

UNIVERSITY OF CENTRAL OKLAHOMA  
Edmond, Oklahoma  
College of Graduate Studies & Research

**MORPHOLOGY AND DEMOGRAPHY OF SONORAN MUD TURTLES  
(*KINOSTERNON SONORIENSE*) ALONG AN AQUATIC HABITAT  
PERMANENCE GRADIENT**

A THESIS

SUBMITTED TO THE GRADUATE FACULTY

In partial fulfillment of the requirements

For the degree of

MASTER OF SCIENCE IN BIOLOGY

By

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Edmond, Oklahoma

2009

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APPROVED FOR THE DEPARTMENT OF BIOLOGY

**December 2009**

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## ACKNOWLEDGEMENTS

There are many people for whom I would like to thank for their contributions because without them this project would not have been possible. Specifically, I would like to thank all the field assistants who volunteered their time and effort in New Mexico. Specifically, this list includes Ken Locey (who camped with me for four months in the Peloncillo Mountains), Marie Babb-Stone, Zachary Stone, Roxie Hites, Matt Curtis, Sandra Thomas, Whitney Johnson, Erica Becker, Curtis Behenna, and Kelly Smith. I would also like to thank the many students who assisted in the sorting and identification of invertebrates in the lab. Specifically, this list includes Erica Gentry, Shay Still, Adam Gardner, and Leah Bates-Albers. I would like to thank the Gault, Hadley, and McDonald families for providing land access and encouraging our efforts. I would like to thank Dr. Phil C. Rosen for lending me the SBNWR dataset. I would like to thank the Department of Biology at UCO for allowing me to be a teaching assistant and adjunct during this process. I would like to thank the Joe C. Jackson College of Graduate Studies and Research for financial support. I would like to thank my friends and family for their continued love and support during these last few years.

I would like to thank all the members of my committee; Dr. David Bass for his continued assistance in the identification of invertebrates, and for letting me use his equipment both in the lab and in the field, Dr. Chris Butler for his continued assistance with statistical analyses, all things computer program related, and for his assistance in the field. Finally, I would like to thank my major advisor Dr. Paul Stone, who has done so many things for me that they are too numerous to list. Most importantly I would like to thank him for serving as my mentor but also for being a great friend.

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## ABSTRACT

Aquatic habitats exist along a permanence gradient and are characterized by the degree of interactions between abiotic (desiccation) and biotic (predation) factors, which are identified as characteristics that regulate body size and population demographics. Sonoran mud turtles (*Kinosternon sonoriense*) occur in aquatic habitats that span the permanence gradient and are potentially impacted by environmental variables associated with these habitats. I sampled aquatic habitats in the Peloncillo Mountains (32°12'N, 108°60'W) and classified them as ephemeral, intermittent, or permanent. I investigated the influence of aquatic habitats on body size, population density, and juvenile recruitment of Sonoran mud turtles. Body size was significantly larger in turtles from permanent aquatic habitats. Juvenile recruitment was related to population density and was highest in intermittent aquatic habitats. These data reflect a distribution pattern that favors intermittent aquatic habitats with desiccation and predation limiting populations in ephemeral and permanent aquatic habitats, respectively. The Sonoran mud turtle is listed as a vulnerable species and my research identifies anthropogenic factors threatening habitat sustainability and population viability.



## I. INTRODUCTION

Many freshwater organisms are impacted by the permanence of an aquatic habitat (Wellborn et al., 1996; Dodds, 2002). Permanence ranges along an ecological axis from small ephemeral habitats to large permanent habitats (Wellborn et al. 1996). Whether modeling lentic or lotic freshwater habitats, aquatic regimes can be classified according to a permanence transition (Wellborn et al., 1996). The permanence transition describes the boundary that separates temporary aquatic habitats from permanent aquatic habitats. Due to temporal variability, it is difficult to classify permanence from a glance. Therefore, invertebrate assemblages and fish are often used as bioindicators of permanence (Wellborn et al., 1996; Williams, 1996). Fish, which need permanent water to survive, are sometimes keystone predators that play important roles in structuring prey assemblages (Wellborn et al., 1996). Generally, temporary aquatic habitats lack fish and have short hydroperiods. Permanent aquatic habitats commonly support fish populations and have long hydroperiods.

Nutrient availability and productivity are often positively correlated with increasing permanence (Skelly, 1995; Wellborn et al., 1996). Permanent aquatic habitats are stable and have high resource availability, whereas temporary aquatic habitats are relatively unstable and have varying resource availability (Skelly, 1995; Wilbur, 1997). However, productivity can be high in temporary aquatic habitats. For example, when dry habitats are refilled, it results in the release of many nutrients and minerals, and thus provides an explosion of resources (Skelly, 1995; Wilbur, 1997). However, these resources become limited as the habitat is reduced (Wilbur, 1997). Habitat duration is important in determining species colonization, reproduction, and survival (Wellborn et

al., 1996). Successful occupants of temporary aquatic habitats are able to utilize the habitat before it becomes unsuitable.

Risks of temporary aquatic habitats include mortality due to habitat loss and reduced fitness due to limited resources (Crump, 1989; Leips et al., 2000; Hamer et al., 2002). Desiccation is the primary abiotic factor affecting fitness and it can eliminate a species altogether (e.g. fish) from a habitat that completely dries. Temporary aquatic habitats have limited hydroperiods which limits resource availability (Wilbur, 1987). Reduction in resources combined with increased competition may limit body size, growth, population density, and survival (Wilbur, 1987; Skelly, 1995; Wellborn et al., 1996; Adams, 2000). For example, many anurans display rapid growth in order to attain optimal size before the habitat vanishes. Although growth is rapid, smaller terminal body size is attained when compared to permanent aquatic habitats, where resources and growth are steady, eventually resulting in larger terminal body size (Skelly and Werner, 1990; Skelly, 1995). However, temporary aquatic habitats provide refuge, enabling prey species to reproduce and grow without threats from top predators (Smith, 1983; Woodward, 1983; Wilbur, 1987; Skelly and Werner, 1990). Therefore, anurans such as *Bufo americanus*, *Rana pipiens*, and *Hyla versicolor* (Collins and Wilbur, 1979) and some coleopterans (Dytiscidae) may concentrate efforts on breeding in temporary aquatic habitats (Merritt and Cummins, 1996).

Permanent aquatic habitats harbor increased number and diversity of predators (Woodward, 1983). Increased predation may reduce prey population density, increase prey mortality, and even cause local extinctions (Murdoch and Bence, 1987; Sih et al., 1992). In permanent aquatic habitats, predation is the strongest biotic factor affecting

growth (Reznick and Endler, 1982; Brown and DeVries, 1985; Skelly, 1995), body size (Figiel and Semlitsch, 1990; Skelly and Werner, 1990), population density (Smith, 1983; Bendell, 1986; Sih et al., 1992), reproduction (Smith, 1983; Brown and DeVries, 1985), and survival (Reznick and Endler, 1982; Woodward, 1983; Hamer et al., 2002; Gunzburger and Travis, 2004). In high predation environments, prey often decrease activity and increase use of refugia, which may negatively impact growth and reproduction (McPeck, 1990; Tikkanen et al., 1996). Predation is usually the primary biotic factor influencing prey attributes (Woodward, 1983; Bendell, 1986; McPeck, 1990; Ortubay et al., 2006). Competition is an important biotic factor (Wilbur, 1984), but it appears to be secondary in comparison to predation, except when occupant densities are high and there are no primary predators (Bendell, 1986).

Predators play a crucial role in structuring prey assemblages. Naturally occurring predator-prey communities have co-evolved and often persist together. Introduced predators can decimate native assemblages and are responsible for declining native populations worldwide (Vitousek et al., 1997; Chapin III et al., 2000). Exotic fish species are one of the most well-studied and harmful introductions (Lachner et al., 1970). The concentrated effort of government, state, and local agencies, and the careless and/or ignorant acts of citizens have combined to intentionally transplant or introduce non-native fish species to many of the freshwater ecosystems of North America for the purposes of angling (Lachner et al., 1970). Introduced fish species either directly or indirectly affect many organisms in the ecosystem (Lachner et al., 1970). For example, introduced fish are indirectly responsible for reducing avian populations by reducing the avian prey base in steppe lakes of Patagonia (Ortubay et al., 2006).

Semi-aquatic organisms usually must select between temporary aquatic habitats and permanent aquatic habitats. Organisms that require aquatic habitats for some portion of their life cycle are presented with a suite of trade-offs associated with choosing either type of aquatic habitat: Is it better to reproduce and live in a more productive environment with an increased risk of predation and competition or an environment with limited resources but low risk of predation and competition? Do individuals avoid predators by only reproducing in resource-limited aquatic habitats or do individuals tolerate predation because they cannot survive the short hydroperiod of temporary habitats? Such trade-offs are recognized by examining species distribution patterns along a permanence axis (Wellborn et al., 1996).

Species distribution patterns along the aquatic permanence axis are influenced by species-specific responses to predation and competition (Smith, 1983; Woodward, 1983; Reznick and Endler, 1982; Werner and McPeck, 1994; Skelly, 1995) and the challenges of desiccation (Skelly, 1996; Wellborn et al., 1996). Several studies have examined biological variation of species across an aquatic permanence gradient (Woodward, 1983; Skelly and Werner, 1990; Werner and McPeck, 1994; Skelly, 1995; Lardner, 2000). However, freshwater turtles have received little attention in this regard, despite documented variation in demography and life history characteristics (Iverson, 1977; Congdon et al., 1983; Mitchell, 1988). Freshwater turtles are likely impacted by biological and environmental changes associated with the permanence axis. Turtles living in permanent aquatic habitats interact with fish as potential predators (Cagle, 1950), prey (Gibbons, 1970), or competitors (Chessman, 1988). Turtles with affinities for temporary

aquatic habitats must have adaptations for terrestrial survival, due to the increased likelihood of encountering a desiccating habitat (Ligon and Peterson, 2002).

Many studies have investigated aquatic turtles in fluctuating aquatic habitats (Gibbons, 1970; Moll, 1990; Iverson, 1991; Buhlmann and Gibbons, 2001; Stone, 2001; Tuma, 2006) but rarely have these studies made comparisons across a permanence axis. Some aquatic turtles are confined to permanent aquatic habitats, such as the river cooter (*Pseudemys concinna*), which only leaves the water to nest and bask (Ernst et al., 1994). All turtle species inhabiting environments that risk drying must be adapted for extended terrestrial activity (i.e. migration and/or estivation). Terrestrial activity associated with drying habitats may be a response to adverse conditions that include desiccation, increased water temperature, competition, and predation (Bennett et al., 1970; Wygoda, 1979; Buhlmann and Gibbons, 2001). Of the aquatic turtle species that are capable of extended terrestrial activity, some of the most successful belong to the genus *Kinosternon*, the mud turtles. There are 18 recognized species of *Kinosternon*, which are distributed throughout the Western hemisphere (Iverson, 1992a). Twelve kinosternids are known to occupy temporary aquatic habitats (Ernst and Barbour, 1989) and at least nine are known to migrate or estivate (Ernst and Barbour, 1989; Ernst et al., 1994). Most *Kinosternon* are capable of complete shell kinesis, which aids in predator defense (Bramble et al., 1984) and promotes water conservation (Wygoda and Chmura, 1990). The proclivity for extended terrestrial activity allows some mud turtles to exploit aquatic habitats only when water is available (Iverson, 1989). As conditions worsen, turtles migrate to new habitats (Moll, 1990) or estivate until conditions improve (Buhlmann and Gibbons, 1991; Ligon and Stone, 2003a; Tuma, 2006). Mud turtles inhabit both

permanent and temporary aquatic habitats ranging from rivers and lakes to small ephemeral pools and streams (Ernst et al., 1994). However, studies of mud turtle natural history suggest a tendency to favor temporary aquatic habitats (Bennett et al., 1970; Gibbons, 1970; Wygoda, 1979; Iverson, 1991; Morales-Verdeja and Vogt, 1997; Stone, 2001). While this distribution pattern is well-documented, few studies have aimed at determining why mud turtles favor temporary habitats.

The Sonoran mud turtle (*K. sonoriense*) is a relatively small turtle, with carapace lengths ranging up to 17.5 cm (Ernst et al., 1994). Sonoran mud turtles are distributed throughout central Arizona, southwest New Mexico, and northern Sonora (Ernst et al., 1994). A few disjunct populations once occurred in southeast California (Ernst et al., 1994); however, these populations are likely extinct (Jennings, 1983). Sonoran mud turtles inhabit slow moving rivers, streams, stock tanks, springs, and ephemeral ponds but are mostly absent from large lakes and rivers (Hulse, 1974; Rosen, 1987; Ernst et al., 1994; Stone, 2001). The Sonoran mud turtle is an opportunistic carnivore, generally feeding on invertebrates (Hulse, 1974), but occasionally may take vertebrate prey (Ligon and Stone, 2003b; Stone et al., 2005b, Stanila et al., 2008). Therefore, habitats with large invertebrate assemblages are probably preferred habitat (Hulse, 1974). However, Sonoran mud turtles may shift towards omnivorous feeding when benthic fauna is limited (Hulse, 1974). Original reports describe Sonoran mud turtles as “totally aquatic” (Hulse, 1974), but recent evidence contradicts this description (Peterson and Stone, 2000; Stone, 2001; Ligon and Peterson, 2002; Ligon and Stone, 2003a). Laboratory experiments have shown that Sonoran mud turtles are capable of estivation and rivaled yellow mud turtles (*K. flavescens*), which in other experiments has gone up to two years without water (Peterson

and Stone, 2000; Rose, 1980). Ligon and Peterson (2002) concluded that Sonoran mud turtles from New Mexico are physiologically more adapted for estivation than ones from Arizona. Individuals used in estivation experiments were collected from a perennial spring (AZ) and an intermittent stock tank (NM) and therefore, may reflect differences in habitat permanence and not geography.

Despite reports of Sonoran mud turtles occurring frequently in temporary aquatic habitats and evidence of terrestrial activity such as estivation, asynchronous behavior, and overland migrations (Stone, 2001; Ligon and Stone, 2003a, Hall and Steidl, 2007), most research has been conducted in aquatic habitats that have permanent water (Hulse, 1974; Rosen, 1987; Van Loben Sels et al., 1997; Rosen et al., 2005). The lack of studies focused in temporary aquatic habitats suggests that an investigation into permanence related variation is warranted. Recent research on Sonoran mud turtles has been focused on its estivation capabilities (Peterson and Stone, 2000; Ligon and Peterson, 2002; Ligon and Stone, 2003a), demographics (Stone, 2001), life history characteristics (Rosen, 1987; Van Loben Sels et al., 1997), and spatial movements (Hall and Steidl, 2007).

The aim of my study is to investigate micro-geographic variation of the Sonoran mud turtle across a permanence axis. I will examine two questions in this study. First, do increased negative biotic interactions impact Sonoran mud turtle populations, either through competition or predation? And second, do resource limitations via limited hydroperiods negatively impact Sonoran mud turtle populations? I address these questions by examining Sonoran mud turtles in aquatic habitats along a permanence axis and by comparing variation in morphology and demography. These characteristics are important in determining the success of populations, and have shown variation along the

permanence axis in studies of other fauna (Werner and McPeck, 1994; Wellborn et al., 1996). I derived two hypotheses from the literature that predict outcomes across the permanence axis. These hypotheses focus on the trade-off associated with living in specific aquatic habitats.

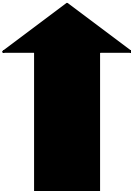
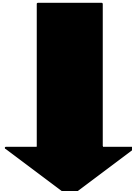
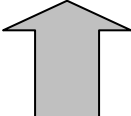
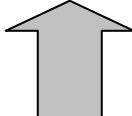


The biotic limitation hypothesis predicts that aquatic habitats with increased biotic interactions (i.e. competition and predation) will result in negative responses in Sonoran mud turtles, whereas a release from biotic interactions will result in positive responses in Sonoran mud turtles. The abiotic limitation hypothesis predicts reduced resource availability via reduced hydroperiods will result in negative responses in Sonoran mud turtles, whereas increased resource availability due to increased hydroperiods will result in positive responses in Sonoran mud turtles. Therefore, predictions can be made across the permanence axis for permanent, intermittent, and ephemeral aquatic habitats.

In permanent aquatic habitats, the biotic limitation hypothesis predicts decreases in body size, population density, and juvenile recruitment due to increased negative biotic interactions. The abiotic limitation hypothesis predicts increases in body size, population density, and juvenile recruitment in permanent aquatic habitats due to increased resource availability through increased hydroperiods. In intermittent aquatic habitats, the biotic limitation hypothesis predicts increases in body size, population density, and juvenile recruitment due to reduced negative biotic interactions. The abiotic limitation hypothesis also predicts increases in body size, population density, and juvenile recruitment in intermittent aquatic habitats due to increased resource availability during the wet seasons. In ephemeral aquatic habitats, the biotic limitation hypothesis predicts increases in body size, population density, and juvenile recruitment due to reduced negative biotic



interactions. The abiotic limitation hypothesis predicts decreases in body size, population density, and juvenile recruitment in ephemeral aquatic habitats, due to decreased resource availability through decreased hydroperiods (Table 1).

However, the predictions also form gradients. The biotic limitation hypothesis predicts increases in body size, population density, and juvenile recruitment for ephemeral and intermittent aquatic habitats due to decreased biotic interactions. Therefore, body size, population density, and juvenile recruitment in ephemeral aquatic habitats should be greater than those in intermittent aquatic habitats, because there are likely increased biotic interactions in intermittent aquatic habitats compared to ephemeral aquatic habitats. Likewise, the abiotic limitation hypothesis predicts increases in body size, population density, and juvenile recruitment for intermittent and permanent aquatic habitats due to increased resource availability through increased hydroperiods. Therefore, body size, population density, and juvenile recruitment in permanent aquatic habitats should be greater than those in intermittent aquatic habitats because permanent aquatic habitats have longer hydroperiods and therefore would have increased resource availability compared to intermittent aquatic habitats (Table 1).

<b>Permanence</b>	<b>Parameters</b>	<b>Biotic Limitation Prediction</b>	<b>Abiotic Limitation Prediction</b>
<i>EPHEMERAL</i>	Body size		
	Population density		
	Juvenile recruitment		
<i>INTERMITTENT</i>	Body size		
	Population density		
	Juvenile recruitment		
<i>PERMANENT</i>	Body size		
	Population density		
	Juvenile recruitment		

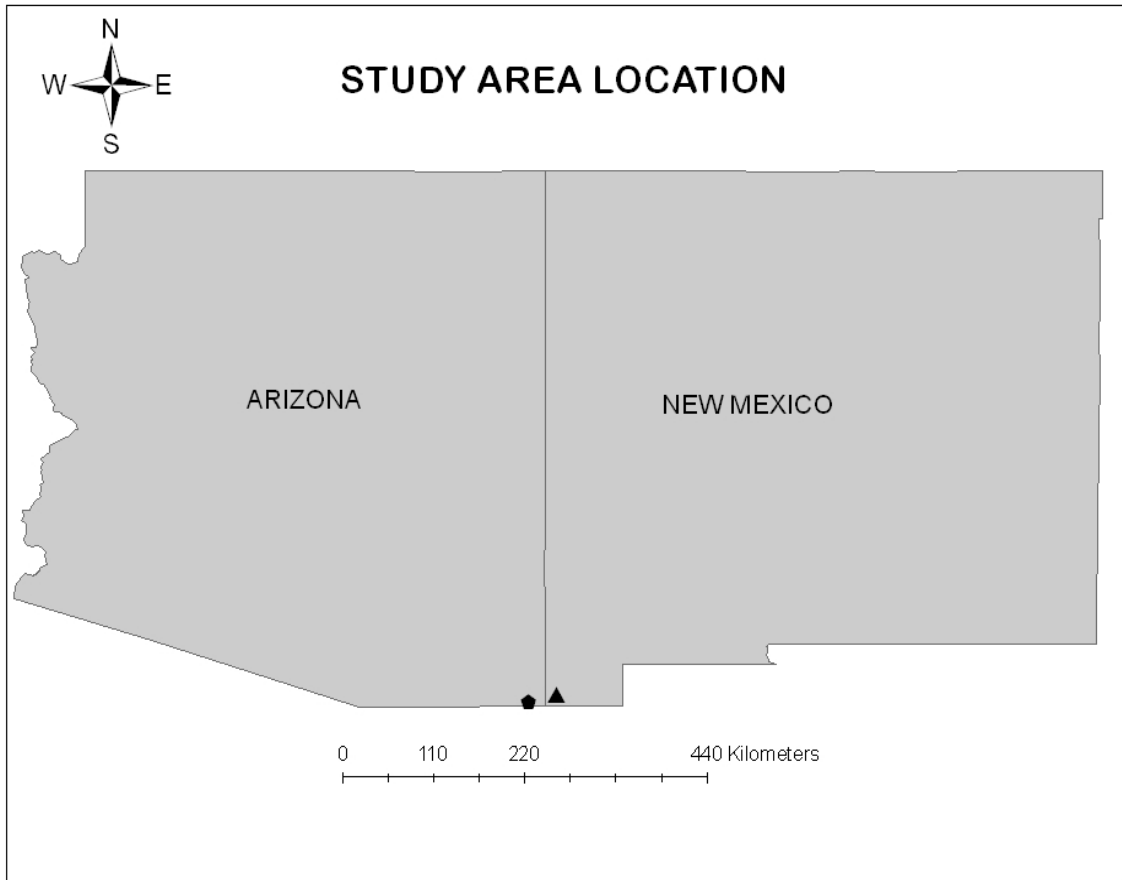
**TABLE 1.** Predictions for body size, population size, and juvenile recruitment according to abiotic and biotic limitation hypotheses. Large dark arrows represent an increase or decrease in the associated variable and smaller gray arrows indicate a relative reduction compared to larger arrows pointing in the same direction.

## II. MATERIALS AND METHODS

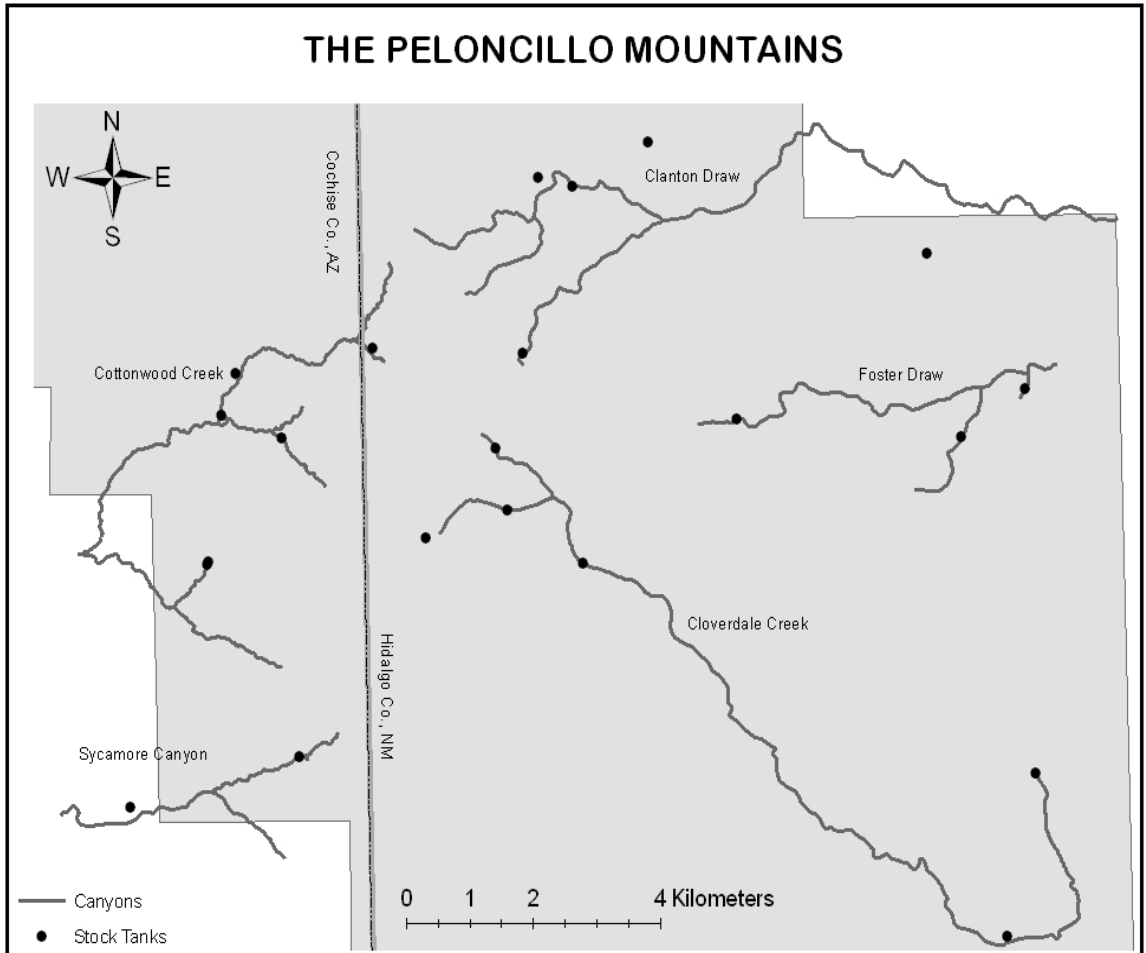
### STUDY AREA

The study area was located in the Peloncillo Mountains (32°12'N, 108°60'W), Hidalgo County, New Mexico and Cochise County, Arizona (Figure 1 and 2). The Peloncillo Mountains run north-south approximately 110 km along the New Mexico-Arizona border, and into the northern portion of Sonora, Mexico. The Peloncillo Mountains are characterized by rugged, rocky, and narrow canyons that empty into the Animas Valley and the San Bernardino Valley to the east and west, respectively. Within the study area there are three distinct watersheds; the Animas, Cloverdale, and Sonoran hydrological basins, which support a number of creeks and draws (Bodner et al., 2003). The Peloncillo Mountains are part of the San Madrean Archipelago, which consist of pine-oak and oak savanna woodland mountain ranges separated by “seas” of semi-arid chaparral, Chihuahuan desert-scrub, short-grass prairie, and desert grasslands. The range also lies at the boundaries of the Sonoran and Chihuahuan Deserts, the Great Plains, and the Great Basin (Bodner et al., 2003). In fact, the southern portion of the Peloncillo Mountains was recently named a Global Diversity Hotspot by Conservation International (Bodner et al., 2003).

Weather conditions are variable within the range, and from year to year. Mean maximum monthly temperatures occur in June and July (23-24° C) and mean minimum monthly temperatures occur in December and January (6-7° C) (Moir et al., 2000). The Peloncillo Mountains experience bi-seasonal precipitation patterns that oscillate between Sonoran and Chihuahuan. A Sonoran pattern is most common with the majority of precipitation occurring in the winter and summer monsoon season, while spring (March-



**FIGURE 1.** Locations of the main study areas. The Peloncillo Mountains (triangle) extend along the state boundary, between Hidalgo Co., New Mexico and Cochise Co., Arizona. The San Bernardino National Wildlife Refuge (pentagon) is located 12 km west of the Peloncillo Mountains in Cochise Co., Arizona.



**FIGURE 2.** The Peloncillo Mountain study area is located mostly within the Coronado National Forest (grey outline). I sampled every stock tank within this area. I did not sample all canyon reaches but those near stock tanks were sampled.

June) and fall receive very little precipitation. Occasionally, a Chihuahuan precipitation pattern occurs with concentrated precipitation during the summer monsoon season (Bodner et al., 2003). Seasonal variation in precipitation increases the likelihood of drought during arid periods, with the most severe droughts usually occurring prior to the onset of the summer monsoon (Bodner et al., 2003).

A majority of the Peloncillo Mountains are owned and managed by the USDA Forest Service, Arizona and New Mexico State Land Departments, and Bureau of Land Management. However, a small portion of the Peloncillo Mountains is privately owned by ranchers. Cattle are grazed on both public and private land. The Peloncillo Mountains are remote with only one dirt road and a few four-wheel drive trails. Non-native fish such as largemouth bass (*Micropterus salmoides*), green sunfish (*Lepomis cyanellus*), longear sunfish (*L. megalotis*), and redear sunfish (*L. microlophus*) have been introduced.

I classified aquatic habitats as permanent, intermittent, and ephemeral. I based classifications on personal communications, hydroperiod scores, and bio-indicators. Hydroperiod scores were determined by dividing the number of times a study site had water by the number of times a study site was visited (Roe and Georges, 2008). Perennial aquatic habitats had a perfect score of 1.0, intermittent aquatic habitats had a score of 0.99-0.50, and ephemeral aquatic habitats had a score of < 0.5 (Roe and Georges, 2008). Hydroperiod scores were useful in separating intermittent from ephemeral aquatic habitats. Ephemeral aquatic habitats gain water via precipitation and runoff and have limited hydroperiods that persist temporarily after precipitation. Intermittent aquatic habitats are defined as having hydroperiods that persist throughout the wet seasons but evaporate during the dry seasons (Pielou, 1998). Due to the temporally short duration of

my study (3 years) and because the bulk of my study efforts were conducted during the monsoon season, some study sites are potentially falsely classified. To assist in permanence classification, I contacted local ranchers (Seth Hadley, Bill McDonald, and Meira Gault), Coronado National Forest Rangeland Managers (Gary Helbing, Marcello Martinez, Glen Klingler, and Joseph Harris), New Mexico Game and Fish Director (Charlie Painter), and Wildlife Refuge Manager (Bill Radke). All of these individuals have worked or live within the study area, and have extensive knowledge of historical water levels. For example, Meira Gault revealed that Buckhorn Tank has gone dry several times during the past 10 years, although it did not completely dry during my study. I also used several bio-indicators such as introduced fish, Chiricahua leopard frogs (*Rana chiricahuensis*), and emergent macrophytes. I considered personal communications more accurate than hydroperiod scores and bio-indicators because personal communications reflect historical permanence which is more meaningful to long-lived animals such as turtles.

Seasonal pools and stock tanks form the two basic types of aquatic habitats in the Peloncillo Mountains. Seasonal pools developed along canyon streambeds and were the direct result of precipitation. These pools were isolated, developed fast, and dried quickly (Stone, 2001). Seasonal pools were ephemeral, but persistent enough to support invertebrates, tadpoles (*Bufo punctatus* and *Hyla arenicolor*), and green algae (Division Charophyta). Emergent macrophytes and waterfowl were never observed in or near seasonal pools. However, bullhead minnows (*Pimephales vigilax*) were observed in pools along a canyon streambed in May 2007 but were absent two months later. Prior to this

observation, fish had never been documented in this canyon, and their occurrence was likely the result of winter flooding in the area.

Stock tanks were more persistent than seasonal pools and were created by reinforcing natural depressions with concrete, stone, or earthen dams. Stock tank permanence ranged from ephemeral to perennial. Several structural variations of stock tanks existed in the study area. First, some stock tanks were artificial impoundments (n=6) created by a dam bisecting the canyon streambed. Artificial impoundments were subject to flooding, especially after intense monsoon rainfall, and were also subject to desiccation, particularly during the arid seasons (Ligon and Stone, 2003a). Artificial impoundments were greatly influenced by precipitation and runoff, and were capable of filling after a single night of heavy rain (Ligon and Stone, 2003a). Artificial impoundments were capable of supporting invertebrate assemblages and algae. Rarely were fish or aquatic macrophytes observed. Only one artificial impoundment (Buckhorn Tank) supported fish (*L. cyanellus*) and aquatic macrophytes, and no other artificial impoundment supported either.

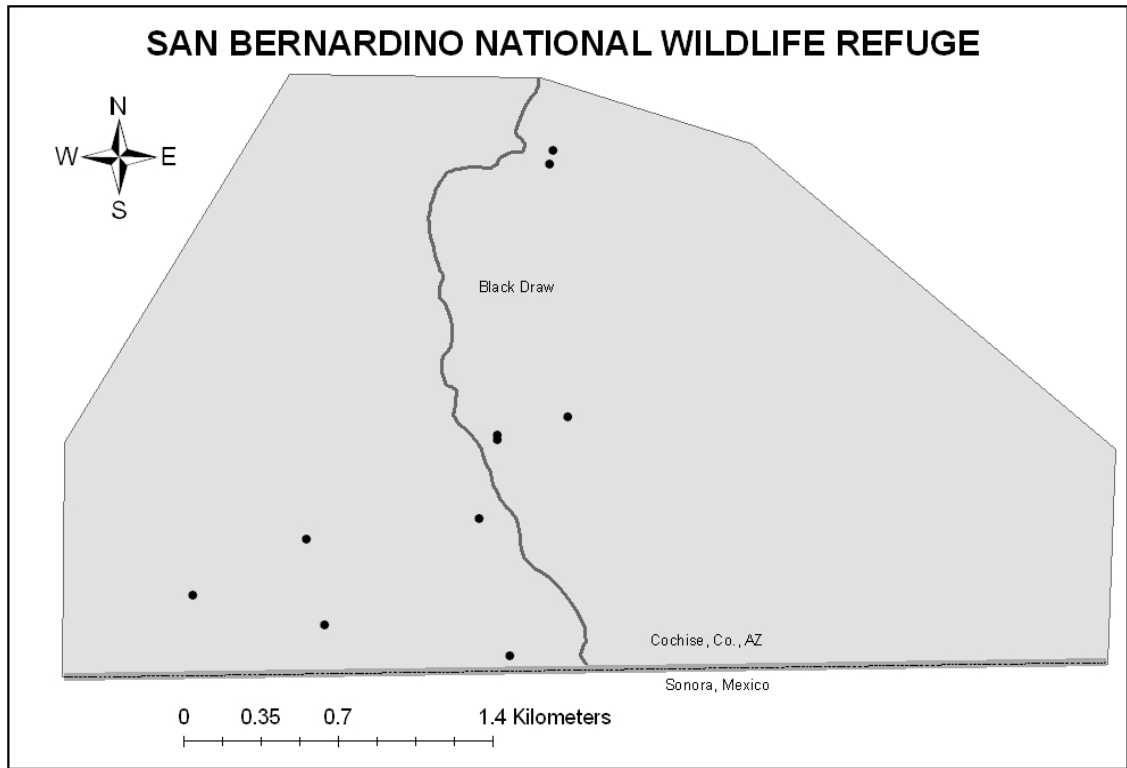
Second, stock tanks were built in open areas where local topography caused water to accumulate creating an artificial pond. Artificial ponds (n=3) spanned the permanence axis, were not associated with canyons, and never supported fish or emergent macrophytes. Artificial ponds were reinforced with small stone or earthen dams that acted to corral water and were mostly dependent on precipitation and runoff for filling. However, one pond (Stateline Tank) had a hydroperiod that persisted throughout the duration of the study and supported a reproducing population of Chiricahua leopard frogs. Stateline Tank lacked emergent macrophytes and terrestrial vegetation grew



around the perimeter of the habitat. Following heavy rains, the vegetation was flooded and possibly mimicked emergent macrophytes in terms of providing habitat and refugia for invertebrates.

Third, stock tanks were constructed at or near springs where groundwater seeped to the surface. Spring-fed stock tanks existed as small concrete tanks or as spring-fed ponds. Concrete tanks (n=4) were designed by ranchers to collect the majority of spring water that seeped from underground for the purpose of watering livestock. However, these were not considered optimal habitat because of their small size and the cement walls appeared to limit turtle entrance. Spring-fed ponds (n=4) were larger, deeper, and more permanent than all other types of stock tanks. Spring-fed ponds persisted annually and were not subject to rapid fluctuations in water levels. All spring-fed ponds supported introduced fish, invertebrate communities, aquatic vegetation, and waterfowl such as great blue herons (*Ardea herodias*), mallards (*Anas platyrhynchos*), and American coots (*Fulica americana*).

Data from the San Bernardino National Wildlife Refuge (SBNWR) was from three years (1997-1999) of a 20-year dataset that was obtained from Dr. Phil C. Rosen (University of Arizona, School of Natural Resources). Mark-recapture data at SBNWR is sparse with sampling occasions occurring once every few years. However, the three-year period (1997-1999) included intense sampling and it is these data that I will integrate into my analyses. The SBNWR is located near the western limits of the Peloncillo Mountains, Cochise Co., AZ (Figure 1 and 3). Aquatic habitats in the SBNWR consist of spring-fed ponds and an ephemeral draw that stretches approximately 1050 m. These spring-fed stock tanks are not connected to the draw. The SBNWR eradicated non-native fish



**FIGURE 3.** The San Bernardino National Wildlife Refuge study area located near the edge of the Peloncillo Mountains. Black Draw runs through the middle of the study area. No stock tanks are connected to Black Draw and all are classified as permanent spring-fed ponds.

populations in the 1970's and has since restored native fish populations and aquatic vegetation (Bill Radke, pers. comm.).

The Peloncillo Mountains probably contain several meta-populations of Sonoran mud turtles because of their ability to undergo long distance overland migrations (Stone, 2001; Ligon and Stone, 2003a, Stone, unpub. data). However, I am interested in local environmental factors directly associated with each study site. Therefore, I considered each study site a separate population if they were in different canyons, were separated by mountains, and showed little to no turtle migration between them. Three study sites (Javalina Tank, Maverick Spring, and Peloncillo Tank) were considered to be one population by my definition, and were treated as such in my analyses.

## TURTLES

### *Sampling*

Seven sampling trips were made from 17 May 2006 to 9 August 2008 (Table 2). During this period, 18 locations were sampled on a rotating schedule. Aquatic habitats were sampled with hoop nets, by hand, and with seines. Hoop nets were used to sample all stock tanks. Single and double-throated hoop nets ranged from 1.8-3.65 m in length, 0.6-1.2 m in diameter, and 2.5-3.8 cm in mesh size. In deep stock tanks (>2 m), hoop nets were placed around the perimeter of the aquatic habitat. In shallow stock tanks, hoop nets were placed throughout the aquatic habitat. Hoop nets were partially submerged so turtles could breathe after entering the net. The number of hoop nets used per stock tank varied, but generally the number of hoop nets used increased as a function of the increasing surface area of stock tanks. Hoop nets were almost always baited with sardines. Variation from this baiting strategy included; one week where raw chicken legs were used in place

<b>Sampling Trip</b>	<b>Date</b>	<b>Research Group</b>
1	17 May – 20 May 2006	Brian D. Stanila, Paul A. Stone, Marie E. Stone
2	27 July – 2 August 2006	BDS, PAS, MES, Zachary S. Stone, Kenneth J. Locey
3	31 August - 5 September 2006	BDS, KJL, PAS, John B. Iverson
4	15 May – 20 May 2007	BDS, PAS, MES, Roxie R. Hites, Matt S. Curtis
5	1 July – 13 October 2007	BDS, KJL
6	13 May – 20 May 2008	BDS, PAS, KJL, Erica C. Becker, Whitney L. Johnson
7	3 August - 9 August 2008	BDS, PAS, RRH, ECB, Curtis J. Behenna, Kelly A. Smith

**TABLE 2.** Sampling trips, range of dates of sampling trips, and field assistants.

of sardines, and two occasions in which hoop nets were baited with Vienna sausages and beef jerky. Nets were set and checked within 24 hours; this constituted one trap night. Hand collecting or “noodling” was used exclusively to sample canyon pools and sometimes used to sample shallow desiccating stock tanks. This consisted of actively searching the habitat with our hands. Hoop netting and “noodling” are common sampling techniques used for studying mud turtle populations (Iverson, 1991; Van Loben Sels et al., 1997; Stone, 2001). Occasionally, seines (3 m by 1.83 m with 0.62 cm mesh size) were used to sample stock tanks that were too shallow for hoop nets but were too large to effectively hand sample. Seines were dragged through all sections of the habitat.

### *Processing*

All turtles were marked and/or identified by a unique series of notches filed in the marginal scutes of the carapace (Cagle, 1939). However, hatchling turtles initially batch marked were only given a unique number after their midline carapace length (MCL; see below) reached at least 40 mm. For each capture, several parameters were recorded including date, location, age, sex, and trap type. Shell dimensions were recorded to the closest 0.1 mm using SPI 2000 dial calipers. Shell measurements included; MCL, midline plastron length (MPL); greatest carapace width (GCW), greatest plastron width (GPW), and shell height (SH). Of these, MCL is the most accurate shell measurement for body size (Iverson, 1985; Stone, 2001). Body mass was measured to the nearest gram with Pesola scales. Sex was determined by sexually dimorphic characteristics, particularly the enlarged tail and indented plastral hinge of males (Ernst et al., 1994). Female Sonoran mud turtles attain sexual maturity at a minimum of 86 mm MCL (Rosen, 1987). No data have been collected on minimum age or size at maturity for the study population.

Therefore, all turtles <86 mm are considered juveniles, unless obviously male (Rosen, 1987; Stone, 2001).

### *Body Size*

In some kinosternid populations there is evidence of sexual size dimorphism (SSD). Generally, the trend is for males to attain larger body size than females (Cox et al., 2007). If my study populations exhibited SSD, males and females would need to be analyzed separately in interpopulational comparisons. If SSD is not exhibited, males and females can be grouped together. To test for SSD, I pooled all body size data and ran a Mann-Whitney rank sum test with MCL as the dependent variable and sex as the independent variable. Consistent with the general trend, males (n= 259, mean  $\pm$  se =  $118.8 \pm 1.14$  mm) were slightly larger than females (n=326,  $116.7 \pm 0.9$  mm) however, these differences were not significant (Z=-1.04, P=0.29). Therefore, I pooled males and females together and categorized them as adults. Body size data appeared positively skewed and failed the Shapiro-Wilk's normality test (P<0.05). Body size data also failed Bartlett's test for homoscedasticity (P<0.05). Therefore, non-parametric tests were used for body size analyses. I compared variation in adult body size across the permanence axis using a Kruskal-Wallis analysis of variance of ranks, with MCL as the dependent variable and permanence classification as the independent variable. Dunn's method was used to determine significant differences among all pair-wise comparisons.

I also compared the relative variation of body size in my study area to that range wide. I used body size data already reported in the literature (Hulse, 1974; Rosen, 1987; Van Loben Sels et al., 1997). I used a coefficient of variation (CV) to make this comparison.

### *Population Size, Habitat Area, and Population Density Estimates*

I used Program MARK (White and Burnham, 1999) to estimate population size and recruitment in turtle populations based on mark-recapture encounter histories. Encounter histories were divided into sampling intervals and the individual turtle was recorded as either absent or present during a sampling interval. A sampling interval was any complete sampling of the study site/population. Captures from incomplete sampling intervals were omitted from these analyses. Sampling intervals varied in length but most lasted three to four days. No new sampling interval was started without at least a three-day hiatus from a previous sampling interval. This ensured ample time for turtles to respond to being captured and handled (Stone et al., in review).

I used a version of the Jolly-Seber open population model known by the acronym POPAN. I used POPAN because it analyzed gross population size ( $N$ ) and allowed for death, recruitment, immigration, and permanent emigration (Arnason and Schwartz, 1999). POPAN uses the encounter histories of uniquely marked individuals from all sampling intervals to make estimations. Specifically, POPAN calculates the probability of survival ( $\Phi$ ), which is the probability that an individual will survive from one sampling interval to the next sampling interval; the probability of recapture ( $p$ ), which is the probability that if the individual is alive, it will be captured during the sampling interval; and the probability of entrance ( $pent$ ), which is the probability of new individuals entering the sampling area during a given sampling interval (Burnham and Anderson, 2002). Furthermore, any of these parameters ( $\Phi$ ,  $p$ ,  $pent$ ) can be categorized temporally as dependent ( $t$ ) or independent of time ( $.$ ). Using the POPAN model structure, I created sub-models and let the probability of survival, recapture, and entrance vary between time

dependent and time independent. Eight sub-model variations were analyzed with MARK and the sub-model with the lowest Akaike's Information Criterion (AIC) was selected as the most parsimonious, following the recommendation by Burnham and Anderson (2002). I used the gross population size (N) computed by MARK as my population size estimate.

For one population (Stateline Tank) I used the Lincoln-Pearson with Bailey's Modification population size estimation because the number of individuals captured was too small (only five) to accurately run in Program MARK, despite eight sampling occasions resulting in 51 trap nights. Lincoln-Pearson with Bailey's Modification works well with samples under 20 and is based on two sampling occasions (Bailey, 1951). Therefore, I grouped captures into prior monsoon and after monsoon sampling occasions.

Habitat area estimates were determined by measuring the total surface area of water in the habitat (canyon pools or stock tank) at a given time. While this estimate disregards terrestrial refugia, it does represent the most logical estimate of habitat because most Sonoran mud turtle activities are conducted in water (Hulse, 1974; Emslie, 1982; Rosen, 1987; Van Loben Sels et al., 1997; Stone, 2001; Ligon and Stone, 2002; Hall and Steidl, 2007). Habitat area data were collected using the tracks function on a Garmin eTrex Vista Cx Global Positioning System (GPS). For both stock tanks and seasonal pools the perimeter of the aquatic habitat was mapped with GPS ( $\pm 4$  m resolution). In some instances, seasonal pools were too small to accurately map ( $<16$  m<sup>2</sup>) and therefore, were classified as either small ( $\leq 1$  m<sup>2</sup>), medium (1-8 m<sup>2</sup>), or large (8.1-16 m<sup>2</sup>). For a series of pools or pool complexes, the number of small, medium, and large pools were counted while pools exceeding 16 m<sup>2</sup> were mapped. These data were



imported into a Geographic Information System (GIS), where polygons were traced around all large pools and stock tanks. Surface area estimates were derived using the area calculator in Hawth's Tools <<http://www.spatial ecology.com/htools>> (Beyer, 2004), an extension of ArcGIS.

The habitat area of SBNWR tanks were estimated in a different manner. Area estimates were derived from an ortho-image of Cochise Co., AZ (2007, UTM, NAD 1983, Zone 12N) provided by the National Agricultural Imagery Program. This image was imported into a GIS, on which polygons of observable tanks were traced. Images were cross-referenced with Phil Rosen to ensure accuracy. SBNWR habitat area estimates were derived using the area calculator in Hawth's Tools (Beyer, 2004). All habitat area estimates estimated in ArcGIS were converted from square meters (m<sup>2</sup>) to hectares (ha).

Population densities were derived by dividing population estimates into habitat area estimates and are reported as turtles/ha. Population densities are dynamic and change as a function of habitat area (Connor et al., 2000). Aquatic habitat area was subject to fluctuations in water level, ranging between flooding and complete desiccation, which would create unreliable and undefined population densities, respectively. Therefore, I report population density using the highest habitat area estimates recorded (non-flood) for every location. This consisted of times when the majority of canyon pools held water and stock tanks were full, which is normal for the monsoon season. This is the most biologically meaningful because of increased turtle activity during persistent hydroperiods (Emslie, 1982; Van Loben Sels et al., 1997; Stone, 2001; Ligon and Stone, 2003a). Population density data appeared non-normal but passed Shapiro-Wilk's

normality test ( $P > 0.05$ ) and failed Bartlett's homoscedasticity test ( $P < 0.05$ ). Therefore, I used non-parametric statistics for population density analyses. I compared variation in high water population densities across a permanence axis using a Kruskal-Wallis analysis of variance of ranks, with turtles/ha as the dependent variable and permanence classification as the independent variable. Dunn's method was used to determine significant differences among all pair-wise comparisons.

### *Juvenile Recruitment*

Accurate juvenile recruitment estimates were unable to be derived using Program Mark because unique markings were needed to detect presence and absence during sampling intervals. Therefore, juvenile recruitment was estimated as the number of sub-adults observed at each study site. For the purpose of this analysis sub-adults were considered to be hatchlings, young of year (YOY), and juveniles. Hatchlings were identified by the presence of an egg tooth and yolk scar, and had little to no growth. YOY were identified by the absence of both yolk scar and egg tooth, and had noticeable growth. Juveniles were individuals  $< 86$  mm that were unable to be accurately sexed and were not obviously male (Rosen, 1987; Stone, 2001). Juvenile recruitment data appeared non-normal and failed Shapiro-Wilk's normality test ( $P < 0.05$ ) and Bartlett's test for homoscedasticity ( $P < 0.05$ ). Therefore, I used non-parametric statistics. I compared variation in sub-adult abundance across a permanence axis using a Kruskal-Wallis analysis of variance of ranks, with sub-adults serving as the dependent variable and permanence classification as the independent variable. Dunn's method was used to determine significant differences among all pair-wise comparisons.

## INVERTEBRATES

### *Sampling*

I sampled permanent (n=4) and intermittent (n=5) stock tanks for invertebrates to estimate resource availability. I used an aquatic D-loop net with 500 micron mesh to sample emergent macrophytes for invertebrates. The D-loop net was placed in, underneath, and around all aquatic vegetation. The net was shaken vigorously in order to dislodge any invertebrates among the vegetation. I sampled all the different types of aquatic vegetation observed at each study site and around the perimeter of each tank. If no aquatic vegetation existed, then no sample was taken. Net collecting effort was timed with a stopwatch only during active agitation. Time spent collecting invertebrates ranged from 2 min–3 min 45 sec, and the mean time spent collecting was 2 min 37 sec. In some cases, I sampled flooded terrestrial vegetation because I believed it served a similar purpose as emergent aquatic vegetation. The core sampler consisted of a PVC pipe (3.8 cm diameter by 15.2 cm length) and a rubber stopper. The core sampler was shoved into the sediment as deep as possible, plugged with the rubber stopper (creating suction), and removed from the sediment. At least five core samples were obtained at each site per visit. Both methods are common techniques used for sampling freshwater invertebrates (Merritt and Cummins, 1996; Voshell, 2002).

Once collected, all samples were washed in a Watermark sieve bucket (#30) and stored in 500 ml and 1L plastic Nalgene wide-mouthed jars and 1L Wheaton wide-mouthed glass jars with 70% ETOH. I collected a total of 122 core samples and 19 net samples from nine different locations. All samples were brought back to the lab for sorting and identification. In the lab, samples were washed through a U.S. standard soil

sieve (#35) and remnants were placed in a Gage plastic sorting tray (45 cm by 31 cm). Samples were examined and sorted, with all potential invertebrates separated into glass vials and stored in 70% ethanol for further identification. Sorting effort for core samples ranged from 15 – 90 min, with an average core sample sorting effort of 28 min. Sorting effort for net samples ranged from 60 – 520 min, with an average net sample sorting effort of 224 min. After sorting, contents were placed under a dissecting microscope and invertebrates were counted and identified to family or lowest possible taxon. I used Pennack (1953), Merritt and Cummins (1996), and Voshell (2002) to identify invertebrates. Invertebrates were not identified to similar taxonomic level and therefore are referred to as other taxonomical units (OTU).

Invertebrate diversity and abundance were assumed to be indicators of resources for two reasons: (1) invertebrates are the main food source for Sonoran mud turtles (Hulse, 1974) and (2) high resources would be required to support substantial invertebrate diversity. Invertebrate diversity was determined using software (EcoSim; Gotelli and Entsminger, 2004) created for the purpose of measuring species diversity and related indexes. Invertebrate abundance is measured using indexes created from core samples and aquatic vegetation samples.

Invertebrate diversity was analyzed using EcoSim, which runs boot-strapping simulations from random samples of the overall dataset. EcoSim uses abundance based data to determine species richness, which is the number of species in a given sample. However, for my analyses I used OTU richness, which is the number of OTU's in a given sample. EcoSim also determines species abundance, which is the number of individuals among species from a given sample. Again, I substituted OTU for species. Richness and

abundance are two components of species diversity and are needed in generating rarefaction curves (Hurlbert, 1971). A rarefaction curve is a statistical technique that compares richness from samples of different sizes and controls for the number of individuals (Hurlbert, 1971). A rarefaction curve results in a plot of the species richness (in this case OTU richness) as a function of the number of individuals sampled (evenness). A steep slope in a rarefaction curve suggests that a large portion of the species have not been sampled. A flattened slope indicates that a large portion of individuals have been sampled. Two rarefaction curves are significantly different if 95% confidence intervals (CI) do not overlap, while curves with overlapping 95% CI are not significantly different (Hurlbert, 1971). I compared OTU rarefaction curves between permanence classifications (perennial and intermittent) to determine variation in OTU diversity.

Invertebrate abundance was estimated using two indexes created from core and aquatic vegetation samples. To estimate benthic fauna abundance, all invertebrates from core samples were sorted, counted, and divided by the total number of core samples taken (invertebrates/core). To estimate littoral fauna abundance all individuals from aquatic vegetation samples were sorted, counted, and divided by the number of seconds spent sampling (invertebrates/sec). I did this to correct for unequal sampling effort due to variation in habitat area and vegetation composition of study sites. I used these indexes to examine the differences in benthic and littoral organism abundance between permanence regimes. Data appeared non-normally distributed and failed Shapiro-Wilk's normality test ( $P < 0.05$ ) and Bartlett's test for homoscedasticity ( $P < 0.05$ ). I used a Mann-Whitney

rank sum test to determine variation in number of invertebrates/core and number of invertebrates/sec between permanent and intermittent aquatic habitats.

### **III. RESULTS**

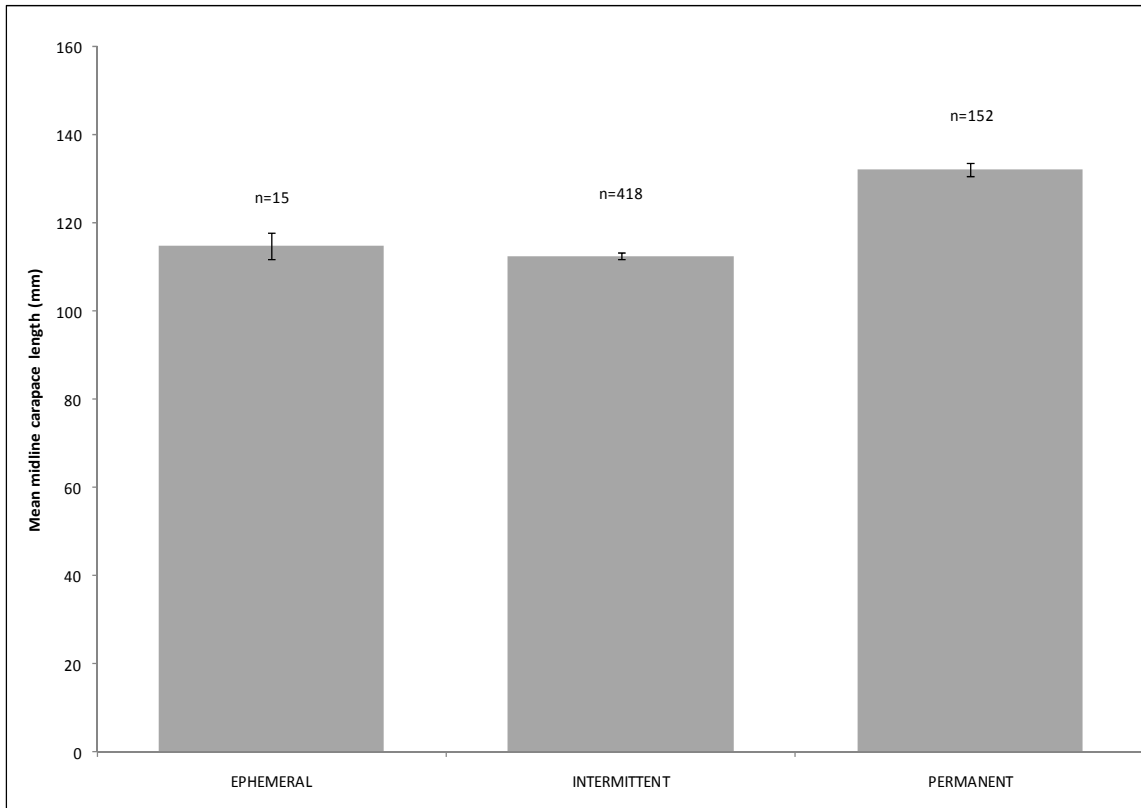
#### **TURTLES**

Seven trips were taken to the study area from 17 May 2006 to 9 August 2008 (Table 2). There were 1791 captures of 843 individual Sonoran Mud Turtles. Sampling effort included a conservative estimate of 1730 hours spent hand sampling and 569 trap nights. Of the 843 individuals captured, there were 185 males and 295 females. There was a significant female-biased sex ratio (1.6:1,  $\chi^2=27.58$ ,  $df=1$ ,  $P<0.001$ ). The remaining individuals captured were juveniles ( $n=119$ ) and hatchlings ( $n=244$ ). Of the 1791 total captures, 933 (52%) were captured by hoop net, 842 (47%) were captured by hand, 13 (<1%) were found dead, two were captured by seine, and one was a ranch owner's pet found as a hatchling, and was marked and released into the wild as a juvenile. Of the 18 study sites, three yielded no captures, five yielded <10 captures, four yielded 10-50 captures, and five yielded >50 captures. No other turtle species was captured microsympatrically.

Similar summary data are available for the SBNWR. During 1997-1999, 109 individuals were captured 307 times at the SBNWR. Of the 109 individuals captured, 74 were male, 31 were female, and four were juveniles. There was a significant male-biased sex ratio at the SBNWR (2.4:1,  $\chi^2=17.6$ ,  $df=1$ ,  $P<0.001$ ). No hatchlings were captured at the SBNWR. Of the 307 total captures, nearly all were made with hoop nets ( $n=304$ ); the remaining three captures were made by hand. Trapping methods consisted mostly of baited hoop netting.

### *Body Size*

Despite the geographic proximity of the study sites, MCL varied significantly among adults ( $H=218.02$ ,  $df=13$ ,  $P<0.0001$ ). Per population, MCL of adults (mean  $\pm$  se) ranged from  $106.1 \pm 0.99$  mm to  $135.7 \pm 1.7$  mm. Variation in body size among populations appears to be related to permanence. In permanent habitats, body size was  $132.1 \pm 1.5$  mm ( $n=152$ ) and ranged from 80.0 mm to 165.7 mm. In intermittent habitats, body size was  $112.5 \pm 0.7$  mm ( $n=418$ ) and ranged from 81.4 mm to 159.0 mm. In ephemeral habitats body size was  $114.7 \pm 3.0$  mm ( $n=15$ ) and ranged from 89.1 mm to 141.9 mm. Adult body size significantly varied across the permanence axis according to a Kruskal-Wallis test ( $H=121.2$ ,  $df=2$ ,  $P<0.001$ ). Dunn's method revealed that adult body size was significantly larger in permanent habitats compared to intermittent ( $P<0.05$ ) and ephemeral habitats ( $P<0.05$ ), with no significant difference between intermittent and ephemeral habitats ( $P>0.05$ ) (Figure 4). Turtles from perennial habitats were on average nearly 19 mm larger than turtles from intermittent habitats or ephemeral aquatic habitats and the largest maximum size was recorded from a permanent aquatic habitat. The coefficient of variation (CV) of body size within the Peloncillo Mountains ( $SD=11.3$ ,  $mean=121$  mm,  $CV=9.3$ ) is similar to the CV of body size throughout the entire range of Sonoran mud turtles ( $SD=13.2$ ,  $mean=128$  mm,  $CV=10.3$ ).



**FIGURE 4.** Mean midline carapace length (MCL  $\pm$  se) of Sonoran Mud Turtles in the Peloncillo Mountains, New Mexico and Arizona. Sample size listed above error bars. Turtles from permanent habitats were significantly larger than turtles from intermittent ( $P < 0.05$ ), and ephemeral aquatic habitats ( $P < 0.05$ ). Adult mean body size from was not significantly different between intermittent and ephemeral habitats ( $P > 0.05$ ).

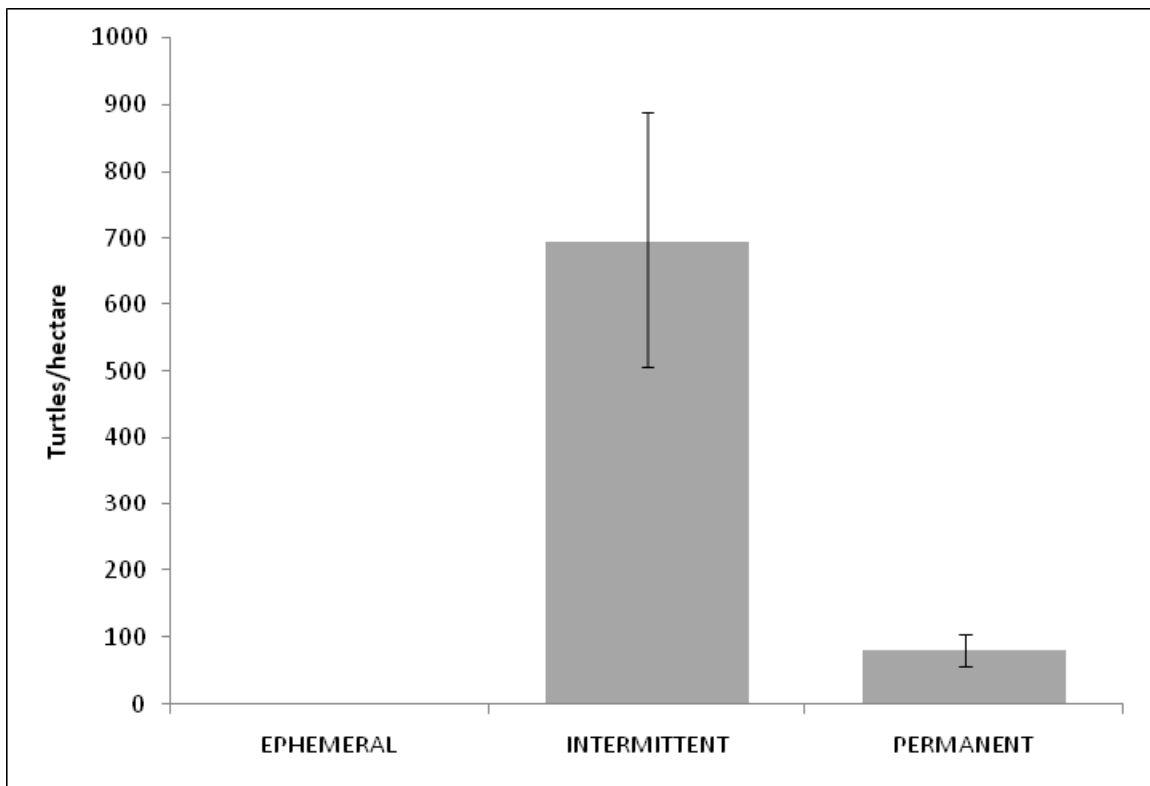


## *Demography*

I estimated population size and density for five intermittent, five permanent, and two ephemeral study sites. Population size estimates (pop. est.  $\pm$  se) ranged from  $41.8 \pm 18.3$  to  $437.7 \pm 132.7$  turtles/ha for intermittent study sites and 0 to  $159.7 \pm 10.5$  turtles/ha for permanent study sites (Table 3). I could not estimate the population size of four ephemeral study sites due to few captures and a lack of recaptures during separate sampling occasions. Population size and density was zero for one perennial and two ephemeral study sites. Population densities at intermittent study sites during high water periods ranged from 215-1305 turtle/ha and mean population density was estimated at  $696.6 \pm 191.4$  turtles/ha. Population densities at permanent study sites ranged from 0 to 123 turtles/ha and mean population density was estimated at  $80.7 \pm 23.2$  turtles/ha. Population density significantly varied across the permanence axis according to a Kruskal-Wallis test ( $H=9.065$ ,  $df=2$ ,  $P<0.001$ , Figure 5). Dunn's method revealed that intermittent study sites had significantly higher population densities than ephemeral ( $Q=2.652$ ,  $P<0.05$ ) and ( $Q=2.28$ ,  $P<0.05$ ). Permanent and ephemeral aquatic habitats were not significantly different ( $Q=0.93$ ,  $P>0.05$ ) but the trend was for higher densities at perennial study sites. Ephemeral aquatic habitats lacked population density estimates due to a paucity of captures.

SITE	Permanence	N	95 % CI	Model	Density	Sub-Adults
Black CCC (31.50° N, -108.95° W)	Ephemeral	0	0		0	0
Prospect Tank (31.48° N, -109.05° W)	Ephemeral	0	0		0	0
Blackwater Hole (31.49° N, -109.02° W)	Intermittent	337.7	267-408	Phi(.)P(t)pent(t)	867	132
Buckhorn Tank (31.48° N, -108.94° W)	Intermittent	168.6	162-175	Phi(.)P(t)pent(t)	378	41
Horse Pasture Tank (31.44° N, -108.93° W)	Intermittent	94.1	72-116	Phi(t)p(.)pent(t)	717	9
Miller Canyon, NM (31.47° N, -109.02° W)	Intermittent	437.7	178-698	Phi(.)p(t)pent(t)	1305	143
Swahili Tank (31.48° N, -108.98° W)	Intermittent	41.8	6-78	Phi(.)P(t)pent(t)	215	8
Clanton Tank (31.52° N, -108.99° W)	Permanent	0	0		0	0
Cloverdale Spring (31.41° N, -108.94° W)	Permanent	44.4	20-69	Phi(.)p(.)pent(t)	59	3
Geronimo Seep Tank (31.52° N, -109.01° W)	Permanent	24.5	15-33	Phi(.)p(.)pent(.)	120	0
SBNWR (31.34° N, -109.26° W)	Permanent	159.7	139-180	Phi(.)p(t)pent(t)	102	5
Stateline Tank (31.49° N, -109.04° W)	Permanent	5	3-7	Lincoln-Pearson	123	0

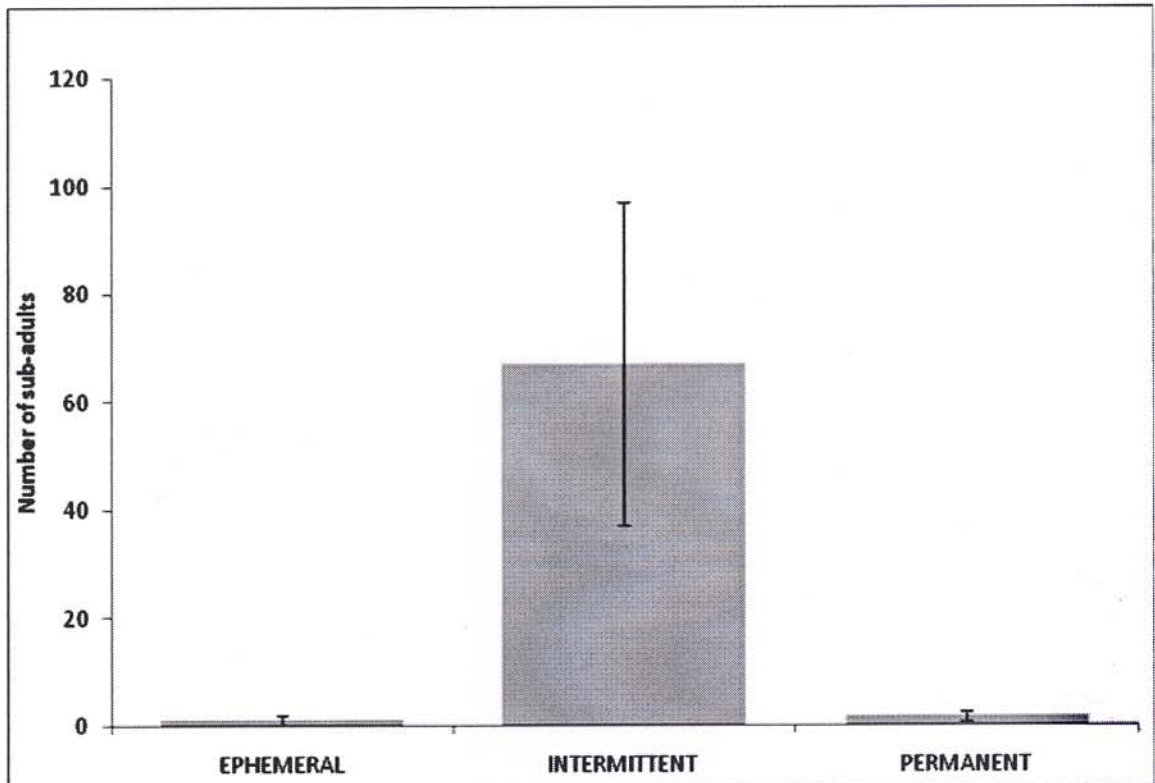
**TABLE 3.** Population size, density estimates, and juvenile recruitment for Sonoran mud turtles in Peloncillo Mountains, New Mexico and Arizona. Study sites are sorted by permanence classification with locations (NAD 83, Lat/Long) for 12 study sites. Population size (N) and 95% CI as derived from population models in Program MARK. Density estimates derived from population size divided by amount of surface area (ha).



**FIGURE 5.** Mean population density (pop. density  $\pm$  se) of Sonoran mud turtles in the Peloncillo Mountains, New Mexico and Arizona. Graph presents density estimates of two ephemeral, five intermittent, and five permanent populations. Population density varied across the permanence axis ( $P < 0.001$ ). Population density was significantly higher in intermittent aquatic habitats compared to ephemeral ( $P < 0.05$ ) and permanent aquatic habitats ( $P < 0.05$ ). Population density estimates in permanent and ephemeral aquatic habitats were not significantly different ( $P > 0.05$ ).

### *Juvenile recruitment*

Sub-adults were captured less frequently than adults and were completely absent from several study sites classified as permanent or ephemeral (Table 3). In permanent habitats, the number of sub-adult captures ranged from 0 to 5 and averaged  $1.6 \pm 1.0$  sub-adults per study site ( $n=5$ ). Permanent aquatic habitats had three study sites with zero captures and two study sites with less than five. In ephemeral aquatic habitats, the number of sub-adult captures ranged from 0 to 4 ( $n=6$ ), with one ephemeral study site (Cedar Tank) having four sub-adult captures, while all other ephemeral study sites had zero sub-adult captures. In intermittent aquatic habitats, the number of sub-adult captures ranged from 8 to 143 and averaged  $66.6 \pm 29.6$  per study site ( $n=5$ ). A Kruskal-Wallis analysis showed that sub-adult abundance varied significantly across the permanence axis ( $H=11.3$ ,  $df=2$ ,  $P=0.004$ ). Dunn's method revealed that sub-adult abundance was significantly higher in intermittent aquatic habitats compared to perennial ( $Q=2.424$ ,  $P<0.05$ ) and ephemeral aquatic habitats ( $Q= 2.977$ ,  $P<0.05$ ). Sub-adult abundance was not significantly different between ephemeral and perennial habitats ( $Q=0.445$ ,  $P>0.05$ , Figure 6). A Spearman rank correlation revealed a significant positive relationship between juvenile recruitment and both population size ( $r_s=0.93$ ,  $df=10$ ,  $P<0.0001$ ) and population density ( $r_s=0.86$ ,  $df=10$ ,  $P=0.0003$ ).



**FIGURE 6.** Sub-adult abundance (mean  $\pm$  se) in aquatic habitats of the Peloncillo Mountains, New Mexico and Arizona. The number of sub-adults captured was significantly higher in intermittent habitats compared to ephemeral ( $P < 0.05$ ) and permanent aquatic habitats ( $P < 0.05$ ). There was no significant difference in the number of captures between ephemeral and permanent habitats ( $P > 0.05$ ).

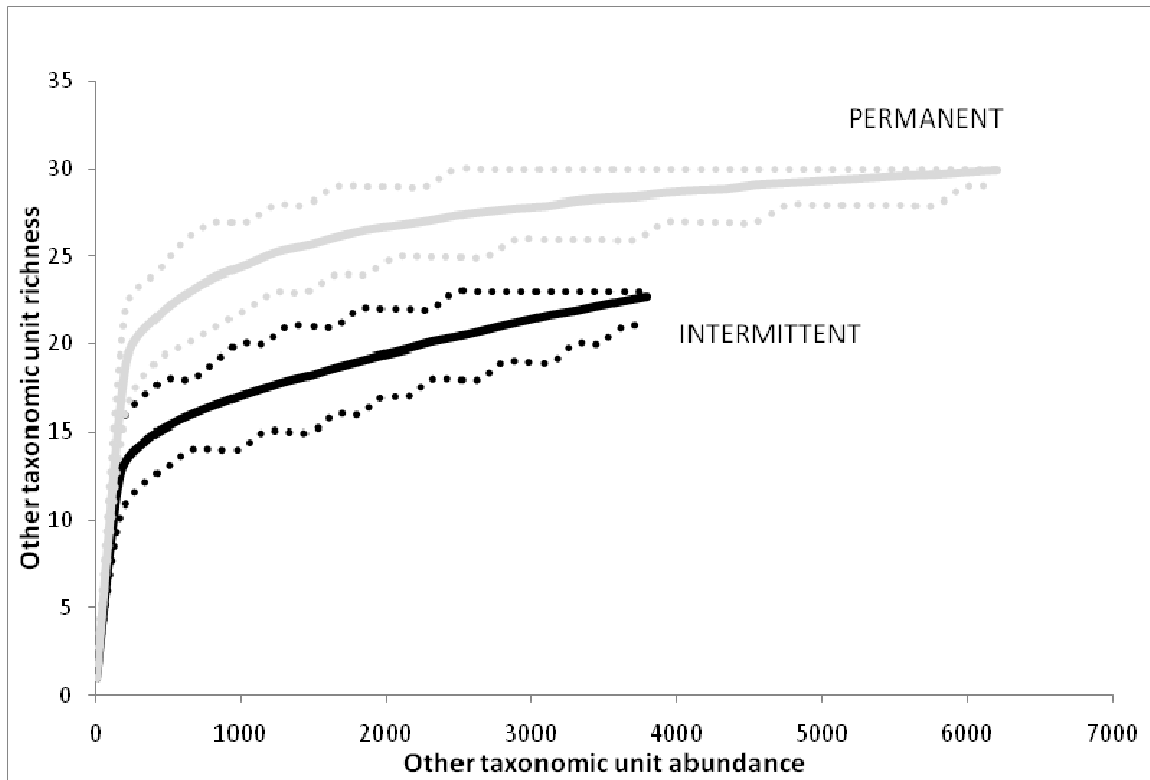
## INVERTEBRATES

I sampled four permanent and five intermittent stock tanks for invertebrates. Rarefaction curves revealed that OTU diversity was significantly higher in permanent habitats compared to intermittent habitats ( $P < 0.05$ ) (Figure 7). Taxonomic comparisons reveal that intermittent habitats had a total of 23 different OTU's while permanent habitats had 30 different OTU's, eight of which were not present in intermittent habitats (Table 5). Only one OTU was not present in permanent aquatic habitats. These data support the rarefaction curve interpretation that OTU diversity is higher in permanent aquatic habitats. OTU diversity is unknown in ephemeral aquatic habitats. Only predacious diving beetles (Dytiscidae), whirligig beetles (Gyrinidae), backswimmers (Notonectidae), water striders (Gerridae), and water boatmen (Corixidae) were consistently observed at ephemeral study sites. Based on these observations and the limited hydroperiods, diversity in ephemeral habitats is assumed lower than in intermittent and perennial habitats.

Abundance indexes indicated that intermittent aquatic habitats had similar benthic invertebrate abundance ( $13.2 \pm 4.4$  invertebrates/core) compared to permanent aquatic habitats ( $9.8 \pm 2.3$  invertebrates/core). A Mann-Whitney test indicated these data were not significantly different ( $U=11.0$ ,  $df=1$ ,  $P > 0.05$ ). Intermittent and permanent aquatic habitats had similar littoral abundance ( $3.3 \pm 1.3$  invertebrates/sec and  $3.4 \pm 1.3$  invertebrates/sec, respectively) and a Mann-Whitney test revealed these data were not significantly different ( $U=9.0$ ,  $df=1$ ,  $P > 0.05$ , Figure 8). Invertebrate abundance in ephemeral aquatic habitats is unknown, but the above mentioned invertebrates were observed in high numbers when water was present.

<b>Study Site</b>	<b>Core Samples (n)</b>	<b>Benthic Abundance</b>	<b>Net Samples (n)</b>	<b>Littoral Abundance</b>
Blackwater Hole	16	30.2	1	3.4
Buckhorn Tank	16	7.7	3	2.3
Clanton Tank	17	15.1	3	2.4
Cloverdale Spring	17	11.4	3	4.6
Geronimo Seep Tank	15	4.4	3	0.3
Horse Pasture Tank	7	12.2	1	1.4
Javalina Tank	13	5.5	2	1.4
Stateline Tank	14	8.3	2	6.1
Swahili Tank	7	10.4	1	8.1

**TABLE 4.** Study sites sampled for benthic and littoral fauna in the Peloncillo Mountains, NM. Benthic fauna abundance reported as mean number of invertebrates per core sample. Littoral fauna abundance reported as mean number of invertebrates captured per second sampled.

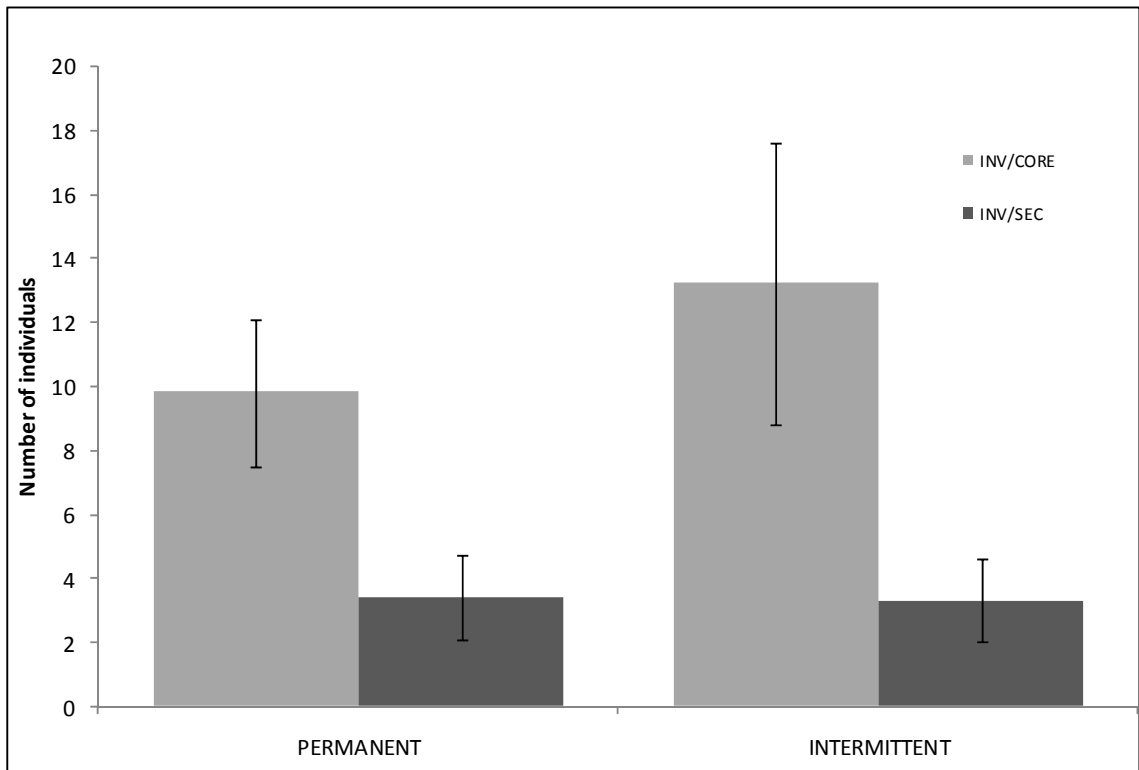


**FIGURE 7.** Rarefaction curves of invertebrate diversity in permanent and intermittent aquatic habitats of the Peloncillo Mountains, New Mexico. Solid lines represent the plot of OTU richness versus OTU abundance in intermittent and permanent aquatic habitats, with dotted lines representing the confidence intervals. Confidence intervals do not overlap and therefore, invertebrate diversity is significantly higher ( $P < 0.05$ ) in permanent aquatic habitats.



Other Taxonomic Unit	% Occurrence	
	Permanent	Intermittent
Chironomidae	45	43
Coenagrionidae	16	5
Baetidae	13	13
Oligochaeta	3	16
Dytiscidae	3	3
Aeshnidae	3	<1
Lestidae	3	2
Notonectidae	2	1
Amphipoda	2	0
Planorbidae	1	0
Halipidae	1	2
Hirudinea	1	<1
Ostracoda	1	1
Culicidae	1	6
Chaobridae	1	<1
Hydrophilidae	1	1
Siphonuridae	<1	0
Ceratopogonidae	<1	0
Tabanidae	<1	<1
Libellulidae	<1	1
Corixidae	<1	<1
Belostomatidae	<1	<1
Hydrachnida	<1	<1
Gerridae	<1	<1
Ephydriidae	<1	0
Gyrinidae	<1	0
Nepidae	<1	<1
Sialidae	<1	0
Dryopidae	<1	0
Veliidae	<1	0
Anastroca	0	7

**TABLE 5.** Taxonomic comparison of the frequency occurrence of OTU's in intermittent and permanent aquatic habitats. Only one OTU did not exist in permanent aquatic habitats that existed in intermittent habitats. However, there were eight OTU's absent from intermittent aquatic habitats.



**FIGURE 8.** Invertebrate abundance (mean  $\pm$  se) in aquatic habitats of the Peloncillo Mountains, New Mexico. Mean benthic fauna abundance (INV/CORE) did not significantly differ between intermittent and permanent aquatic habitats ( $P > 0.05$ ). Mean littoral fauna abundance (INV/SEC) did not significantly differ between intermittent and permanent aquatic habitats ( $P > 0.05$ ).

## IV. DISCUSSION

Body size, population density, and juvenile recruitment all varied along the aquatic permanence axis. In permanent habitats, turtle body size was large, population density was low, and juvenile recruitment was low. In intermittent habitats, turtle body size was small, population density was high, and juvenile recruitment was high. In ephemeral habitats, turtle body size was small, population density was low, and juvenile recruitment was low. Juvenile recruitment was positively correlated with population density. In the aquatic Coahuila box turtle (*Terrapene coahuila*), a similar pattern of large body size with low population density in permanent habitats and small body size with high population density in intermittent habitats has been observed (Brown, 1971).

### BODY SIZE

Body size is an important life history characteristic and variation may result from natural selection, sexual selection, genetic influences, or environmental variables (Peters, 1983; Savage et al., 2004; Woodward et al., 2005). My data suggest body size varies along a permanence gradient ranging from ephemeral to permanent aquatic habitats. Sonoran mud turtles appear to reach larger body sizes as habitats become increasingly permanent. The abiotic limitation hypothesis predicted increased turtle body size with increasing permanence. Data fit these predictions well with turtles being significantly larger in permanent habitats compared to intermittent and ephemeral aquatic habitats. Data did not fit the predictions of the biotic limitation hypothesis. This suggests variation in body size is due to abiotic factors, primarily hydroperiod length, suggesting permanence is a selective pressure that influences body size. Increasing body size along the permanence gradient has been observed in predatory salamanders, aquatic box turtles,

coleopteran larvae, and odonate larvae (Brown, 1971; Skelly, 1996). Flow permanence regulated body size in stream macroinvertebrates, with larger invertebrates occurring in more permanent flowing streams (Chakona et al., 2008). In *Salamandrina perspicillata*, mean body size was larger in individuals occurring in water bodies that were consistent compared to water bodies that dried and flooded annually (Angelini et al., 2008). In turtles, an association between permanence and body size has been demonstrated for Coahuila box turtles (Brown, 1971). Body size has also been demonstrated to be positively correlated with increasing habitat surface area in the Mexican rough-footed mud turtle (*K. hirtipes*; Iverson, 1985) and the painted turtle (*Chrysemys picta*; Rowe, 1996). This association may be similar to the pattern observed across the permanence gradient assuming larger aquatic habitats dry less often. Variation in body size can be explained by factors associated with the permanence gradient, such as increased food resource availability and increased stability. These factors likely contribute to larger body size in permanent aquatic habitats.

Variation in body size (among other traits, such as growth and reproduction) is thought to be positively correlated with food resource availability and food quality (Gibbons, 1967; Danstedt, Jr., 1975; Gortazar et al., 2000; Lindsay and Dorcas, 2001). Sonoran mud turtles are thought to feed exclusively in the water, with carnivorous diets consisting mostly of aquatic invertebrates (Hulse, 1974; Emslie, 1982). Therefore, invertebrate diversity and abundance are assumed to be indicators of resource availability. Invertebrate diversity was significantly higher in permanent aquatic habitats, suggesting these habitats provide a more diverse selection of prey. Invertebrate abundance was not significantly different between permanent and intermittent aquatic

habitats. This suggests these habitats support similar invertebrate abundance. However, invertebrate data were only collected when habitats had water. When a stock tank or canyon pool dries, aquatic invertebrates (and thus all food resources) disappear. This suggests resource availability is higher in permanent aquatic habitats, simply due to persistent hydroperiods. It is not surprising that larger turtles are found in these habitats because they offer prolonged food availability and a more diverse dietary selection.

Permanent aquatic habitats are stable and lack the fluctuations in water that occur at non-permanent study sites (intermittent and ephemeral). Non-permanent study sites often experience complete desiccation which prevents some aquatic invertebrates from occurring and imposes foraging limitations on Sonoran mud turtles by reducing food availability. This creates a scenario in which a longer foraging season is possible for turtles inhabiting permanent study sites. Turtles inhabiting permanent aquatic habitats may avoid forced estivation due to non-desiccating habitats. The disappearing habitat forces aquatic turtles to estivate or migrate to other aquatic habitats. Both behaviors would limit foraging opportunities. During estivation, Sonoran mud turtles must cope with a loss in body mass, reduced metabolic rate, and anhomeostasis (Peterson and Stone, 2000; Ligon and Peterson, 2002). It is clear that while estivating, turtles are not dedicating energy towards growth. Even when water is present, Sonoran mud turtles undergo asynchronous aquatic activity (Stone, 2001) and thus their own behavior limits foraging opportunities. Furthermore, intraspecific competition for limited resources in high density populations (*See Demography*) may also result in small sized turtles (Damuth, 1981; Branch and Branch, 1982).

Interpopulational variation in body size has been previously reported in several species of turtles including Sonoran mud turtles (Gibbons, 1967; Iverson, 1985; Rosen, 1987; Congdon and Van Loben Sels, 1991; Rowe, 1996). Rosen (1987) reported MCL means as high as 145 mm from eight populations throughout Arizona. Hulse (1974) documented variation in female body size (103 mm vs. 134 mm) from two stream populations in Arizona. Sonoran mud turtles in my study populations showed exceptional variation in body size despite being geographically proximate. The CV of body size between my study populations and the rest of the range is very similar (9.3 to 10.3, respectively) and there was no significant difference in MCL. In other words, the same amount of variation in body size exists within the Peloncillo Mountains as exists throughout the Sonoran mud turtle's entire geographic range. This suggests that body size is correlated with factors associated with local environments, such as the permanence gradient and not with range-wide environmental gradients such as latitude and longitude.

Permanent aquatic habitats provide benefits such as increased hydrological stability and increased resource availability. These factors appear to promote larger body size. However, I will later show that although permanent aquatic habitats are favorable for increased body size, they are likely unfavorable for supporting large populations.

## DEMOGRAPHY

### *Population Density and Juvenile Recruitment*

Population density and juvenile recruitment varied along the aquatic permanence gradient, with significantly higher population density and juvenile recruitment occurring in intermittent aquatic habitats. Both permanent and ephemeral aquatic habitats had low population density and low juvenile recruitment. It is striking that every intermittent

aquatic habitat has higher population density than any permanent aquatic habitat (Table 4). Data supported predictions made by both the abiotic and biotic limitation hypotheses. The abiotic limitation hypothesis was supported by low population density and low juvenile recruitment at the ephemeral end of the permanence axis, whereas the biotic limitation hypothesis was supported by low population density and low juvenile recruitment at the perennial end of the permanence axis. Abiotic limitations negatively impacting demographics in ephemeral aquatic habitats appear to be related to limited hydroperiods. Biotic limitations negatively impacting demographics in permanent aquatic habitats appear to be increased predation pressure and competitive interactions.

### **Abiotic Limitations**

Population density and juvenile recruitment was low in ephemeral aquatic habitats, and support the pattern predicted by the abiotic limitation hypothesis. Low population densities are likely the result of poor recruitment and appear to be a reflection of the physiological challenges imposed by limited hydroperiods in ephemeral aquatic habitats. Ephemeral aquatic habitats were dry at least half the times they were visited, suggesting poor habitat quality and instability within the habitat. Even after persistent rain, water soaked into silt-filled canyon streambeds and quickly evaporated. Limited hydroperiods may force Sonoran mud turtles to undergo estivation and spatiotemporally limit hydration opportunities. Adult Sonoran mud turtles are capable of complete shell closure which decreases evaporative water loss (Wygoda and Chmura, 1990) and probably aids in their estivation capabilities. For sub-adults, the hydration challenges imposed by limited hydroperiods are intensified due to decreased allometric scaling of surface area to volume ratios (Hill and Wyse, 1989) and the inability of complete shell

closure (pers. obs.). This may put sub-adults at high risk for dehydration and potentially death. Flash floods are another environmental disturbance that may restrict population density and juvenile recruitment. Flash floods were responsible for high mortality of Sonoran mud turtles in ephemeral canyon streams (Stitt and Swanson, 2000). Flash floods were common in both ephemeral and intermittent aquatic habitats, suggesting that floods alone are probably not a limiting factor. However, the cycle of complete habitat desiccation to flash flooding reflects instability in ephemeral habitats, which promote abiotic selection pressures that appear to limit population densities via reduced recruitment.

Limited hydroperiods and instability in ephemeral aquatic habitats may also lead to decreased food availability which would reduce foraging opportunities, and ultimately make the habitat unsuitable. Decreased food resources certainly impact all age classes, but it appears reduced resources would impact juveniles more because they require resources for rapid growth until sexual maturity is attained (Gibbons and Lovich, 1990). Increased food resources have been positively correlated with increased juvenile recruitment in other taxa (Einarsson et al., 2006), so a reduction in resources may lead to reduced recruitment.

Abiotic stress is likely reduced in intermittent aquatic habitats because these habitats hold water during most of the year. Intermittent aquatic habitats fill during the summer monsoon season and water will persist into the winter. However, intermittent aquatic habitats are usually dry by spring. Intermittent aquatic habitats appear to hold water long enough for Sonoran mud turtles to satisfy hydration requirements. Hydroperiod scores indicate that intermittent aquatic habitats held water 70-80% of the



times they were visited. Due to longer hydroperiods relative to ephemeral habitats, intermittent aquatic habitats appear to provide enough food resources to support high population densities and high juvenile recruitment. This suggests that abiotic selection pressures are not acting as strongly on intermittent aquatic habitats as they are on ephemeral aquatic habitats.

### **Biotic Limitations**

Population density and juvenile recruitment was low at permanent study sites, supporting the pattern predicted by the biotic limitation hypothesis. Sonoran mud turtles are generally thought to be more aquatic than other kinosternids (Ernst et al., 1994), so small populations in permanent habitats is intriguing. Permanent aquatic habitats supported increased food availability due to persistent hydroperiods and lacked disturbances, which indicate that invertebrate communities and the habitat itself were stable and consistent. Population density was positively correlated with juvenile recruitment. Low juvenile recruitment probably reflects the challenges associated with increased predation and competition. Predator density and abundance increases near permanent aquatic habitats (Woodward, 1983) and increases along a permanence axis (Skelly, 1995). Potential aquatic predators and competitors in the study area include introduced non-native fish (*M. salmoides*, *L. microlophus*, *L. megalotis*), bullfrogs, and Chiricahua leopard frogs (*R. chiricahuensis*); all of these are absent from non-permanent study sites. Invertebrates may also act to reduce juvenile recruitment, but crayfish (*Orconectes virilis*), which have drastically reduced Sonoran mud turtle recruitment at Sycamore Creek since 1986 (Fernandez and Rosen, 1996), were absent from the study area. However, odonate larvae, which in previous studies have been shown to limit anuran distribution (Smith, 1983),

were abundant in permanent aquatic habitats. Bullfrogs are predators of hatchling and juvenile Sonoran mud turtles (Schwalbe and Rosen, 1988), and are considered threats to population stability (Van Loben Sels et al., 1997). Bullfrogs were observed at the SBNWR and maybe responsible for reducing juvenile recruitment at the SBNWR.

Largemouth bass are another exotic species potentially reducing recruitment in populations of Sonoran mud turtles. Largemouth bass are particularly harmful because of the wide range of prey organisms taken, including both aquatic and terrestrial items (Hodgson and Hansen, 2005). It is unlikely that an adult turtle would be prey for predatory fish, but juveniles and hatchlings are documented prey (Bennett et al., 1970; Gibbons, 1970; Ernst and Barbour, 1972; Ernst, 1986; Mitchell, 1988; Mitchell, 1994). Britson and Gutzke (1993) found that largemouth bass were capable of capturing live hatchling red-eared sliders (*Trachemys scripta*) and painted turtles, but were unable to consistently ingest them. Their results suggest that both turtles have behavioral mechanisms that allow them to escape fish predation. Compared to turtle species used in these experiments, Sonoran mud turtle hatchlings are typically smaller (Ernst et al., 1994) and less aggressive (pers obs). Largemouth bass are capable of eating food items up to 50% of their gape (Richard and Wainwright, 1995) and in experiments performed by Britson and Gutzke (1993) bass were able to eat the maximum sized hatchlings (MCL=39.5 mm). Hatchling Sonoran mud turtles in the Peloncillo Mountains average MCL=23.8 ± 0.8 mm (n=103) upon initial capture, and their high activity rates may increase their exposure to predation. Furthermore, red-eared sliders and painted turtles have more widespread distributions across the United States (Ernst et al., 1994), and have evolved alongside predatory fish. In aquatic habitats that contain fish, the yellow mud

turtle and the eastern mud turtle (*K. subrubrum*) were both consistently found at lower densities than red-eared sliders (Gibbons, 1970; Stone et al., 1993; Tuberville et al., 1996; Stone et al., 2005a). Rosen (1987) reported the lowest population densities of Sonoran mud turtles in habitats with largemouth bass. Sonoran mud turtles are nearly absent from lakes and rivers (Ernst et al., 1994), which typically support introduced largemouth bass. This suggests that Sonoran mud turtles may not have evolved adequate anti-predatory mechanisms to reach high abundance in habitats with predatory fish.

Turtles compete with many animals within the aquatic habitat but fish (introduced or not) are probably the strongest competition due to dietary overlap. Sonoran mud turtles may avoid permanent aquatic habitats to avoid competition with fish. For example, Chessman (1984) documented variation in stomach content volume, which was eight times higher in Australian snake-necked turtles (*Chelodina longicollis*) from temporary habitats without fish, compared to permanent habitats with fish. Chessman (1988) concluded that Australian snake-necked turtles preferred temporary aquatic habitats to avoid competition with fish. Permanent aquatic habitats may have reduced juvenile recruitment because competitors best juvenile turtles in the procurement of food, thereby reducing the population. This supports a negative fish-turtle trophic interaction and suggests that turtle abundance might be limited by fish.

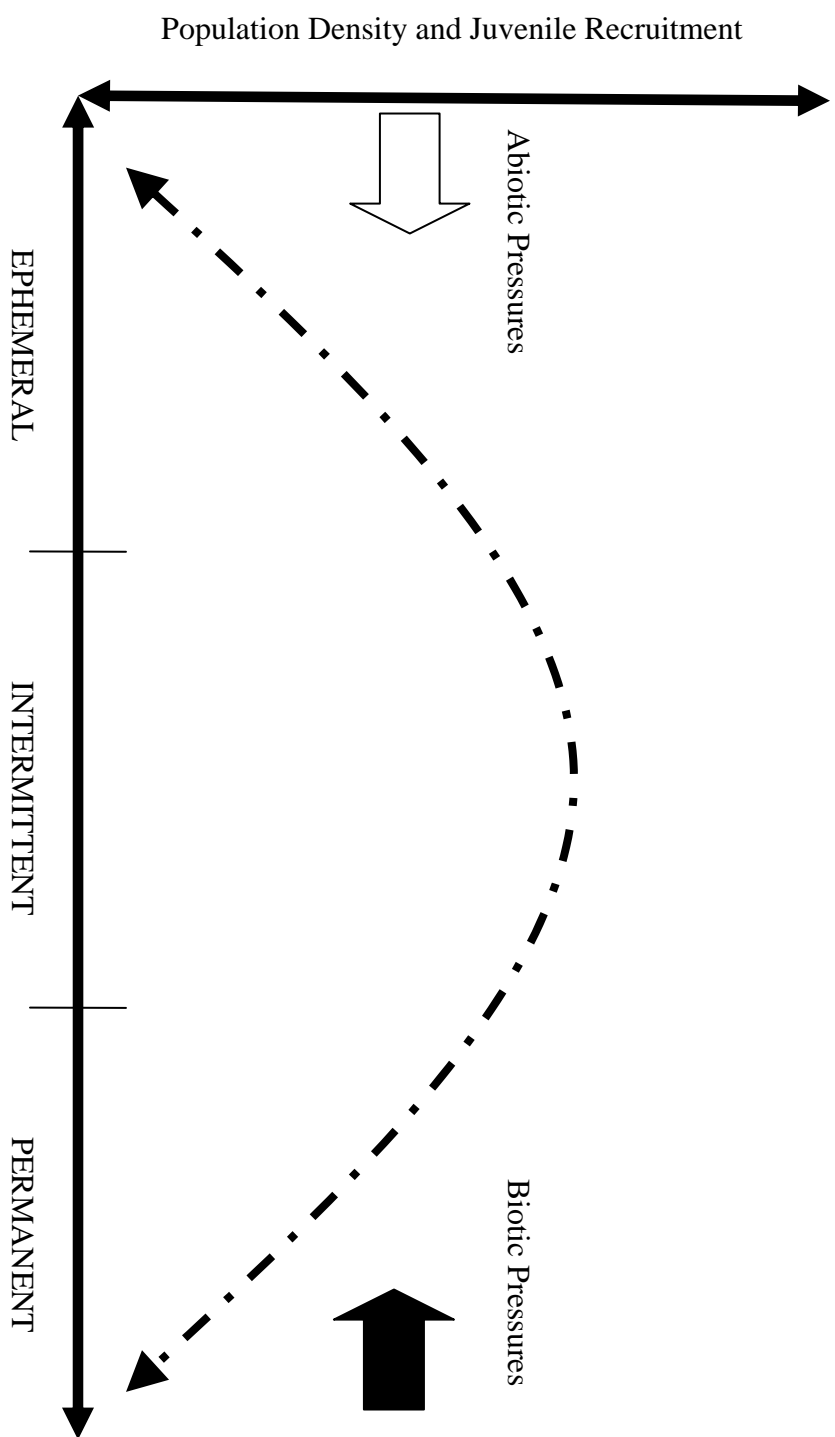
Low juvenile recruitment in permanent aquatic habitats could be a function of biased trapping methods. Juvenile and hatchling Sonoran mud turtles have been noted for their secretive behavior and several studies have reported difficulties locating hatchling kinosternids (Hulse, 1974; Van Loben Sels et al., 1997; Forero-Medina et al., 2007). Our research group had no troubles finding juvenile and hatchling Sonoran mud turtles. In

fact, they were quite conspicuously active in the water column and frequently swam away from the shoreline upon approach. Almost all hatchling captures were made by hand (96%), while only half of juvenile captures were by hand (54%). Hoop netting was most commonly used at permanent study sites and hatchlings could easily fit through the mesh of hoop nets. While this does explain the lack of hatchlings at permanent study sites, it does not explain why so few juveniles were captured (which could not fit through the mesh). Therefore, I consider the sub-adult pattern not biased by trapping methods.

Nest predation is also a potential factor in reducing juvenile recruitment. Permanent aquatic habitats have increased predator density and diversity (Woodward, 1983). Increased predators could potentially lead to increased nest predation. Potential nest predators observed included coyotes (*Canis latrans*), skunks (*Mephitis mephitis*), snakes (*Crotalus* spp.), javelinas (*Tayassu tajacu*), and coatis (*Nasua narica*). High nest predation rates are often reported for freshwater turtles (Iverson, 1991; Burke et al., 1998; Tuma, 2006). Rosen (1987) found evidence of nest predation at one site, Montezuma Well, the most permanent water source in the Sonoran mud turtles geographic range. While nest predation is a viable explanation for low juvenile recruitment, I have no evidence to support this hypothesis because nests were never observed at any study site.

The general pattern of low population density and low juvenile recruitment at the ends of the permanence gradient, and high population density and high juvenile recruitment in the middle of the permanence gradient reflect a distribution pattern that appears to favor intermittent aquatic habitats (Figure 9). Intermittent aquatic habitats appear to optimum habitat for several species of mud turtles (Ernst and Barbour, 1989). This pattern is also shared by the green frog (*R. clamitans*) and striped chorus frog

(*Pseudacris triseriata*; Smith, 1983; Werner and McPeck, 1994; Skelly, 1996). Predation and short hydroperiods were shown to affect these anuran's distribution patterns with limiting factors at the ends of the permanence gradient (Werner and McPeck, 1994; Skelly, 1996). This may indicate that abiotic and biotic selection pressures are strongly acting on the ends of the permanence gradient but are restrained in middle (Figure 9). The pattern and predictions these counteracting selection pressures create is similar to the pattern and predictions made by the intermediate disturbance hypothesis (IDH). The IDH makes predictions about species diversity based on frequency of disturbances (Connell, 1971). The IDH predicts species diversity will be increased in areas with an intermediate number of disturbances, and diversity will be decreased in areas with a low or high number of disturbances (Connell, 1971). Predictions of the IDH about species diversity are similar to the demographic pattern observed (Figure 9). While the organization level is different (one species vs. species diversity), the principle of intermediate habitats being optimal should still hold, making a modified IDH an attractive model for combining predictions of the abiotic and biotic limitation hypotheses.



**FIGURE 9.** Abiotic and biotic selection pressures across a permanence gradient. Factors are strongest at the ends of the permanence gradient, but appear relaxed in the middle. The dotted arc reflects population density and juvenile recruitment in each of the permanence classifications.

Population density estimates ranged from zero to 1305 turtles/ha (Table 4) and are within the range already reported in the literature. Hulse (1974) estimated population density at Tule Stream (AZ) to be 750-825 turtles/ha and could not estimate population density at Sycamore Creek (AZ), but suggested that the Tule Stream population was larger due to reduced flooding and an increase in preferred habitat. Thirteen years later, Rosen (1987) estimated population density to be 1902 turtles/ha at Sycamore Creek, much higher than that of Tule Stream. Rosen (1987) also reported population densities ranging from 188/ha to 8829/ha for six populations inhabiting permanent aquatic habitats throughout Arizona. In an ephemeral stream less than 1 km from Lake Pleasant (AZ), population density estimates ranged from 270/ha to 406/ha depending on water levels (Frank Hensley, pers. comm.). Finding patterns within these data are difficult due to fluctuating hydroperiods, discrepancies in age classes used, and variation in models used to estimate population size. All the studies listed above conducted research in areas where at least some of the aquatic habitat persisted annually.

## CONSERVATION

There continues to be growing concern over the loss of biodiversity in ecosystems. Herpetofauna are disappearing at alarming rates (Gibbons et al., 2000). Of the 285+ species of turtles (Zug et al., 2001), 140 are currently listed as threatened (IUCN Red List, 2009). Of those, 12 species of *Kinosternon* are on the Red List, but only three are listed as vulnerable, including the Sonoran mud turtle (IUCN Red List, 2009). An animal is considered “vulnerable” if the best available evidence indicates that the animal is facing high risk of extinction in the wild (IUCN Red List, 2009). This highlights the importance of understanding the biological and ecological impacts threatening Sonoran

mud turtles. Habitat loss and degradation, introduced species, pollution, disease, harvesting, and climate change are often thought to be the main factors affecting population stability (Gibbons et al., 2000). These factors may naturally reduce populations or declines may be exacerbated through anthropogenic effects. Interestingly, the aquatic habitats that supported increased population densities and high juvenile recruitment were artificial impoundments, which are anthropogenic. This suggests that anthropogenic effects may be positively affecting population demographics in the Peloncillo Mountains.

Threats to Sonoran mud turtles in the Peloncillo Mountains include habitat loss due to siltation and dam failures, and the introduction of non-native fish. Although impoundments may be artificially increasing population densities, it is clear that if these impoundments are not properly maintained a population crash is inevitable. Silt threatens to fill every artificial impoundment and has filled at least four impoundments in the Peloncillo Mountains. For example, Sonoran mud turtles were often observed at Cedar Tank prior to the tank becoming filled with silt (Bill McDonald, pers. comm.). Afterwards, turtles were scarcely observed (Bill McDonald, pers. comm.) and our sampling suggests that very few turtles now inhabit this study site. Unfortunately, Blackwater Hole (one of the major populations) is threatened by siltation, but efforts to dredge Blackwater Hole have been tepidly received. Dam failure results in quickened draining of the artificial impoundment. Blackwater Hole also has a dam failure, which drains the impoundment, greatly shortening the hydroperiod. If proper action is not taken to fix the leaking dam and remove the silt, then the population at Blackwater Hole is



likely doomed. Both dam failures and siltation result in degradation or loss of aquatic habitat.

The introduction of non-native fish is another anthropogenic factor that threatens life in aquatic habitats. Non-native fish are partly responsible for reducing the distribution and abundance of several frog species in the western United States (Fisher and Shaffer, 1996) and the introduction of largemouth bass to Japanese freshwaters has all but eliminated native fishes (Takamura, 2007). The effect of non-native fish on freshwater turtles is not well understood, and the interactions may be direct or indirect. The eradication or removal of introduced non-native fish from the Peloncillo Mountains appears to be a task worth undertaking.

## **V. CONCLUSIONS**

It is clear that the permanence gradient affects the distribution, abundance, and size of Sonoran mud turtles in the Peloncillo Mountains. The permanence gradient appears to influence variations in body size, with larger turtles occupying the most permanent aquatic habitats. I hypothesize that increased body size is a reflection of increased growth rates due to longer activity periods made possible by temporally persistent hydroperiods. Likewise, decreased body sizes are a reflection of temporarily interrupted hydroperiods. Body size distribution along the permanence gradient resemble the predictions made by the abiotic limitation hypothesis and suggest that aquatic permanence should be a factor considered when reporting body size variation in freshwater turtles. The permanence gradient also appears to influence population demographics, specifically population density and juvenile recruitment, which were positively correlated. Populations with low density and low recruitment were found at the

ends of the permanence gradient, while populations with high density and high recruitment were found in the middle of the permanence gradient. I hypothesize that limited hydroperiods impose physiological challenges that limit population density by reducing recruitment in ephemeral aquatic habitats and that predation imposes survival challenges that limit population density by reducing recruitment in permanent aquatic habitats. These challenges appear relaxed in intermittent aquatic habitats because hydroperiods appear long enough to support adequate hydration requirements but are short enough to exclude aquatic predators, such as fish. It appears that data related to demographics closely resemble predictions of both the abiotic and biotic limitation hypotheses suggesting that both limitations are acting on populations concurrently and that these limitations should be considered when studying populations of freshwater turtles.

The IUCN lists the Sonoran mud turtle as a vulnerable species and therefore close attention should be focused on determining which factors threaten population demographics and dynamics throughout its geographic distribution. Anthropogenic introductions of non-native animals (i.e. bullfrogs, crayfish, bass) threaten recruitment throughout much of the Sonoran mud turtles range. Ironically, habitat degradation and loss through dam failures and siltation threaten the very impoundments created to artificially support aquatic organisms. In the future, proper steps towards managing and protecting both the organism and its habitat will hopefully lead to positive recruitment and growth of populations.

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