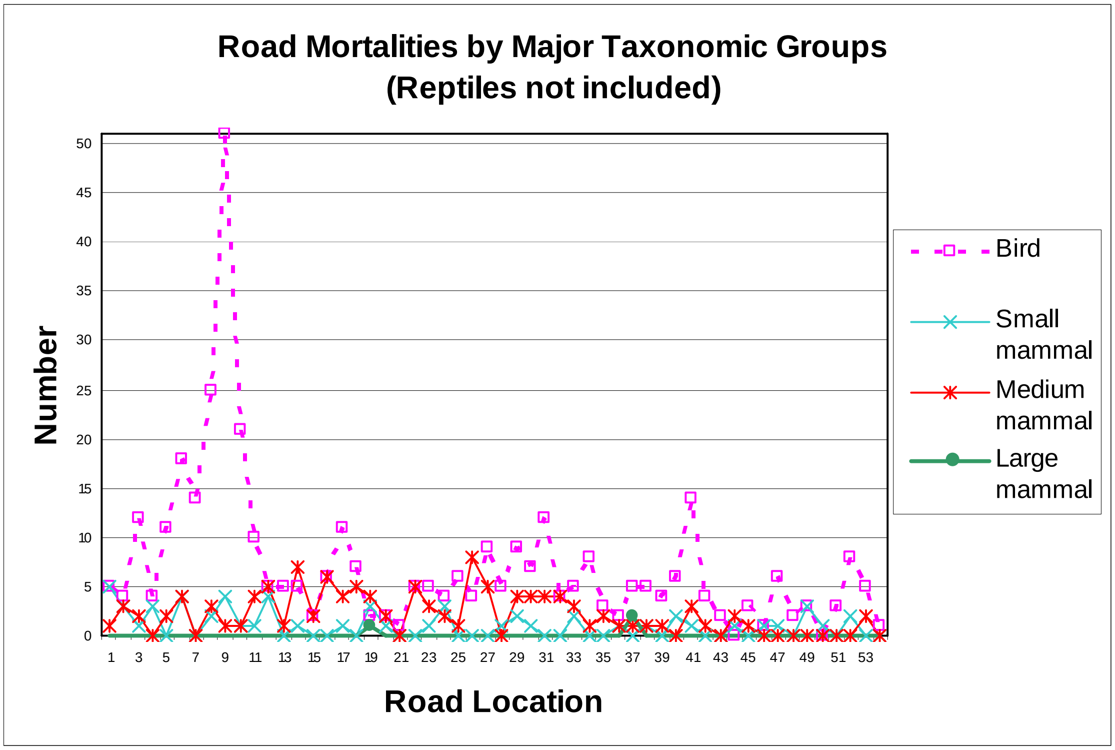

Figure C-1. The number of road mortalities of major taxonomic groups (no reptiles/amphibians) from 2002-2004 encountered along Highway 93 between Gunlock-Olson Road and Beaverhead Lane. Reptiles not included.

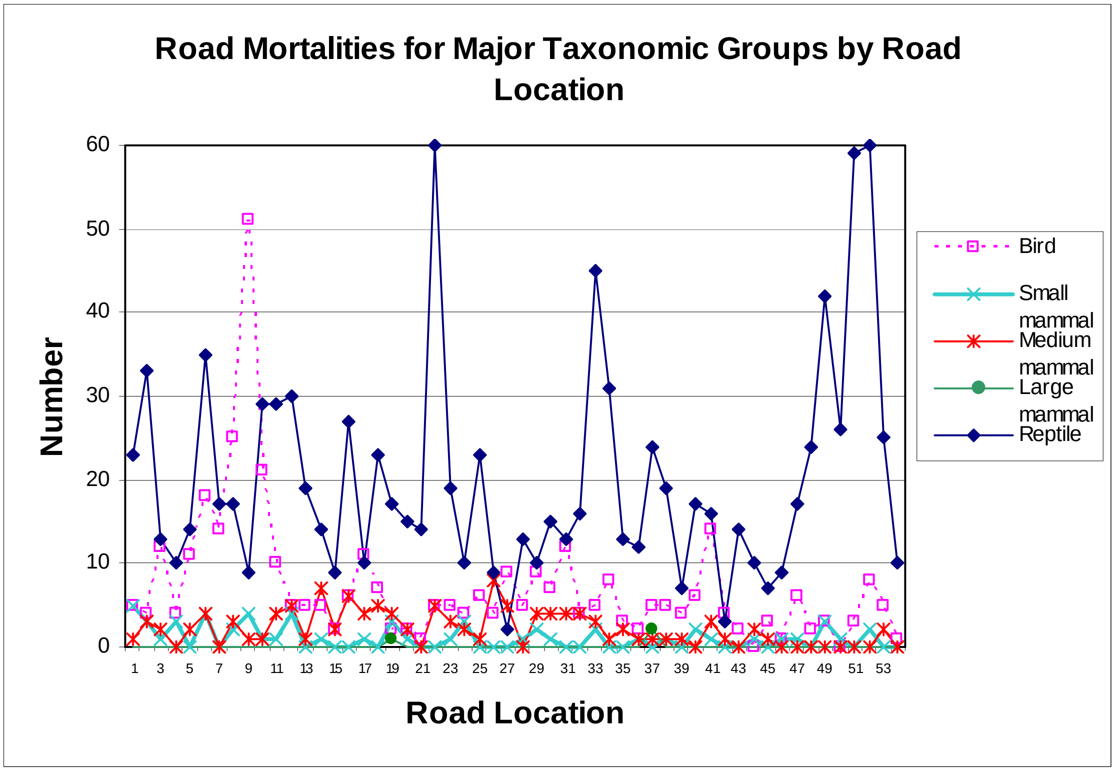

Figure C-2. The number of road mortalities of major taxonomic groups from 2002-2004 encountered along Highway 93 between Gunlock-Olson Road and Beaverhead Lane.