Comparative Demography and Habitat Use of Western Pond Turtles in Northern California: The Effects of Damming and Related Alterations

by

Devin Andrews Reese

B.A. (Harvard University) 1986

A dissertation submitted in partial satisfaction of the

requirements for the degree of

Doctor of Philosophy

in

Integrative Biology

in the

GRADUATE DIVISION

of the

UNIVERSITY of CALIFORNIA at BERKELEY

Committee in charge:

Professor Harry W. Greene, Chair
Professor Mary E. Power
Professor Reginald Barrett

1996

The dissertation of Devin Andrews Reese

is approved by:

Harry W. Greene May 13, 1996
Chair Date

Mary E. Power May 14 1996
Date

Reginald H Barrett May 13, 1996
Date

University of California at Berkeley

1996

Comparative Demography and Habitat Use of Western Pond Turtles in Northern California: The Effects of Damming and Related Alterations

by

Devin Andrews Reese

Abstract

Comparative Demography and Habitat Use of Western Pond Turtles in Northern California: The Effects of Damming and Related Alterations

by

Devin Andrews Reese

Doctor of Philosophy in Integrative Biology

University of California at Berkeley

Professor Harry W. Greene, Chair

Despite their tenure in California for more than two million years, a period including extreme changes in the landscape, western pond turtles (*Clemmys marmorata*) are now declining. Survival and viability of populations are impacted by a range of factors, including damming, residential development, agricultural practices, introduced predators, and direct harvest. Some of the few remaining large populations occur in the Klamath River hydrographic basin. From 1991-1995, I examined demography and habitat associations of western pond turtles on a dammed tributary (mainstem Trinity River) and an undammed tributary (south fork Trinity) using mark-recapture techniques and radiotelemetry. In addition, radiotracking of turtles in a set of agricultural ponds in Santa Rosa provided an assessment of movements in a fragmented aquatic landscape.

Although both Trinity River populations were sparse compared to large, extant populations in lower order streams, the mainstem population was more sparse and significantly more adult-biased. Riverine western pond turtles were associated with basking sites of low slope in areas of deep, pooled waters that provided aquatic refugia. Lewiston Lake, the reservoir formed by the dam, supports a small, adult-biased population of turtles. Modifications of the river channel for fisheries enhancements are too shallow and exposed to improve conditions for turtles. Small wetlands adjacent to the river, including vernal pools, play a significant role in the life cycle of western pond turtles. The riverine sites and agricultural ponds host a complex set of terrestrial movements for nesting, overwintering, estivation, basking, and travel between multiple bodies of water.

The relatively low densities of western pond turtles in the Trinity River system may be attributable to a more diffuse distribution of resources in higher order streams. However, the adult-biased age structure indicates possible recruitment declines along the dammed mainstem. Dam-induced changes, including filling of pools with sediment, increased water velocities along the shoreline, and lowered water temperatures, are probably deleterious to turtles. Restoration attempts geared towards recreating a wide, braided channel should include recovery of warm, pooled areas with structural complexity. Management efforts throughout the range of this species must take place at the landscape scale, including protection of suitable upland habitat and maintenance of aquatic connectedness.

Harry W. Greene May 13, 1996

Chair Date

DEDICATION

to my father

Thomas S. Reese

for the example he set as a research scientist

and

to my mother

Anne H. Reese

for her dedication to humanitarian work

and

to the hundreds of western pond turtles

who unwittingly participated

in these studies

TABLE OF CONTENTS

LIST OF FIGURES ix
LIST OF TABLES xii
LIST OF APPENDICES xv
ACKNOWLEDGEMENTS xvi
CHAPTER l: INTRODUCTION 1

CHAPTER 2: METHODS OVERVIEW

  Study Sites 8
  Field Methods 12
  Statistical Analyses 14

CHAPTER 3: DEMOGRAPHY OF WESTERN POND TURTLE POPULATIONS IN THE TRINITY RIVER IN THE CONTEXT OF DAM-INDUCED ALTERATIONS.

  ABSTRACT 16
  INTRODUCTION 17

  METHODS
    Field Methods

      Mark-recapture 18
      Float Surveys 20

    Data Analysis
      Population Size

        A. Mark-recapture 21
        B. Remaining mainstem reaches 26
      Population Density 26
      Population Structure 27

  RESULTS
      Population Size

        A. Mark-recapture 29
        B. Remaining mainstem reaches 36
      Population Density 38
      Population Structure 38
  DISCUSSION 41

CHAPTER 4: SITE CHARACTERISTICS AND BASKING BEHAVIOR OF WESTERN POND TURTLES IN THE MAINSTEM TRINITY RIVER

ABSTRACT 46

INTRODUCTION 47

METHODS
- Study sites 48
- Field Methods 49
- Data Analysis
  - Examination of basking intensity 52
  - Comparison of turtle basking site used to availability 54
  - Analysis of lifestage differences in basking site characteristics 56
  - Assessment of underwater habitat use 57

RESULTS
- Examination of basking intensity 58
- Comparison of turtle basking site used to availability 60
- Analysis of lifestage differences in basking site characteristics 62
- Assessment of underwater habitat use 62

DISCUSSION
- Examination of basking intensity 65
- Comparison of turtle basking site use to availability 69
- Analysis of lifestage differences in basking site characteristics 70
- Assessment of underwater habitat use 70

ACKNOWLEDGEMENTS 71

CHAPTER 5: HABITAT USE BY WESTERN POND TURTLES IN AN ALTERED SYSTEM, THE TRINITY RIVER BASIN OF NORTHWESTERN CALIFORNIA

ABSTRACT 72

INTRODUCTION 73

MATERIALS AND METHODS
- Study Sites 77
- Field Methods 77
- Data Analysis
  - Comparison of available habitat on mainstem and south fork 81
  - Comparison of turtle habitat use to availability 82

RESULTS 84
Comparison of available habitat on mainstem and south fork 85
Comparison of habitat use to availability on the mainstem 88
Comparison of habitat use to availability on the south fork 91

DISCUSSION 97

ACKNOWLEDGEMENTS 103

CHAPTER 6: INVESTIGATION OF WESTERN POND TURTLE POPULATIONS IN LEWISTON LAKE

ABSTRACT 104

INTRODUCTION 105

METHODS AND ANALYSIS
Study Site 107
Surveys 107
Aquatic Habitat Analysis 112
Nesting Searches 114

RESULTS
Surveys 116
Aquatic Habitat Analysis 117
Nesting Searches 119

DISCUSSION 123

ACKNOWLEDGEMENTS 126

CHAPTER 7: HABITAT QUALITY OF ARTIFICIAL SIDE CHANNELS AND BANK FEATHERED EDGES FOR WESTERN POND TURTLES IN THE TRINITY RIVER

ABSTRACT 127

INTRODUCTION 128

STUDY AREA 132

METHODS
Surveys 134
Aquatic Habitat Comparisons and Evaluations 135

ANALYSIS

Surveys 136
Aquatic Habitat Comparisons 136
Aquatic Habitat Evaluations 138

RESULTS
Surveys 139
Aquatic Habitat Comparisons 141
Aquatic Habitat Evaluations 144

DISCUSSION 148

ACKNOWLEDGMENTS 150

CHAPTER 8: MOVEMENTS AND MICROHABITAT USE OF HATCHLING AND JUVENILE WESTERN POND TURTLES IN THE TRINITY RIVER BASIN

ABSTRACT 151

INTRODUCTION 152

METHODS
Field Methods
Juvenile Searches 154
Radiotelemetry 155
Habitat Measurements 157
Data Analysis
Juvenile Searches 159
Habitat Measurements 160
Radiotelemetry 161

RESULTS
Juvenile Searches 162
Habitat Measurements 164
Radiotelemetry 168

DISCUSSION 171

ACKNOWLEDGEMENTS 176

CHAPTER 9: USE OF THE TERRESTRIAL AND AQUATIC LANDSCAPES BY WESTERN POND TURTLES: A COMPARISON OF THREE LOCALES

ABSTRACT 177

INTRODUCTION 178

METHODS
- Study Sites 181
- Field Methods 183
- Data Analysis 187
  - I. Terrestrial Movements
    - A. Overview 188
    - B. Overwintering: Behavior 189
    - C. Overwintering: Timing 190
    - D. Overwintering: Distance 191
  - II. Aquatic Movements 193

RESULTS
  - I. Terrestrial Movements
    - A. Overview 195
    - B. Overwintering: Behavior 206
    - C. Overwintering: Timing 208
    - D. Overwintering: Distance 214
  - II. Aquatic Movements 218

DISCUSSION 222

ACKNOWLEDGEMENTS 232

CHAPTER 10: DISCUSSION 234

LITERATURE CITED 241

LIST OF FIGURES

Figure Number and Title Page

2-1 Location of study reaches along the mainstem Trinity River, Trinity County, California. 9

2-2 Location of study reaches along the south fork Trinity River, Humboldt and Trinity Counties, California. 10

2-3 Diagram of marking and measuring techniques for western pond turtles. Adapted from Holland 1994. 13

3-1 Percent of captured turtles that were adults and juveniles at each of three sites. 40

4-1 Proportion of captured turtles that were sighted basking prior to capture along the mainstem Trinity. 59

4-2 Distribution of turtle-use perches and potential perches across substrate types at the mainstem Trinity. 64

5-1 Graph of the first two principal components for habitat measurements from mainstem and south fork random quadrats. 87

5-2 Distribution of random habitat quadrats at the mainstem and south fork study sites across shoreline vegetation types. 90

5-3 Distribution of turtle habitat quadrats and random habitat quadrats across shoreline vegetation types at the mainstem site. 93

5-4 Distribution of turtle habitat quadrats and random habitat quadrats across shoreline vegetation types at the south fork site. 96

5-5 Depiction of favorable habitat for western pond turtles. 102

6-1 Map depicting the location of Lewiston Lake in relation to the Central Valley Project. From USDI Bureau of Reclamation 1992. 108

6-2 Diagram of baited trap used to capture turtles in Lewiston Lake. 109

6-3 Map of Lewiston Lake showing trap stations and locations of ponds. 111

Figure Number and Title Page

6-4 Plot of classification error rates across threshold values for logistic regression of turtle presence against habitat characteristics. 121

7-1 Schematic profile of side channel sites before and after construction. 130

7-2 Schematic profile of bank feathering sites before and after construction. 131

7-3 Side channel and feathered edge sites sampled on the mainstem Trinity River. 133

7-4 Percent of sample sites at side channel and feathered edges with suitable habitat for juvenile western pond turtles. 145

8-1 Proportion of juvenile and adult turtles inhabiting sites at the south fork Trinity River. 163

8-2 Proportion of juvenile and adult turtles inhabiting sites at the mainstem Trinity River. 165

9-1 Map of Santa Rosa study site showing ranches and ponds in which western pond turtles were captured. 182

9-2 Comparison of mainstem Trinity River site and Santa Rosa site with respect to what proportion of turtles made journeys onto land during 1992-3. 196

9-3 Comparison of south fork and mainstem Trinity River sites with respect to what proportion of turtles made journeys onto land during 1993-4. 196

9-4 Proportion of radioed males and females on the mainstem Trinity River that made journeys onto land during each month. 197

9-5 Overwintering modes of radioed turtles in ponds at Santa Rosa study site during 1992-3 and 1993-4 winters. 205

9-6 Terrestrial stops made prior and subsequent to hibernation by western pond turtles on the mainstem Trinity River. 210

9-7 Depiction of the timing of overwintering behaviors by male and female western pond turtles on the mainstem Trinity River during the 1993-4 winter. 213

Figure Number and Title Page

9-8 Overwintering locations of female western pond turtles on the mainstem Trinity River during 1992-1994 winters. 219

9-9 Overwintering locations of male western pond turtles on the mainstem Trinity River during 1992-1994 winters. 220

9-10 Overwintering locations of western pond turtles on the south fork Trinity River during 1993-1994 winters. 221

LIST OF TABLES

Table Number and Title page

3-1 Tests for the Jolly-Seber model (A), the death but no immigration model (A'), the constant survival model (B), and the constant capture and survival model (D) for western pond turtles in reaches 10 and 11 of the mainstem. 31

3-2 Jolly-Seber estimates and approximate standard errors under the Jolly-Seber model (A) and the constant survival model (B) for western pond turtles in the mainstem Trinity River, reaches 10 and 11, captured during nine sampling periods from 1991-1993. 31

3-3 Jolly-Seber estimates and approximate standard errors under the death but no immigration model (A') for western pond turtles in reach 3 of the mainstem Trinity River captured during seven sampling periods from 1992-1993. 33

3-4 Tests for the Jolly-Seber model (A),the death but no immigration model (A'), and the constant capture and survival model (D) for -western pond turtles in reaches 1, 3, and 4 of the south fork Trinity River. 33

3-5 Jolly-Seber estimates and approximate standard errors under the Jolly-Seber model (A), the death but no immigration model (A'), and the constant survival and capture model (D) for western pond turtles in reaches 1, 3, and 4 of the south fork Trinity River captured during nine sampling periods from 1992-94. 34

3-6 Jolly-Seber estimates and approximate standard errors under the death but no immigration model (A') for western pond turtles in reach 2 of the south fork Trinity River captured during seven sampling periods from 1992-1994. 35

3-7 Summary table of capture histories for western pond turtle caught on the mainstem Trinity River during nine sampling periods from 1991-93. 35

3-8 Estimates of western pond turtle population size derived from counts of basking turtles along 16 reaches of the mainstem Trinity River. 37

3-9 Density of western pond turtle populations along the mainstem Trinity River. 39

4-1 Results often two-group discriminant analyses of habitat from 90 occupied basking sites and 90 potential basking sites (subsampled) for western pond turtles on the mainstem of the Trinity River. 61

Table Number and Title Page

4-2 Values of habitat variables (means and standard deviations) for turtle-occupied basking sites and potential basking sites at the mainstem Trinity River. 63

4-3 Habitat characteristics of underwater capture locales for male and female western pond turtles on the mainstem Trinity River and result of t-tests comparing males to females (with Bonferroni adjustment). 66

5-1 Range of values of random habitat measurements (Appendix 5-A) from the mainstem (n=93) and the south fork (n=84) study sites. 86

5-2 Comparison of available habitat at the south fork and the mainstem Trinity study sites. 89

5-3 Two-group stepwise discriminant analysis of available habitat and utilized habitat for western pond turtles at the mainstem Trinity study site. 92

5-4 Two-group nonparametric discriminant analysis of available habitat and used habitat for western pond turtles at the south fork Trinity study site. 95

6-1 Water temperatures of Lewiston Lake during July of 1995. 118

6-2 Logistic regression of turtle presence/absence against habitat characteristics at Lewiston Lake traps. 120

6-3 Habitat characteristics of potential nesting areas and nest sites within 500 m of turtle capture locales. 122

7-1 Number of turtles captured within side channel and feather edge projects and number of turtles captured in the adjacent river during 1995 surveys. 140

7-2 Two-group stepwise discriminant analysis of side channel habitat and river habitat along the mainstem Trinity. 142

7-3 Two-group stepwise discriminant analysis of feather edge habitat and river habitat along the mainstem Trinity. 143

7-4. Number of habitat quadrats that were NOT suitable for adult western pond turtles in terms of values of each habitat variable. 146

7-5 Number of habitat quadrats that were NOT suitable for juvenile western pond turtles in terms of values of each habitat variable. 147

Table Number and Title Page

8-1 Values of habitat variables for juvenile-occupied sites and random riverine sites sampled at the south fork and mainstem of the Trinity River. 166

8-2 Results of ten two-group discriminant analyses of habitat from 47 occupied sites and 84 random riverine sites (subsampled) for western pond turtles on the south fork of the Trinity River. 167

8-3 Results of ten two-group discriminant analyses of habitat from 19 occupied and 93 random sites (subsampled) for western pond turtles on the mainstem of the Trinity River. 169

8-4. Table of radiotelemetered juveniles. 170

9-1 List of journeys onto land by radioed turtles at the mainstem Trinity site, the south fork Trinity site, and the Santa Rosa site. 198-203

9-2 Overwintering habitat of western pond turtles during the 1992-94 winters. 207

9-3 Analysis of the effects of site and sex on the number of terrestrial stops made by overwintering turtles on the mainstem and south fork Trinity during 1993-4. 209

9-4 Analysis of the effects of year on the timing of overwintering by western pond turtles at the mainstem and south fork Trinity during 1992-1995 211

9-5 Analysis of the effects of sex and site on the timing of overwintering by western pond turtles on the mainstem and south fork Trinity during 1993-4. 212

9-6 Analysis of the effects of site and sex on the duration of overwintering by western pond turtles on the mainstem and south fork Trinity during 1993-4. 215

9-7 Analysis of the effects of site and sex on the duration of overwintering by western pond turtles on the mainstem and south fork Trinity during 1993-4, excluding time spent in ponds after hibernation. 215

9-8 Distances of turtle overwintering points to the watercourse (m) at the mainstem and south fork Trinity River, as well as distances between successive overwintering points for each individual that was monitored for multiple years. 216

Table Number and Title Page

9-9 Location of overwintering locales relative to the river corridor for western pond turtles on the mainstem and south fork of the Trinity River during 1991-1994. 217

9-10 Aquatic home range sizes of western pond turtles on the mainstem and south fork Trinity generated from radiotelemetry and mark-recapture data. 222

LIST OF APPENDICES

Appendix Number and Title Page

2-A DESCRIPTION OF HABITAT CLASSIFICATION PROCEDURES Based on McCain et al. 1990 15

4-A METHODS OF HABITAT MEASUREMENT (Chapter 4) 50-51

5-A METHODS OF HABITAT MEASUREMENT (Chapter 5) 79-80

6-A METHODS OF HABITAT MEASUREMENT (Chapter 6) 113

8-A METHODS OF HABITAT MEASUREMENT (Chapter 8) 158

9-A MONITORING DATES FOR RADIOED TURTLES 184-185

9-B ILLUSTRATION OF TECHNIQUE TO MEASURE DISTANCES OF TURTLE OVERWINTERING POINTS IN THE GIS MAP USING INFORMATION ON ELEVATION 193

9-C POTENTIAL FUNCTIONS OF OVERLAND TRAVEL BY AQUATIC TURTLES 227

ACKNOWLEDGEMENTS

I thank my major professor, Harry Greene, for his continual encouragement and enthusiasm during my tenure as a graduate student. I also thank Mary Power and Reginald Barrett for their participation in my oral exams and dissertation review. I am very grateful to Hartwell Welsh, who provided and guided a fruitful cooperation with the U.S. Forest Service, without which I could not have accomplished this research. Amy Lind has been an incredibly valuable colleague and friend, providing statistical advice, logistical help, editorial assistance, knowledge of the Trinity River system, and moral support. To Douglas Welsh, I am grateful for urging me to devote my studies to the clade that most fascinates me, the Chelonians. His patience, ideas, assistance in the field, and ceaseless excitement about this endeavor have boosted me over many hurdles. Dan Holland has been a role model of dedication to the study of western pond turtles, as well as a teacher, colleague, and friend. I could not have asked for a better duo of field biologists than Don Ashton and Kary Schlick who, with competence, flexibility, motivation, and persistence, have tackled countless river rapids and other challenges. Polly Taylor deserves praise for courage, good humor, familiarity with the Trinity River landscape, and willingness to offer her home to the "turtle project". The Santa Rosa studies could not have succeeded without the encouragement, knowledge, and assistance of Greg DeNevers. A very special thanks to the agency primarily responsible for finding this research, the U.S. Bureau of Reclamation. I am grateful to Ted Case's lab at U.C. San Diego for providing assistance during the final stages. Numerous other people and organizations contributed time and money and are acknowledged in the relevant chapters.

CHAPTER 1

INTRODUCTION

Management of our natural resources has long been plagued by a weak link between basic research and decision-making. Although basic research has identified ecological processes and problems, decision-making has been primarily guided by utilitarianism (Western 1991). Two related culprits can be implicated in this failure to translate knowledge into action. One is our political system, in that high-level positions in natural resource management are not necessarily held by scientists. Thus, while a sizeable group of ecologists gather information on population biology, habitat use, and community dynamics, the scientific journals in which the majority of results are published are not likely to be read by people making management decisions.

Another culprit is the minimal role that scientists assume in fostering sound management practices. In the face of global degradation of habitats and impending extinctions, our charge as scientists has been broadened to include ensuring that the information we gather is accessible to decision-makers. In addition to literal accessibility (such as publication in journals or other media with wide readership), this entails a commitment to gathering, interpreting, and reporting data in a manner that is usable by managers. As Western (1991) pointed out, conservation biology must become more relevant by generating applicable results as opposed to abstract theories. By the time that general principles crystallize from the research and "trickle down" to managers, numerous decisions have already been made about particular ecosystems and the individual species they support.

The impacts of management actions taken without regard to biological information may be serious and difficult to mitigate. For example, the construction of dams in the United States proceeded with minimal regulation well into the 1960s, despite evidence that they might cause huge reductions in fish populations. The repercussions of dams appear to have been anticipated as early as 1852, when the first state fishing statute limited construction of weirs or other obstructions to anadromous fish (CA State Lands Commission, 1993). Dams were, nevertheless, built in response to the demand for hydropower and flood control. With the National Wild and Scenic Rivers Act in place (1968) and the U.S. Fish and Wildlife Service contending with a recent glut of listing petitions for salmonids (e.g. West Coast Steelhead, West Coast Coho Salmon, Chinook Salmon, Sockeye Salmon, Pink Salmon, Chum Salmon; Federal Registers 1994 & 1995), efforts are finally underway to understand dam induced alterations in river ecology and make the necessary restorations. The Trinity River Basin Management Program initiated in 1979 (Pests 1984) constitutes one such effort and, after nearly twenty years, has illuminated the challenges of retrospective consideration of ecological factors.

This problem of decision-making in a knowledge vacuum is particularly true for herpetofauna, whose standing in the decision-making arena is recently acquired and tenuous. For the most part, charismatic megavertebrates, such as elephants and pandas, or species of economic value, such as salmon and deer, have garnered attention (Mittermeier and Carr 1994). The recent publicity gained by declining amphibian populations challenges this precedent. Through concentrated efforts to enlighten the public (Barinaga 1990, Blaustein and Wake 1990, Pechmann et al. 1991, Phillips 1990, Wake 1991, Wyman 1990), world-wide interest and resources have been focused on frogs and toads. This illustrates the potential for strong linkages between science, conservation, and ultimately management.

The western pond turtle (*Clemmys marmorata*) is an ideal subject for forging a close connection between research and management. Its status as a "Species of Special Concern" in California, as Sensitive-Critical in Oregon, and as Endangered in Washington, as well as its previous status as a Federal candidate species (Category 2, Federal Register 1993) mandates that it receive consideration by managers. For example, because of its designation as a U.S. Forest Service "sensitive" species, all operations on National Forest Lands must be preceded by a biological assessment that includes an evaluation of potential impacts to western pond turtles. Ecological studies of this species are still possible because sizeable populations remain in a few areas, despite the rangewide declines. Relative to other species, such as the grizzly bear, for which habitat destruction has been accompanied by extreme range shrinkage (Schneider 1977), the range of the western pond turtle has become drastically fragmented, but only reduced by 15-20%. Thus, two criteria for applied research, that the subjects be available for study and that they be of interest to managers, are satisfied.

The history of western pond turtles in California presents a picture of colonization and endurance through radical alterations in the landscape. The aquatic turtle fauna inhabiting California during the Eocene was more diverse, including members of the families Chelydridae, Trionychidae, and Kinosternidae (Hay 1908). Drying trends of the Oligocene and early Miocene caused most of the aquatic reptiles in the state to be extirpated. Despite the subsequently wetter climate, the California turtle fauna remained depauperate. Hutchison (1982) proposed that the topography of California, namely the prevalence of steep east-west drainages and the lack of a major north-south dispersal corridor, inhibited repopulation. *Clemmys*, however, appears to have entered and spread through California during the late Pliocene or early Pleistocene by crossing drainage divides from the north. Thus, its ability to move overland in search of suitable, wet habitat may have conferred an advantage (Chapter 9).

The survival of western pond turtle populations today is jeopardized by a host of factors, including introduced species, conversion of habitat to urban or agricultural land, drought, damming, and other alterations of riparian systems (Jennings and Hayes 1994). Often, juveniles are most impacted, such that recruitment declines occur and populations become adult-biased. Thus, many populations currently exist that are deceptively large, but are composed primarily of aging adults (Holland 1994). This aggravates the task of protecting the species, given that their widespread occurrence creates an illusion of prosperity. However, if the numerous adults capable of reproducing still collectively encompass some genetic diversity, it may provide an opportunity for recovery that is absent for many declining species.

The characteristics that have enabled *Clemmys marmorata* to persist are also those that make it a difficult to study, namely that it is a long-lived, late-reproducing species with cryptic habits and generalist requirements. Although the lifespan of western pond turtles has not been established, they are known to live at least 40 years (Holland 1991) and may live considerably longer judging from the longevity of other aquatic turtles (Gibbons 1987). Reproduction does not occur until 7-12 years of age and then continues over many years (Holland 1991). Females may produce eggs as infrequently as every other year and their clutches are small relative to other aquatic turtles. Consequently, survivorship must be high to sustain populations. Western pond turtles have been labeled habitat generalists (Holland 1994, Washington Department of Wildlife 1993) because they occupy a diversity of aquatic habitats, including lakes, ponds, large rivers, intermittent and perennial streams, and vernal pools. They appear robust to changes not only because of their persistence through geologic transformations, but also because of their ability to survive in contaminated or otherwise altered wetlands. Although juveniles are perhaps less adaptable, adults can be found in reservoirs, agricultural waterways, and sewage treatment plants (Holland 1994). Their cryptic coloration and use of underwater refugia serves to conceal them from predators.

The ramification of this combination of features is that it is difficult to evaluate the status of populations via demographic parameters or habitat conditions. The apparent resilience of adults combined with the classic, K-selected suite of life history characteristics (Begon at al. 1986) introduces a lag time in the response of western pond turtle populations to impacts. Recruitment declines may occur, but not be immediately apparent, and adults may survive in areas that do not sustain viable populations. Habitat requirements may be difficult to isolate, given the wide tolerance limits. Consequently, research on western pond turtles over the last couple of decades has focused on illuminating the natural history and behavior, as well as gathering baseline data on population structure and range-wide densities (Bury 1972, Holland 1985, Holland 1991). Experimental work has been conspicuously absent, undoubtedly because it would require an extremely long-term study to monitor the outcome of a treatment. Although habitat has been described, quantification of relevant features has been minimal. A recent surge in radiotelemetry studies (Rathbun et al. 1992, Goodman 1994, Holland 1994, Reese and Welsh 1996) has provided information that contributes to the development of appropriate management plans for this species, but there remains a pressing need for prescriptive results.

This project was initiated with that need in mind. Wilson et al. (1991) and Lind et al. (1992) reported relatively large populations of turtles inhabiting the mainstem Trinity River in Trinity County, California (Chapter 2). Completed thirty years earlier, the dams on this section of river ultimately triggered significant alterations in flow regimes, water temperatures, and downstream aquatic habitats with potential impacts on riparian and aquatic wildlife. This proved to be an appropriate political and biological setting for examining the basic ecology of western pond turtles as well as evaluating their response to long-term impacts. Describing those impacts and developing recommendations for restoration relative to turtles required a mufti-faceted approach that emphasized habitat utilization. In the absence of information on resident turtle populations prior to construction of the dams, the evaluation relied on inferences from comparison to the South fork Trinity, an adjacent but undammed portion of the Trinity watershed (Chapter 2). To enhance our understanding of the terrestrial components of landscape utilization, comparison was also made to a set of ponds near Santa Rosa, California (Chapter 9).

My objectives were defined as follows:

1) To further our knowledge of demography, habitat use, and movement patterns of western pond turtles.

2) To describe that knowledge from a quantitative perspective that facilitates application to management.

3) T o make deductions about the impacts of the dams on pond turtle populations in the Trinity River and predictions about the impacts of future alterations or alterations at other sites.

Chapter 2 provides basic background information, including a description of the study sites and an overview of the statistical procedures used for analysis. Chapter 3 examines the demography of western pond turtle populations in the dammed mainstem Trinity and the undammed south fork relative to the demography of a stable population. Chapters 4 reviews the use of basking sites relative to life history parameters. Chapter 5 address aquatic habitat utilization at a larger scales in the context of how habitat is likely to have been altered by the dams. Chapter 6 describes turtle populations and habitat quality in the reservoir formed by the dam. Chapter 7 evaluates the potential of restoration projects on the mainstem Trinity to generate more suitable habitat. Chapter 8 focuses on movements and habitat use of juvenile western pond turtles. Chapter 9 characterizes movements by adults with particular attention paid to overland travel. Chapter 10 is a discussion of the overall results.

CHAPTER 2

METHODS OVERVIEW

Study Sites

Research was conducted at three study sites:

1) The mainstem Trinity River in Trinity County, California.

2) The south fork Trinity River, which forms the boundary of Humboldt and Trinity counties, California.

3) A set of agricultural ponds in the vicinity of Santa Rosa, Sonoma County, California (see Chapter 9 for details).

The mainstem Trinity River study site consists of a 63 kilometer stretch that runs between the Lewiston/Trinity dams and the confluence with the North Fork Trinity (Figure 2-1). Wilson et al. (1991) divided the mainstem site into 16 unequal length segments, hereafter referred to as "reaches", with several "gaps" occurring where access to the river was limited by private landholdings. The reaches varied from 2.41 to 4.02 kilometers in length (averaging 3.14 kilometers). Some reaches (1, 3, 10, 11) received more intensive study as described in each chapter. The south fork study site consists of a 15 kilometer stretch of river that runs between Surprise Creek and Sandy Bar (Figure 2-2). This site was divided into 4 reaches, ranging from 2.5 to 5.7 kilometers in length. At both study sites, the beginnings and ends of reaches were defined primarily on the basis of access points, particularly on the south fork where road access is limited. Survey flags placed every 250-300 meters on the mainstem served as reference points for western

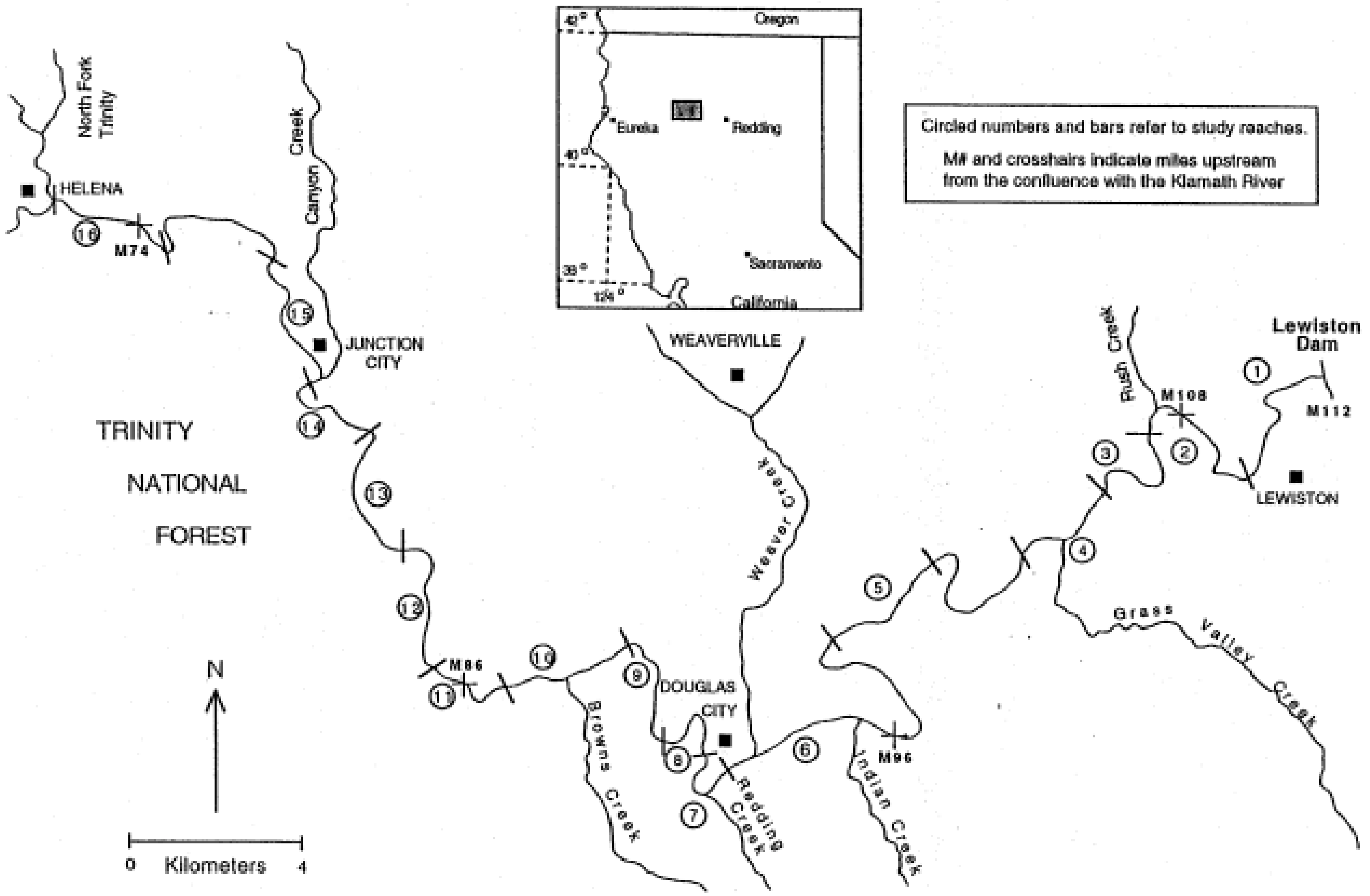


Figure 2-1. Location of study reaches along the mainstem Trinity River, Trinity County, California.

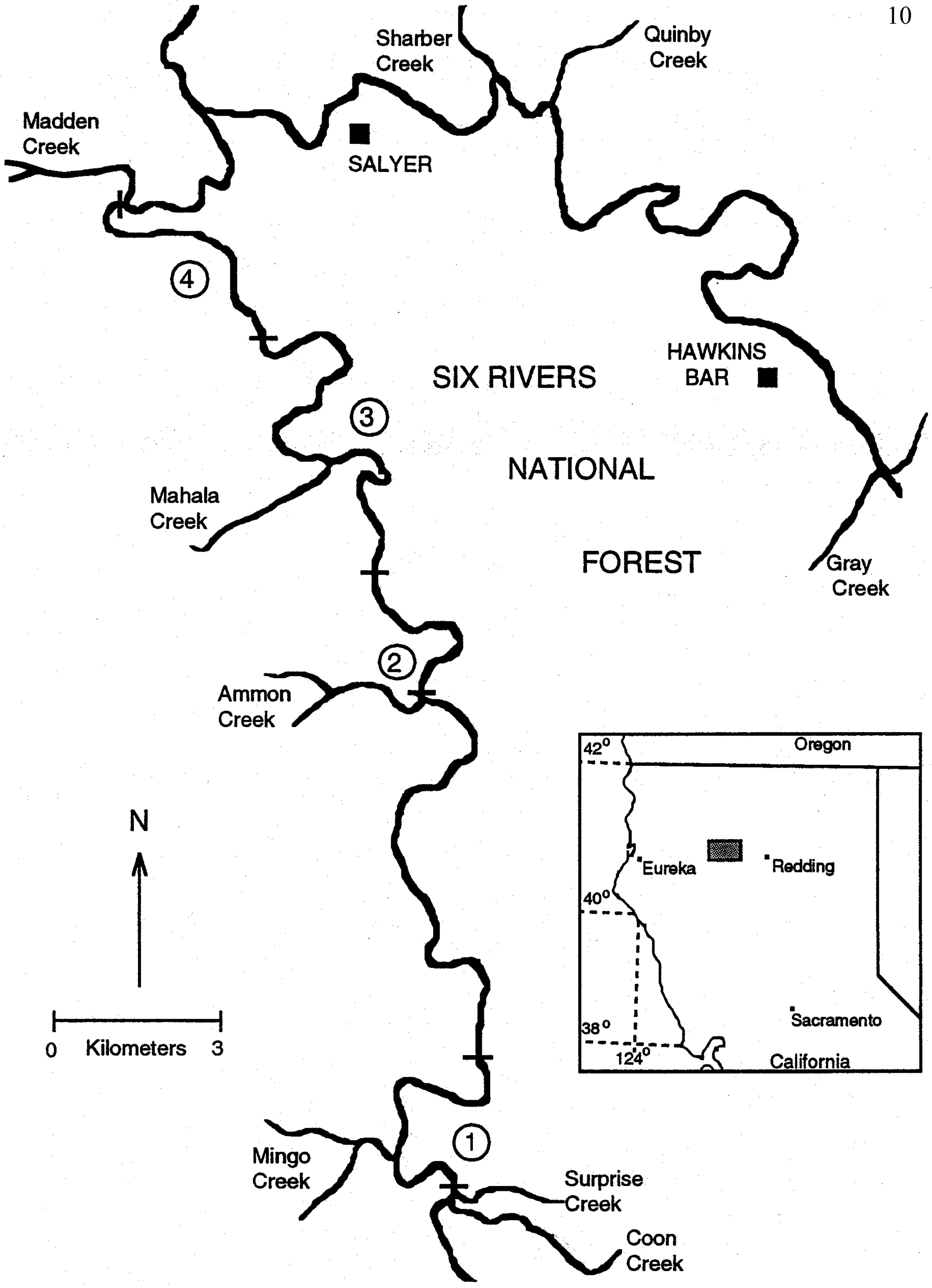


Figure 2-2. Location of study reaches along the south fork Trinity River, Humboldt and Trinity Counties, California.

pond turtle (*Clemmys marmorata*) locations. On the south fork, they were placed at the upstream ends of gravel bars, which occurred at least every few hundred meters.

All the mainstem reaches are downstream of the Lewiston/Trinity dam complex and are, thus, subject to its influences. The dams were constructed in the early 1960s, after which fish and wildlife mitigations were addressed with a minimum flow requirement of 150 cubic feet per second (cfs). Declines in anadromous fish were subsequently detected, as well as changes in channel morphology. Formation of a statewide task force to study the problems associated with the dams prompted the implementation of a schedule of increased flow releases (USDI-FWS 1995). The upper reaches (e.g. Reach 3) are most impacted by the controlled flows; further downstream, tributaries contribute natural, variable flows (USDI-BLM 1995). The south fork tributary is undammed. The mainstem at Helena drains an area of 2,968 km^2; the south fork at its mouth drains an area of 2,460 km^2. The south fork has an average annual flow of 1.1 million acre-feet (California Department of Water Resources 1982), which is comparable to the average annual flow of the mainstem at Lewiston prior to the dam (1.2 million acre-feet; Trinity River Restoration Program 1994).

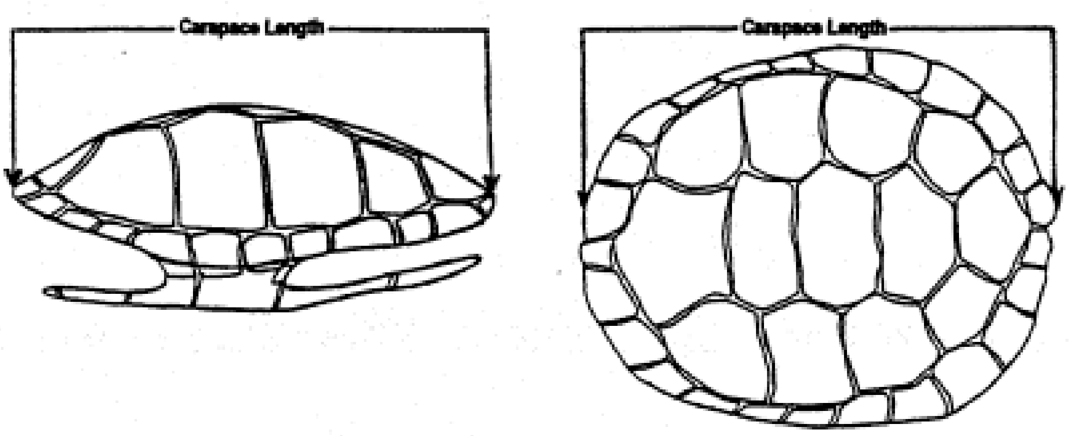
The upland habitat of both study sites may be categorized as montane hardwood-conifer or montane hardwood on north-facing and south-facing slopes respectively (Mayer and Laudenslayer 1988). Common tree species include Douglas-fir (*Pseudotsuga menziesii*), California black oak (*Quercus kelloggii*), tanoak (*Lithocarpus densiflorus*), Pacific madrone (*Arbutus menziesii*), ponderosa pine (*Pinus ponderosa*), ghost pine (*Pinus sabiniana*), and knobcone pine (*Pinus attenuata*) (Wilson et al. 1991, USDA-FS 1992). Dominant tree species in the riparian zone include white alder (*Alnus rhombifolia*) and yellow willow (*Salix lasiandra*). Both the mainstem and south fork have experienced a history of logging (Pacific Watershed Associates 1994) and the mainstem has experienced a history of mining (Clark 1992) as evidenced by the extensive mining tailings along the lower third of the study area.

Field Methods

A variety of methods were used to capture turtles and assess habitat use, and these are discussed within each chapter. However, a standardized system for handling and marking that has previously been applied to western pond turtles was used throughout (Bury 1972, Holland 1991, Zug 1991). The maximum carapace length of each captured individual was measured using calipers held over the carapace with the long axis parallel to the plastron (Figure 2-3). Each turtle was weighed to the nearest gram using a pesola scale. Sex of adults was ascertained using a set of characteristics described by Holland (1992, 1994), which include carapace shape, plastron concavity, beak orientation, and head coloration. The reproductive condition of females was ascertained by palpation.

Each individual received a unique mark, consisting of a set of notches in the carapace made with a triangular file after Cagle (1939) and Ferner (1979). For hatchlings or small juveniles whose carapaces were still soft, sharp scissors were used to create the notches. This technique provides a mark that is subtle, yet permanent and readable. Thus, turtles could be identified as first-capture or recapture. The numbering system established by Holland (1991, Figure 2-3) was employed using a distinct block of numbers relative to other western pond turtles marked in the state.

Carapace length is measured as the greatest straight-line distance in mm from the anterior end of the carapace to the posterior end, parallel to the centerline of the shell and the plastron. This usually means that the distance measured is from the "front" edge of the 2nd marginals to the back edge of the 12th marginals.



Marking Code Arrangement: Marks are made by use of a small triangular file to notch one or more marginal shields. The sum of the numbers corresponding to the marked marginals represents the total mark.

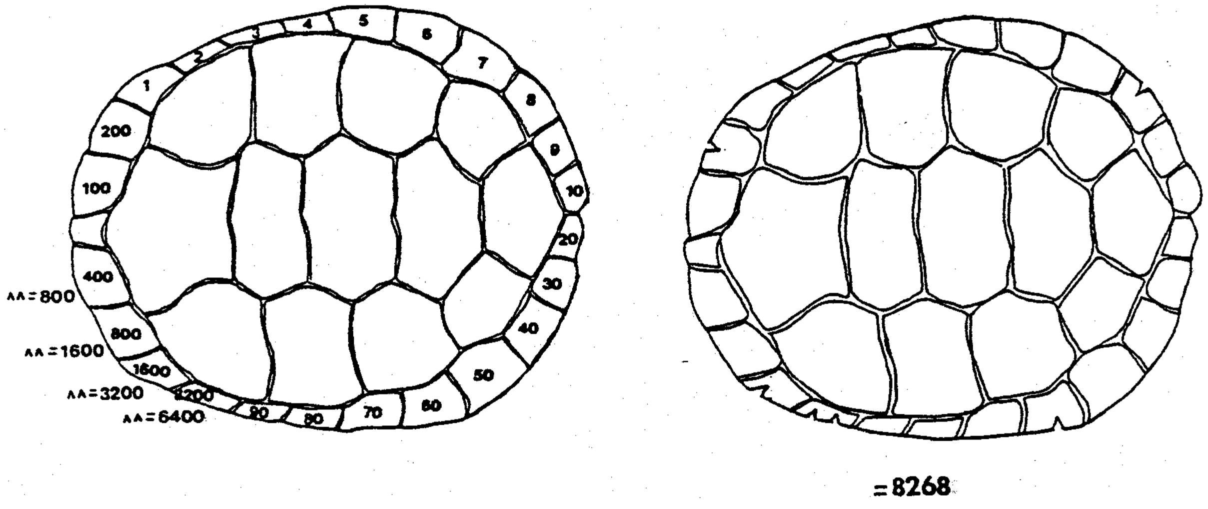


Figure 2-3. Diagram of measuring and marking techniques for western pond turtles. Adapted from Holland 1994.

Juveniles were defined on the basis of carapace length using a known relationship between size and sexual maturity. Because not many gravid females were captured, I lacked adequate information on size at maturity for Trinity River populations. However, the size at which females reach maturity varies rangewide from about 110-130 mm in carapace length (Holland 1991, per. comm. 1995) with females in northern populations tending to mature at a larger size. The cutoff between juvenile and adult turtles was consequently set at 125 mm Juveniles as defined were not identifiable as males or females because they often failed to display sexually dimorphic characteristics.

Habitat measurements varied according to research goals. However, a standard system of flow habitat classification was used for the riverine study sites (McCain et al. 1990). Flow types were either described as edgewater pool, backwater pool, glide, run, or riffle as defined in Appendix 2-A.

Statistical Analyses

A variety of analyses were performed as described in the individual chapters. Prior to application of all parametric techniques, distributions of variables were examined via measures of skewness and kurtosis, as well as normal probability plots (SAS 1991). It was assumed for multivariate analyses that univariate normality of all the variables implied multivariate normality. Deviations from normality were corrected using suitable transformations (log for continuous data, square root for count data, and arcsine for percent data; Sokal and Rolf 1981). If distributions were still nonnormal, non-parametric techniques were applied. Pearson product-moment correlation analysis was used to identify relationships among variables and either discuss or eliminate redundancies.

APPENDIX 2-A

DESCRIPTION OF RIVER HABITAT CLASSIFICATION PROCEDURES
Based on McCain et al. 1990

I. FLOW TYPES

Backwater Pool: Found along channel margins and caused by eddies around obstructions such as boulders, rootwads, or woody debris. These pools are usually shallow and are dominated by fine-grain substrates. Current velocities are quite low.

Edgewater Pool: Quiet shallow area found along the margins of the stream, typically associated with riffles. Water velocity is low and sometimes lacking. Substrate varies from cobbles to boulders.

Glide: A wide shallow pool flowing smoothly and gently, with low to moderate velocities and little or no surface turbulence. Substrate usually consists of cobble, gravel, and sand.

Run: Swiftly flowing reaches with little surface agitation and no major flow obstructions. Often appears as flooded riffles. Typical substrates are gravel, cobble and boulders.

Riffle: Steeper reaches with swiftly flowing, turbulent water with some exposed substrate. Substrate varies from cobbles to boulders and bedrock.

II. FLOW INDEX

Flow types were ranked from low to high according to the gradient as follows:
1. edgepool 2. glide 3. run 4. riffle

Because it was not feasible to define the degree of difference in gradient between each type, they were assumed to be equadistant. The following equation was then developed to represent relative flow gradient:

Flow index = (edgepool x 1) + (glide x 2) + (run x 3) + (riffle x 4)

where edgepool = proportion of target area consisting of edgepool habitat
glide = proportion of target area consisting of glide habitat
etc.

This equation produces values ranging from 1.0 to 4.0 with low values indicating low gradient flow types and high values indicating high gradient flows.

CHAPTER 3

DEMOGRAPHY OF WESTERN POND TURTLE POPULATIONS IN THE TRINITY RIVER IN THE CONTEXT OF DAM-INDUCED ALTERATIONS

ABSTRACT: Western pond turtle (*Clemmys marmorata*) populations were examined on two forks of the Trinity River, one of which is subject to the impacts of damming and one of which is not. Mark-recapture was conducted over a three year period for each population and the Jolly-Seber model was used to calculate estimates of population size. Age structures were compared with reference to potential impacts of damming on this species. Populations on the dammed fork (mainstem Trinity) were found to be slightly but not significantly sparser (turtles/ha) than populations on the undammed fork (south fork Trinity). Both populations were substantially sparser than western pond turtle populations elsewhere for which density of turtles has been assessed. The mainstem population had an adult-biased age structure relative to the south fork population and relative to a population with a known stable age distribution. I suggest that higher order streams, in general, do not support high densities of western pond turtles, possibly because of the sparse distribution of resources. I also suspect that damming of the mainstem Trinity has negatively impacted juvenile turtles.

INTRODUCTION

Populations of western pond turtles (*Clemmys marmorata*) have experienced declines throughout their range (Holland 1991, 1993, 1994). Many of these declines can be attributed to habitat alterations resulting from agricultural development and urbanization. Dams and other water diversion structures, for example, have altered aquatic habitats throughout California. Specific impacts include conversion of lotic to lentic water, reduction in wader quantity and quality, and changes in flow regimes. The mainstem Trinity River, dammed in the early 1960s, has changed dramatically as a result. Slow-moving edgewater habitats have been eliminated, riparian vegetation has expanded and encroached on the banks; and seasonally flooded marshes have become dry. Overall, the river has become more channelized with straighter edges and a lower diversity of depths and flows (Evans 1984, Wilson 1993, Hampton 1995).

Little is known about the impacts of dam-induced alterations on western pond turtle populations. Comparison of the dammed mainstem Trinity with the undammed south fork offers an opportunity to assess these impacts. These adjacent forks of the river are similar in flow volume, channel size, vegetation, and land-use history. The south fork Trinity, with its natural alternation of riffles and deep pools, resembles the mainstem in its predam condition. Habitats preferred by western pond turtles were probably more abundant prior to installation of the dam on the mainstem Trinity (Chapter 5). Several of the changes wrought by the dam, including reduction of water temperature, increased sedimentation, and decreased range of flow velocities, have lowered the availability of suitable aquatic habitat for this species.

Ultimately, a decrease in habitat suitability may manifest in demographic parameters, such as lower growth rates, altered age structures, or reduced population sizes. For example, elimination of microhabitats on which hatchlings depend, such as slow-moving waters (Holland 1991, Chapter 8) might create an adult-biased population. A decrease in water temperature might inhibit growth and/or juvenile survivorship. Although there is no historical information on densities of turtles at either the south fork or mainstem site, it can be speculated that, due to their similarity, they originally may have hosted comparable turtle populations. I propose to compare the two study sites with respect to demography of existing western pond turtle populations.

METHODS

Field Methods

Mark-recapture

Mark-recapture was conducted along four study reaches at the mainstem site that ranged from 2.3 to 2.7 kilometers in length (totalling 7.5 km; reaches 2,3,10,11, Figure 2-1). Four study reaches, totalling 15.3 km, were also examined at the south fork site (Reaches 1,2,3,4, Figure 2-2). Nonrandom site selection was acceptable, provided that a wide range of conditions were sampled; thus, the inclusion of several study reaches spanning a number of kilometers. The mainstem reaches were also selected to contain a range of turtle densities. Previous surveys revealed that reach 3 has few turtles (approximately 50), reach 10 has a moderate number of turtles (approximately 80), and reach 11 has many turtles (approximately 160) relative to the overall turtle distribution along the 63 kilometers between Lewiston Dam and the north fork of the Trinity (derived from Lind et al. 1992).

A total of nine rounds of capture occurred on reaches 10 and 11, two during 1991 and 1992 and five during 1993. Due to logistical constraints, Reach 3 was only sampled during 1992-1993, yielding a total of seven rounds of capture. Reach 2 was eliminated from the study after several sampling rounds yielded no captures and revealed a high level of human disturbance as a result of settlement in the floodplain and adjacent upland areas. All capture rounds were during the months of April-September, before and after which western pond turtles are overwintering (Reese and Welsh 1996, Chapter 9). At the south fork study site, mark-recapture was conducted along reaches 1-4 during 1992-1994. The sampling period started later (May) because high gradient rapids in the study area rendered it unswimmable until that time. A total of nine rounds of capture occurred on reaches 1, 3, and 4: four during the first year, two during the second year, and three during the third year. Due to logistical constraints, Reach 2 was only sampled during 1992 and 1994, yielding a total of seven rounds of capture.

One-half reach was travelled per day (about 1.5 kilometers), such that it took six days to complete each round of capture at each study site. One snorkeler was stationed on each side of the river, moving downstream and searching. All swimmable areas were searched, where "swimmable" was defined as safely navigable by a trained snorkeler. This definition tended to exclude only high gradient riffles (Appendix 2-A) from the search. Offshoots of the main channel, including side channels and backwater pools, were included in the search.

Searching consisted of visually scanning underwater areas for turtles, as well as manually exploring bank undercuts, caves, rock crevices, debris piles, and clumps of vegetation. The search area was limited to within 4 meters of the shoreline because that was the maximum distance a snorkeler could scan visually while moving downstream In addition, beyond four meters the rapid flows often rendered swimming dangerous. Considering that basking sites and cover objects are clustered along shorelines, and that western pond turtles are relatively poor swimmers (Holland 1991), it is likely that the search area harbored the majority of turtles.

Hatchling and juvenile western pond turtles, due to their small size and crypticity, are likely to be more difficult to catch. They also inhabit microhabitats that are not easily accessed by a snorkeler, such as shallow edgewaters (Chapter 8). Specific measures were therefore adopted to increase the probability of finding these younger age classes. These including walking searches of all gravel bars and other areas too shallow to swim and searches of seasonal pools connected to the river. Special attention was given to root wads, emergent vegetation, and other fine-scale aquatic features that might hide hatchlings and juveniles.

All captured turtles were measured (maximum carapace length), weighed, and marked as described in Chapter 2.

Float surveys

Logistical limitations did not permit snorkeling of the remaining thirteen reaches of the mainstem Trinity River study site (Figure 2-1). However, "float surveys" were conducted, which consisted of two observers equipped with binoculars floating the entire 63 kilometers and counting the number of basking turtles on both sides of the river. Floats were only conducted at times when turtles were likely to be basking, namely on clear, sunny days between 0900 and 1730 hours. Observers floated four reaches per day such that it took four days to complete all reaches. Five complete float surveys were conducted during the following months: July 1991, August 1991, May 1992, July 1992, September 1992. In addition, the private land gaps described above were floated during the July 1992 survey.

Because reaches 10 and 11 played such as significant role in my calculations of population size for the whole study area, they were sampled multiple times during each sampling month to increase accuracy of basking turtle counts. They were floated three times each in July 1991, July 1992, and September 1992, four times in August 1991, and five times in May 1992. Counts of basking turtles along these two reaches were averaged within each sampling month. In addition, each mainstem study reaches was floated three times during July of 1992 to obtain estimates of the sampling error.

Data Analysis

Population Size

A. Mark-recapture reaches

The study populations were clearly not "closed" in the sense of having a constant size during the period of investigation (White et al. 1982). Because the sampling spanned a period of three years, additions and deletions to the populations via birth and death undoubtedly occurred. Also, because the study sites consisted of river reaches, turtles had the potential to enter and leave the populations at the upstream and downstream ends of each site as well as making some overland movements (Chapter 9). Open population models, based on the Jolly-Seber model (Jolly 1965, Seber 1965), were used because they allow for birth, death, and migration.

Emphasis has recently shifted to the application of open models for estimation of survival rates as opposed to population size; survival rate estimates are more robust to violations of model assumptions (Lebreton et al. 1992). My purpose, however, was to estimate population size for comparison of turtle densities between the mainstem and south fork study sites. Survival parameters are reported but, given the ecology of the study species, I was unable to distinguish between deaths and emigration or between births and immigration. Western pond turtles leave the Trinity River for temporary terrestrial excursions (Chapter 9), as well as make long-distance aquatic movements. Turtles in other locales have moved as far as several miles within streams and returned up to six months later (Holland 1994). Either terrestrial or aquatic migration could make these individuals effectively invisible in the mark-recapture samples for extended periods of time. Considering that individuals of this species may live forty years or more (Holland 1991), missing individuals are more likely to have emigrated than to have died.

In analyzing the mark-recapture data, each capture round was treated as a separate sample, such that there were nine total samples, and eight sampling intervals, for each study site. In defining the lengths of the sampling intervals, overwintering periods were included because, although the turtles are dormant (Reese and Welsh 1996), mortality does occur during that time. Thus, the sampling intervals from the last capture round of one year to the first capture round of the next were particularly long. Reaches 10 and 11 of the mainstem and reaches 1, 3 and 4 of the south fork were treated as single datasets, respectively, because each of these groups of reaches experienced the same capture rounds. Separate models were applied to reach 3 of the mainstem and reach 2 of the south fork because they experienced fewer capture rounds.

The program RELEASE, which implements the theory of Burnham et al. (1987), was used to determine whether each set of mark-recapture data fit the Jolly-Seber model. It includes goodness of fit tests (contingency table chi-squares) for the assumption of site-specific parameters. Fisher exact tests were used in the case of small cell counts. If test results were nonsignificant at the alpha =.05 level, indicating no evidence for lack of fit to the model, then additional programs were used to compute population estimates.

JOLLYAGE (Hines 1990) allows for the populations of interest to be treated as having two age classes with potentially different survival and capture probabilities. For populations of aquatic turtles, survival rates are generally lower in the younger age classes because of their susceptibility to predation and abiotic factors (Gibbons 1990). There are also likely to be age-related differences in capture probability because the smaller body size and more cryptic habits of juveniles renders them more difficult to capture (Congdon et al. 1993). The JOLLYAGE program, implementing theory from Pollock (1981), tests whether survival and capture rates are different between age classes using contingency table chi-squares. The classes "juveniles" and "adults" were defined on the basis of carapace length as described in Chapter 2.

If the JOLLYAGE tests yielded a nonsignificant result at the alpha=.05 level, the two age classes were combined and the mark-recapture data were analyzed using the program JOLLY (Hines 1990). This program includes a standard Jolly-Seber model (model A; Jolly 1965, Seber 1965), a death but no immigration model (model A′; Darroch 1959), a constant survival model (B) and a constant survival and capture model (D). The standard model is "open" in that it allows for births, immigration, deaths, and emigration. The death but no immigration model has the more restrictive assumption that births and immigration are negligible. The constant survival model assumes that survival probabilities are constant over the course of the study, while the constant survival and capture model additionally assumes that capture probabilities are constant over the course of the study. By reducing the number of parameters to be estimated, these simpler models have the potential to gain better precision of estimates than the standard Jolly-Seber (Pollock et al. 1990).

Both the JOLLY and JOI:LYAGE models assume the following: 1) that marks are retained during the course of the study 2) that captured individuals are released immediately after sampling 3) that individuals have equal capture probabilities in each sample and 4) that marked individuals have equal probabilities of survival to the next sampling period, with the exception of the variance between age classes allowed in JOLLYAGE. As described above, these model assumptions were tested using contingency table chi-squares. The results must be interpreted with the understanding that a nonsignificant goodness-of-fit statistic does not guarantee that all the model assumptions have been met. Small populations with low capture probabilities and survival rates can reduce the power of the test. Also, permanent changes in capture or survival probabilities as a result of marking cannot be detected; the tests are geared to detect short-term influences (Pollock et al. 1990).

Thus, it is worth considering the conceptual validity of the assumptions for the study populations. Individuals are released immediately after capture and marking, and all carapace notches are retained during the course of the study, satisfying the first two assumptions. The assumption of equal capture probabilities may or may not be met. Unequal capture probabilities can either result from trap-shy responses or heterogeneity among individuals. Because turtles were captured by snorkeling as opposed to trapping, trap-shy responses do not occur. And, assuming that snorkellers consistently and thoroughly search turtle refugia, the effect of "snorkel-shy" responses on capture probabilities will probably be negligable. However, it is possible that individuals differ in their likelihood of being captured; the chi-square tests identify this phenomenon. The third assumption of equal survival probabilities is the most difficult to examine. Because the handling and marking techniques are noninvasive, and marks are cryptic with respect to predators, there are not likely to be differences in survival rates between marked and unmarked individuals. Other heterogeneity in survival rates may exist, and is identified to the degree possible by the chi-square tests. Pollock et. al. (1990) proposed that, in natural populations, for the common case of heterogeneous survival rates that are positively correlated for the same individual, biases on population size estimators are likely to be small.

B. Remaining mainstem reaches

Population estimates for the remaining 13 reaches of the mainstem that were not sampled by snorkeling (reaches 1-2, 4-9, 12-16) were derived from the visual survey data. Using the population size estimates for mark-recapture reaches 10 and 11 generated from the mark-recapture data, I was able to derive a ratio of basking turtles to resident turtles for these two reaches. A separate ratio was derived for each of the five sampling periods. Note that although mark-recapture did occur along reach 3, the results were not included in these calculations because the small number of captured turtles there seemed likely to bias the ratio. The ratios of baskers/residents (reaches 10 and 11) for each sampling period were then applied to counts of buskers in the remaining river reaches to derive estimates of residents. Total estimates of population size for the mainstem study site within each sampling period were obtained by summing estimates of residents across the sixteen study reaches. Three separate estimates were obtained for the July 1992 sampling period (which included three float surveys) and compared for error estimation. .

Population Density

Population densities were calculated by dividing the population estimate by an estimate of river surface area for each study site. Mainstem river surface area was obtained from a GIS map of the river contour created from aerial photographs by Wilson (1993). The aerials used were spatially corrected "ortho-photos" taken in August of 1989. South fork river surface area was obtained from a GIS map of the river contour that was created by digitizing the right and left banks from a topographic map. For each site, the GIS river contour was divided into reaches as designated in Figures 2-1 and 2-2 and then an area was calculated for the polygon formed by the right bank, left bank, upstream end, and downstream end of each reach. Individual density estimates for each reach were obtained as well as the density for the entire 63 kilometers of the mainstem and 15 km of the south fork.

Population Structure

In evaluating age structure for turtle populations, growth rings on the plastral shields are typically counted with the assumption that one growth ring is produced per year. In fact, several rings may be produced in a single year, or alternately no rings may be produced (Holland, pers. comm., Moll and Legler 1971). Thus, counts of plastral rings do not correspond directly with age. Additionally, annuli in a significant portion of the population may be uncountable due to wear of the plastral shields. Interpretation of other indicators of age, such as maximum carapace length, is tricky given that growth rates vary among individuals and between populations. Unless some individuals have been measured annually since birth, carapace length can only be used as a relative indicator of age within populations. To compare between populations, models that include growth rate data must be applied. Because this study lacked the longevity and high juvenile capture rate required for growth rate information, I selected a more conservative method of comparing populations, namely to group individuals into just two age classes (juveniles and adults) on the basis of the known relationship between carapace length and sexual maturity (Chapter 2).

Using the capture data, the number of adult and juvenile turtles on the mainstem and south fork sites, respectively, were tallied for each sampling year. Turtles that were recaptured from one year to the next were included in the tally. The mean tallies across years were then calculated to obtain an estimate of average age structure for each site. Average age structure was also derived from 9 years of data from Hayfork Creek, a tributary of the south fork Trinity (Holland and Bury; unpublished results). Hayfork Creek is in close proximity to both the mainstem and south fork Trinity and has a stable size distribution relative to 1968 censuses (Bury, 1972, Holland pers. comm.). Thus, it served as a useful comparison to the lesser-known Trinity populations. Chi-square contingency table analysis as used to assess whether the proportion of juveniles and adults differed between the three populations. Multiple comparison proportion tests (Zar 1984) identified which pair of proportions were responsible for the overall difference.

This approach assumes that the proportions of juveniles and adults captured in a particular sampling period is representative of the true proportion in the population, or at least that the average proportion across sampling periods is representative. Although this assumption is not testable in the context of the current study, the results of the JOLLYAGE analysis described above may be illuminating. They provide a comparison of the recapture rates for adult and juvenile turtles. A difference in recapture rates would indicate that the perceived ratio of age classes is biased relative to the true age structure.

RESULTS

At both study sites, capturing western pond turtles proved difficult and required the intensive search effort described in the Field Methods. These cryptic reptiles utilized a variety of underwater refugia, some of which were difficult or impossible to search. Refugia included undercut banks and mammal (e.g. river otter) caves, beaver dams and other piles of woody debris, sand and silt, large boulders, and root masses. The complexity of refugia and their frequent location in deep water (see Chapter 5) restricted capture to only 10-20% of the population during each sampling period.

Population Size

A. Mark-recapture reaches

For the larger mainstem dataset (reaches 10 and 11), the results of Jollyage provided evidence for an age-dependent effect (overall chi-square = 7.79, p = 0.0053). As anticipated, given the crypticity of juveniles, the recapture probability for juveniles was lower than that for adults. Model A2 (the standard Jolly-Seber with age-dependency), appeared to fit the data; the contingency chi-square table was nonsignificant, indicating no lack of fit to the model (overall chi-square = 11.86, p = 0.22). However, because of low sample sizes of captured juveniles, survival rates for the juvenile age class were not estimable for most sampling periods, and estimates of recruitment (birth plus immigration) were confounded. For the smaller datasets (mainstem reach 3 and southfork reach 2), the effects of small sample size were even more apparent; there were not enough data to perform the Jollyage tests of age-dependence. I abandoned the age-dependent models altogether, deeming them too complex for the data.

A total of 247 unique (i.e. first-capture) turtles were caught on mainstem reaches 10 and 11 during the course of the study. For these reaches, the chi-square contingency table tests in RELEASE indicated no reason to reject the Jolly-Seber model (overall chi-square = 17.85 on 28 df, p = 0.93). Both model A (standard Jolly-Seber) and model B (constant survival) appeared to fit the data (Table 3-1), whereas the goodness-of-fit tests produced significantly larger chi-square values for models A' and D. The test comparing model A to model B does not reject the simpler model (B) in favor of A (chi-square = 3.68, p = 0.72). However, examination of the parameter estimates (Table 3-2) reveals greater precision from model A; the standard errors for the population size estimate and the survival estimate are smaller. Indeed, Pollock et al. (1990) noted that when estimating the average population size across sampling periods, an average of the Jolly-Seber estimates N_i may be more precise than an average of the model B or D estimates. The authors attribute this to the fact that in these simpler models the N_i estimators tend to be positively correlated with one another. I therefore report the mean population size estimate across all sampling periods for these reaches to be 255 individuals with a standard error of 45 (Table 3-2).

A total of 34 unique turtles were caught on mainstem reach 3. Because of the small dataset, only two of the sampling periods had sufficient data for calculation of the goodness-of-fit test in RELEASE. However, overall test results indicated no evidence for lack of fit to the Jolly Seber model (overall chi-square = 1.32 on 13 df, p =.72). Model A'

Table 3-1. Tests for the Jolly-Seber model (A), the death but no immigration model (A'), the constant survival model (B), and the constant capture and survival model (D) for western pond turtles in reaches 10 and 11 of the mainstem Trinity River.

Test	x^2	df	P
Goodness-of-fit to Model A	18.83	13	0.13
Goodness-of-fit to Model A'	41.86	17	0.00
Goodness-of-fit to Model B	22.51	19	0.26
Goodness-of-fit to Model D	42.27	26	0.02
Model B versus Model A	**3.68**	**6**	**0.72**

Table 3-2. Jolly-Seber estimates and approximate standard errors under the Jolly Seber model (A) and the constant survival model (B) for western pond turtles in the mainstem Trinity River, reaches 10 and 11, captured during nine sampling periods from 1991-1993. N_i = population size. o_i = survival rate per unit time.

Period	Date	N_i	SE	o_i	SE
Model A--Jolly-Seber model					
1	June 1991			1.00	0.005
2	July 1991	590	260.4	1.00	0.001
3	April 1992	180	40.1	1.00	0.006
4	May-June 1992	216	47.6	1.00	0.006
5	July 1992	179	44.0	1.00	0.011
6	August 1992	230	70.0	1.01	0.023
7	September 1992	207	129.9	1.00	0.002
8	May 1993	185	55.0		
	$\overline{X}$	**255**	**45.2**	**1.00**	**0.003**
Model B--constant survival model					
2	July 1991	586	224.3		
3	April 1992	215	32.5		
4	May-June 1992	232	30.0		
5	July 1992	196	20.9	0.70[a]	0.072
6	August 1992	262	38.7		
7	September 1992	150	12.6		
8	May 1993	179	29.6		
9	August 1993	243	43.5		
	$\overline{X}$	**258**	**96.8**		

[a] This estimate pertains to all years of the study due to the assumption of constant survival.

(no immigration) appeared to fit the data (overall chi-square = 1.06, p = 0.59) and provided a population estimate of 40 individuals for this reach. Standard errors were not generated, or were survival rates estimated because of the small sample size (Table 3-3).

A total of 230 unique (i.e. first-capture) turtles were caught on south fork reaches 1, 3, and 4. RELEASE indicated no reason to reject the Jolly-Seber model (overall chi-square = 25.5 on 19 df, p = 0.14). Of the models offered in Jolly, models A, A' and D all appeared to fit the data (Table 3-4). The goodness-of-fit tests revealed no significant difference between the fits for model A (standard Jolly-Seber) and the two simpler models Examination of the model A estimates (Table 3-5) reveals that standard errors were not estimable for some parameters during some sampling periods, indicating insufficient data for this model. Comparison of the other two models indicates higher precision for model A'; it yielded smaller standard errors for both the population size and the survival estimate I thus selected model A' (death but no immigration) as the most suitable, yielding a mean population estimate of 447 (standard error = 118, Table 3-5).

A total of 48 unique turtles were captured on reach 2 of the south fork. RELEASE indicated no lack of fit to the Jolly-Seber model (overall chi-square = 6.24 on 10 df, p = 0.79), although two sampling periods had insufficient data due to few captures. Model A' appeared to fit the data (overall chi-square = 0.495, p = 0.78) and provided a population estimate of 53 individuals for this reach (standard error = 13; Table 3-6). Survival rats were not estimated as a result of the small sample size.

Examination of the capture histories for both study sites revealed an unusual trend in the data. Table 3-7 displays the capture history table for reaches 10 and 11 from the

Table 3-3. Jolly-Seber estimates and approximate standard errors under the death but no immigration model (A') for western pond turtles in reach 3 of the mainstem Trinity River captured during seven sampling periods from 1992-1993.

Period	Date	N_i	SE
1	April 1992	28	0.0
2	May-June 1992	63	35.5
3	July 1992	44	18.5
4	August 1992	77	NE
5	September 1992	20	9.9
6	May 1993	8	NE
$\bar{X}$		**40**	**NE**

NE Not estimable due to insufficient data for this model.

Table 3-4. Tests for the Jolly-Seber model (A), the death but no immigration model (A'), and the constant capture and survival model (D) for western pond turtles in reaches 1, 3, and 4 of the south fork Trinity River.

Test	x^2	df	P
Goodness-of-fit to Model A	9.64	6	0.14
Goodness-of-fit to Model A'	13.41	10	0.20
Goodness-of-fit to Model B	22.72	16	0.12
Model A versus Model A'	**Z=1.23***		**0.11**
Model D versus Model A	**13.08**	**10**	**0.22**

*Test described in Pollock 1974.

Table 3-5. Jolly-Seber estimates and approximate standard errors under the Jolly Seber model (A), the death but no immigration model (A'), and the constant survival and capture model (D) for western pond turtles in reaches 1, 3, and 4 of the south fork Trinity River captured during nine sampling periods from 1992-1994.

Period	Date		N_i	SE	o_i	SE
Model A--Jolly-Seber model						
1	July 1992				1.00	0.009
2	Early August 1992		110	100.9	1.01	0.028
3	Late- August 1992		128	87.8	1.04	0.050
4	September 1992		1000	NE	1.00	0.003
5	June-July 1993		287	115.6	1.00	0.005
6	September 1993		314	101.9	1.00	0.001
7	June 1994		243	78.1	1.00	0.015
8	July 1994		271	130.1		
		$\bar{X}$	**336**	**NE**	**1.00**	**0.007**
Model A'--death but no immigration model						
1	July 1992		388	86.7	1.00	0.009
2	Early August 1992		335	69.3	1.01	0.028
3	Late August 1992		407	132.6	1.04	0.049
4	September 1992		979	918.8	1.00	0.003
5	June-July 1993		454	84.1	1.00	0.004
6	September 1993		433	86.2	1.00	0.001
7	June 1994		330	77.4	1.00	0.014
8	July 1994		247	94.4		
		$\bar{X}$	**447**	**118.5**	**1.00**	**0.007**
Model D-constant survival and capture model						
2	Early August 1992		149	40.0		
3	Late August 1992		119	30.8		
4	September 1992		130	31.0		
5	June-July 1993		451	90.3	0.92[a]	0.019
6	September 1993		537	99.7		
7	June 1994		488	94.7		
8	July 1994		426	83.3		
9	August 1994		285	62.7		
		$\bar{X}$	**323**	**141.5**		

[a] This estimate pertains to all years of the study due to the assumption of constant survival.

NE Not estimable as a result of insufficient data for this model.

Table 3-6. Jolly-Seber estimates and approximate standard errors under the death but no immigration model (A') for western pond turtles in reach 2 of the south fork Trinity River captured during seven sampling periods from 1992-1994.

Period	Date	N_i	S E
1	July 1992	43	2.1
2	Early Aug 1992	65	26.8
3	Late Aug 1992	59	30.9
4	September 1992	54	19.3
5	June 1994	32	22.1
6	July 1994	66	56.9
	$\overline{X}$	**53**	**12.3**

Table 3-7. Summary table* of capture histories for western pond turtles caught on the mainstem Trinity River during nine sampling periods from 1991-1993. Dates of sampling periods appear in Table 3-2.

Time of Last	Time of Recapture (period)								
Capture (Period)	1	2	3	4	5	6	7	8	9
1	0	5	5	1	0	1	0	2	2
2	0	0	10	12	7	6	2	8	5
3	0	0	0	6	5	3	2	3	1
4	0	0	0	0	6	1	2	6	4
5	0	0	0	0	0	2	4	4	2
6	0	0	0	0	0	0	2	5	3
7	0	0	0	0	0	0	0	1	1
8	0	0	0	0	0	0	0	0	9
9	0	0	0	0	0	0	0	0	0

* B-Table format from Leslie et al. 1953.

mainstem site. It is notable that numerous individuals captured in the first few sampling periods were not recaptured until the last few sampling periods. For example, eight individuals captured in period 2 were not recaptured until period 8 (two years later). This is in contrast to the more common pattern of individuals being recaptured soon after their first capture and then not recaptured at all.

B. Remaining mainstem reaches

The ratio of basking turtles to resident turtles on reaches 10 and 11, derived from the mark-recapture data, ranged from 2.0% to 20.7% (Table 3-8). With the exception of the September 1992 sample, the ratios are relatively consistent: The low ratio during this late sampling period (resulting from only 4 turtles observed basking) can be attributed to a seasonal effect. Radiotelemetry data (Reese and Welsh 1996) revealed that by September, turtles are leaving the river to travel to terrestrial overwintering sites. It is likely that during this survey, only a small fraction of the population was still resident in the river. Because such low counts are likely to bias the population estimates, this survey was excluded from the analysis.

Population estimates for all 16 study reaches ranged from 899 to 1323 turtles (Table 3-8). The July 1992 survey indicated that the "gap" reaches (Figure 2-1) harbor an additional 157-253 turtles. Comparison of estimates of population size.(including the gap reaches) generated from the multiple surveys during July 1992 indicated as much as a fifty percent difference between estimates taken during the same month (Table 3-8). Taking the mean estimate across sampling periods is likely to mitigate for some of this .

Table 3-8. Estimates of western pond turtle population size derived from counts of basking turtles along 16 reaches of the mainstem Trinity River.

Sampling Period	Ratio of Baskers/Residents (Reaches 10 and 11)	Derived Population Size (All sixteen reaches)
July 1991	41/255 = 16 %	1293 individuals
August 1991	53/255 = 21 %	899 individuals
May 1992	51/255 = 20 %	1022 individuals
July 1992	47/255 = 18 %	904, 1323, 1251 Individuals*
September 1992	5/255 = 2 %	**

* Three replicate surveys conducted during July 1992 to obtain error rates of estimates.

** Not computed due to low sample size of basking turtles.

difference, but overall it suggests that there is an error of +/- two hundred turtles. This large error term is not surprising, given that population estimates were generated from counts of basking turtles. Basking surveys are particularly subject to variability from temporal, environmental factors (Jones and Hartfield 1995). Averaging across all sampling periods, and including gap reaches, an estimated 1318 western pond turtles inhabit the 63 kilometer stretch of river between the Lewiston Dam and the confluence with the North Fork Trinity.

Population Density

Analysis of polygons from the subdivided river contour revealed that mainstem reaches vary from 4.79 to 15.47 hectares in size, yielding a range of density estimates from 0.45 turtles/hectare to 21.75 turtles/hectare (Table 3-9). The overall density, averaging across all reaches was 6.33 western pond turtles/hectare of mainstem river. The south fork reaches varied from 5.89 to 13.51 hectares in size. Using the mark-recapture population estimates, this yields an overall density estimate of 12.39 turtles/hectare for the four reaches.

Population Structure

Size structure histograms for the mainstem, south fork, and Hayfork Creek populations display a difference in the proportion of juveniles to adults, as revealed by the significant chi-square value (chi-square= 6.1, $p < .05$; Figure 3-1). Proportion tests indicated that the mainstem has a significantly smaller proportion of juvenile turtles than

Table 3-9. Density of western pond turtle populations along the mainstem Trinity River. (See Figure 2-1 for location of study reaches)

Reach	Estimated number of turtles (mean across surveys)	Hectares of water surface	Density (turtles/ha)
1	4.3	9.53	0.45
2	85.7	15.47	5.54
3	34.5	8.09	4.26
4	35.2	6.47	5.43
gap*	6.3	9.64	0.66
5	151.3	7.21	20.99
gap*	98.3	10.13	9.71
6	165.3	7.60	21.75
7	24.3	6.77	3.59
8	22.8	4.79	4.77
9	60.0	5.78	10.38
10	13.7	6.70	2.04
11	34.2	6.57	5.21
12	60.7	5.80	10.46
13	64.7	9.65	6.70
14	8.5	7.72	1.10
15	4.7	9.47	0.49
gap*	68.7	13.86	4.95
16	13.8	7.42	1.86

$\bar{X}$ = **6.33 turtles/hectare**

*gaps consist of portions that are unlabelled on Figure 2-1, but were surveyed.

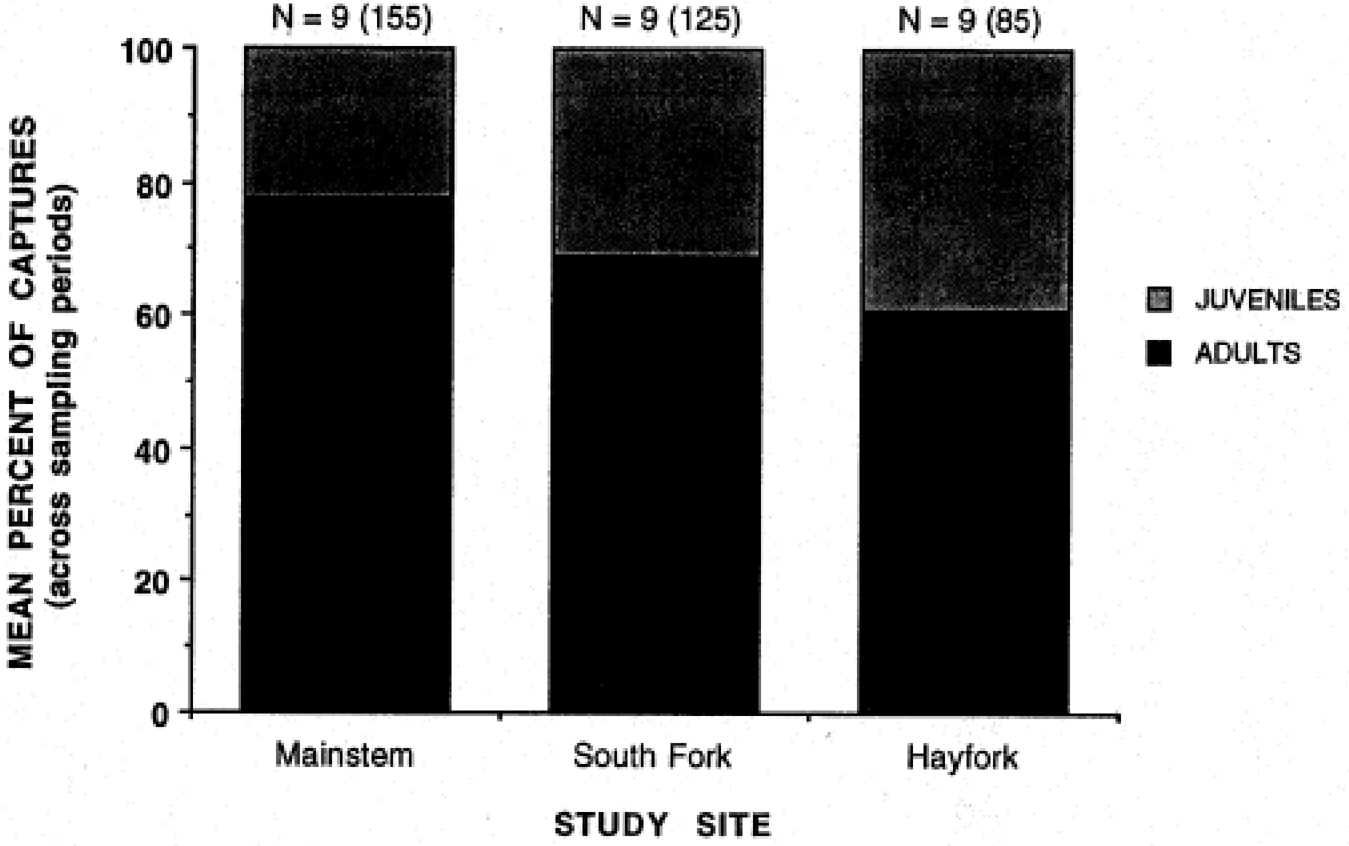


Figure 3-1. Percent of captured turtles that were adults and juveniles at each of three sites. Percents are averaged across sampling periods for each site. N = number of sampling periods (n = # captures).

either the south fork or Hayfork ($q = 2.47$, $p < .05$ and $q = 3.87$, $p < .05$ respectively). The age structures were not significantly different between the south fork and Hayfork ($q = 1.62$, $p > .05$). Examination of the JOLLYAGE results indicates that juvenile turtles at the mainstem site have significantly lower survival and/or capture probabilities than adult turtles (chi-square = 7.79, $p = .0053$, see Results: Population Size). While 39% of captured adult turtles were eventually recaptured, only 15% of juveniles were recaptured. At the south fork site, in contrast, the survival and/or capture probabilities were not significantly different (chi-square = 4.93, $p = .1768$). Twenty-five percent of adults and 23% of juveniles were eventually recaptured.

DISCUSSION

The unusual capture histories for both the mainstem and the south fork populations indicate that some form of temporary emigration is occurring. Some turtles are effectively "disappearing" from the population between their first capture and subsequent captures, whether it be actual departure from the study area or departure from capturability (e.g. turtles becoming capture shy and moving into inaccessible underwater refugia). Results of the goodness-of-fit tests in the JOLLY program do not provide evidence that the temporary emigration is Markovian (i.e. related to previous locations, Nichols, pers. comm. 1995), suggesting that the unusual capture histories stem from random temporary emigration and/or low capture probabilities. Temporary emigration certainly does occur, both within the watercourse and onto land, as evidenced by the radiotelemetry results

(Reese and Welsh 1996). Low capture probabilities also occur because western pond turtles are cryptic and able to access effective refugia. While Markovian temporary emigration leads to biased, estimates of population size, random temporary emigration does not (Nichols, pers. comm. 1995).

The density of western pond turtles in both the mainstem and the south fork of the Trinity River was startlingly low. This species achieves densities as high as 1000 individuals/hectare at other locales (Holland 1991). The density in nearby Hayfork Creek has been as high as 750 individuals/hectare (Bury 1972). The low density in the mainstem is not likely attributable to the dam, since densities in the undammed south fork are only slightly higher. Low densities may result from characteristics of these sites with respect to resource distribution. Namely, they are both large rivers with food, cover, and basking site resources restricted to the shorelines. Although turtles can cross the river, the middle section is not likely to provide suitable habitat (Chapter 5). Thus, the density estimates are deflated by the fact that much of the river area consists of unsuitable habitat.

However, even if these middle portions are excluded from the calculations, the densities are still an order of magnitude lower than Hayfork Creek. Turtle populations may be limited by a sparse distribution of resources in large rivers such as these; Holland (pers. comm. 1995) reported an inverse relationship between stream order and density of western pond turtles. Alternatively, the mainstem and south fork of the Trinity may have both experienced impacts that depressed the size of western pond turtle populations. The mainstem has been dramatically altered by mining, logging, and damming (BLM 1995), and the south fork has experienced substantial logging (U.S. Forest Service 1992).

However, Hayfork Creek has also been impacted by mining and logging (Bury 1972). Further research on rangewide population densities might clarify the significance of the low densities in the Trinity system

The results of the age structure analysis indicate that the mainstem population has a smaller proportion of juveniles than either the south fork Trinity River population or the Hayfork population, the latter of which is known to be stable over a period of more than twenty-five years. This could result from lower recruitment of juveniles into the population, lower survival rates of juveniles, and/or a bias in the study from lower capture rates of juveniles. The latter two hypotheses are likely, given that survival and/or recapture probabilities for juveniles were lower than those for adults in the mainstem, but not in the south fork. The JOLLYAGE tests do not distinguish lower survival probabilities from lower capture probabilities, since these effects have the same outcome in the sampled population. However, there is no reason to suspect that juveniles would be more difficult to recapture on the mainstem, but not on the south fork; identical capture techniques were employed at the two sites. It can, thus, be speculated that lower survival rates of juveniles than adults on the mainstem are responsible for the adult-biased age structure.

The factors causing lower juvenile than adult survival require further investigation. The smaller body size of juveniles poses an increased susceptibility to predation from aquatic predators such as otters (*Lutra canadensis*) and minks (*Mustela vison*). Unnatural factors could also play a role, the most significant being the Lewiston/Trinity Dams. Changes wrought by the dams include a decrease in shallow, lentic edgewaters and a lowering of water temperatures (Hampton 1995, Trinity River Restoration Program 1994). These changes might impact juvenile turtles, who are associated with lentic, warm waters (Chapter 8). The results could also be explained by adult survivorship being relatively high on the mainstem Trinity, although it is not clear why this would occur. The larger proportion of juveniles in the stable Hayfork population leans the interpretation of age structure towards unnatural changes in the mainstem. Assessment of juvenile versus adult survival rates at other sites is warranted.

The combination of low densities and an adult-biased age structure on the mainstem Trinity River is not indicative of a "healthy" population. Because of its size and gradient, the Trinity River may never have been the most productive area for western pond turtles. One area known to have harbored extremely dense populations was the Central Valley prior to large-scale agricultural development (Tulare Lake, Kern Lake, and Buena Vista Lake, Holland 1991, Preston 1981). Habitat provided by the huge, shallow lakes that existed at that time certainly contrasts with the small pockets of lentic water in the Trinity River. Higher order streams such as the Trinity may play a supplementary role in the ecology of the species, serving as corridors for migration and gene exchange between slower streams and adjacent ponds. Indeed, at both the mainstem and south fork sites, turtles make seasonal journeys to other bodies of water (Chapter 9), some of which may be associated with mating. Unfortunately, habitat such as that provided by the Trinity may take on an unnatural significance now that western pond turtle habitat in other locations, such as the Central Valley, has been altered or eliminated.

Western pond turtles typify the order Chelonia in having long lifespans, delayed sexual maturity, iteroparity, and high adult survival rates. This characteristic suite of life history traits results in turtle populations that are limited in their ability to rebound from increased mortality of any age class. Despite high adult survivorship, low fecundity and low nest survival necessitates extremely high juvenile survival to maintain stable populations (Congdon et al. 1993). In general, species with low intrinsic rates of increase face higher extinction probabilities because their populations recover slowly from a depressed condition (Pimm et al. 1988). Long-lived species also exhibit a lagtime in their response to population impacts because of long generation times and consequently slow replacement rates even under natural conditions. Thus, particular attention should be paid to evidence of biased age structures or other indications of population ill-health because they are indicative of long-term impacts to populations with limited recovery capabilities.

ACKNOWLEDGEMENTS

I thank the USDI Bureau of Reclamation and Fish and Wildlife Service for providing the funding for and facilitating this project. Thanks to Don Ashton, Jenny Glueck, Amy Lind, Josh Metz, Sarah Mook, Kari Sadowski, Kary Schlick, Kris Shimizu, Doug Welsh, Cindy Walker, and Randy Wilson for their participation in mark-recapture dives. Thanks also to Don Ashton, Kris Shimizu and Kary Schlick for entering and checking data. Special thanks to Randy Wilson for providing 1991 data from the mainstem Trinity for use in the mark-recapture models and to Dan Holland and Bruce Bury for providing data from Hayfork Creek for comparison.

CHAPTER 4

SITE CHARACTERISTICS AND BASHING BEHAVIOR OF

ABSTRACT: Aerial basking behavior of western pond turtles (*Clemmys marmorata*) was examined along the mainstem Trinity River, Trinity County, California during 1992. In conjunction with data on underwater captures, I obtained estimates of proportion of turtles basking and examined effects of temperature, sex, sizeclass, and month. Air temperature was found to be only weakly associated with basking intensity. No differences were detected between males and females, but a higher proportion of juveniles known to be present were basking over the entire season. Males showed no seasonal effect, while females showed a post-July peak in basking intensity. Analysis of basking site characteristics revealed that basking sites utilized by turtles could be distinguished from random basking sites primarily by their lower slope and association with deeper, more lentic waters. Juvenile and adult basking sites had similar characteristics, with the exception of lower water flows at juvenile sites. In general, basking sites were associated with higher velocity waters than underwater capture locales. This study contributes to our understanding of the timing of basking and selection of basking sites by *C. marmorata* in relation to other life history traits.

INTRODUCTION

Aquatic turtles engage in aerial basking (above water *sensu* Moll and Legler 1971) for a variety of reasons. Potential benefits include thermoregulation, parasite control, drying of the integument, and synthesis of vitamin D. It is generally believed that regulation of body temperature with consequent impacts on metabolic rate is the primary function (Boyer 1965, Brattstrom 1965, Buhlmann and Vaughan 1991, Ernst 1986, Janzen et al. 1992, Lefevre and Brooks 1995). Aquatic turtles can bask to attain body temperatures that exceed air and water temperatures (Ewert 1976, Farrell and Graham 1991). By raising body temperatures, basking may accelerate digestion and assimilation (Janzen et al. 1992). Decreased basking time or increased growth rates and activity levels might then occur (Frazer et al. 1993, Lefevre and Brooks 1995).

The significance of basking is likely to vary with life history traits, including body size, sex, and degree of terrestriality. The most terrestrial member of the genus *Clemmys* (*C. insculpta*), for example, basks less frequently than the sympatric *C. guttata* or *C. muhlenbergii* (Ernst 1986). Juveniles, which warm more quickly due to their higher surface/volume ratio, may bask for shorter periods than adults (e.g. *Chrysemys picta*; Lefevre and Brooks 1995, Spotila and Gates 1975). Juveniles sometimes inhabit shallower, warmer waters (Congdon et al. 1992, Pappas 1992, Chapter 8), which may decrease the time they must spend basking to achieve preferred body temperatures. Increased energy requirements during certain phases of the life cycle, such as egg production by females, may prolong basking (Auth 1975, Hammond et al. 1988, LeFevre and Brooks 1995).

Because basking is essential for most turtle species, attention to basking sites is warranted in programs that manage for the survival of turtle populations. Habitat manipulations to benefit *Clemmys marmorata*, the western pond turtle, have included addition of basking sites to ponds. In most locales inhabited by this species, basking sites are not likely to constitute a limiting factor. However, provision of suitable sites is a relatively easy manipulation that has the potential to enhance metabolism, growth, and survivorship. Potential drawbacks include temporary disturbance to populations or accidental introduction of exotic plant or animals. Although considerable research has been conducted on the timing of basking by *C. marmorata* in relation to environmental cues (Bury 1972, Holland 1985), the characteristics of preferred basking sites are not well understood.

With these data gaps in mind, I evaluated basking sites used by western pond turtles in a lotic system, the mainstem Trinity River. Examination of utilized sites in relation to available sites along the river was intended to identify features that potentially attracted turtles to the utilized sites. The relationships between basking frequency, time of year, sex, and lifestage were also explored. My intent was to further define the significance of basking in the life history of this species.

METHODS

Study sites

Data were gathered along the mainstem Trinity River in Trinity County, California, in conjunction with mark-recapture dives during 1992 (Chapter 3). Two sets of contiguous study reaches, each approximately six kilometers in length, were examined (Reaches 2,3 and Reaches 10,11, Figure 2-1). The study reaches had been chosen for mark-recapture primarily on the basis of their accessibility. I felt that nonrandom site selection was also acceptable for this basking site study provided that we sampled a wide range of conditions; thus, the relatively large sample sizes along study reaches spanning a number of kilometers. In choosing the reaches, the degree to which they contained a range of turtle densities was also considered (an indicator that they were likely to represent a range of conditions). Previous surveys revealed that Reaches 2 and 3 had few turtles, Reach 10 had a moderate number of turtles, and Reach 11 had a high number of turtles relative to the overall distribution along the 39 miles between Lewiston Dam and the North Fork Trinity (Chapter 3, derived from Lind et al. 1992).

Field Methods

Five mark-recapture dives were conducted at the mainstem study site between April and September of 1992 (Chapter 3) during which basking site data were collected. For every turtle that was sighted basking, even those that subsequently eluded capture, the following characteristics of the basking perch were measured: substrate type, river flow type, canopy cover, distance above the water, distance to shore, water depth, water velocity, perch diameter, perch slope, and connectedness to shore (Appendix 4-A). For turtles that had not been sighted basking but were captured underwater, the following underwater characteristics were recorded: river flow type, distance to shore, water depth,

METHODS OF HABITAT MEASUREMENT

Variable	**Methodology**
I. BASKING SITES (PERCHES)	
Substrate Type	Categorized as either boulder, cobble, bedrock, gravel, logs, woody debris, treefalls, live vegetation, root wads, or hummocks.
Flow type	Flow type (Appendix 2-A) of the area under the perch converted to a continuous flow index as described.
Canopy cover	Estimated by eye as the percentage of closed canopy in a 5-meter radius area above the perch locale.
Distance above water	Distance of the perch (cm) above the water surface.
Distance to shore	Distance (m) from perch location to nearest shore.
Water depth	Depth (m) of river directly underneath the perch.
Water velocity	Measurement (m/sec) with a Marsh-McBurney flowmeter halfway between the river bottom and river surface. Measured directly under each perch site.
Perch diameter	Diameter of the perch (cm) at central point.
Perch slope	Slope of the perch (degrees).
Connectedness	Diameter (cm) of the largest connection between the perch and the shore. A zero value indicates that the perch does not connect to shore at any point.

II. UNDERWATER SITES

Flow type	Flow type (Appendix 2-A) of the area where the turtle was captured. These were converted to a continuous flow index as described.
Distance below water	Distance (m) of turtle capture location below the water surface.
Distance to shore	Distance (m) from turtle capture location to nearest river shore.
Water depth	Depth (m) of river at turtle capture location.
Water velocity	Measurement (m/sec) with a Marsh-McBurney flowmeter held at each capture location.

and water velocity. Canopy over the capture location was also assessed. All captured turtles were measured (carapace length) and their sex determined. In the case of baskers that slipped into the water and subsequently escaped, notes were made of their sizeclass and sex based on characteristics that are visible from a distance, including carapace shape, neck coloration, and head shape and coloration (Holland 1991).

In addition to characterizing the perches of basking turtles, we also characterized emergent objects at random sites, the latter intended to represent the characteristics of available perches along the river. To qualify as a potential perch, an object had to be at least 5 cm in diameter and emergent from the water (i.e. not underwater or entirely suspended in the air). Potential perches were chosen by using random numbers to select a survey station, a distance from the station, a direction (upstream or downstream), and a distance from shore. The distance from the station was constrained to 0-100 meters to cover as much area as possible without overlap of downstream measurements from one station and upstream measurements from the next. The distance from shore was constrained to 0-4.0 meters to match the actual area searched for turtles (Chapter 3). The nearest perch to the random spot was then selected.

Data Analysis

Examination of basting intensity

For each study day, the number of basking turtles sighted was divided by the total number of turtles captured (basking or otherwise). This provided daily estimates of the proportion of turtles basking. This proportion is likely to be related to both the frequency and the duration of basking events. Although these factors were not separable in this study, I surmise that an increase in either factor would lead to an increase in the proportion of baskers at a given time.

The proportion of baskers was regressed against daily mean air temperature as well as against the ratio of air/water temperature (U.S. Fish and Wildlife Service, Lewiston gauging station) to look for a relationship. Temperatures were obtained from an established gauging station; although these clearly do not provide a measure of basking site microclimate, they do provided a general index of daily local climate. It was suspected that high air temperatures would be associated with diminished basking activity; Lefevre and Brooks (1995) found that duration of basking by painted turtles (*Chrysemys picta*) decreased as air temperature increased over a 20-35 degree range (Celsius). I also hypothesized that most basking would occur on days when the ratio of air temperature to water temperature was greater than 1.0. Buhlinann and Vaughan (1991) found that aerial basking of *Pseudemys concinna* occurred only when air temperature exceeded water temperature. If the primary function of basking is thermoregulation, then this trend may hold true for other species.

The monthly proportion of turtles basking (number of baskers/total number captured) was plotted to look for shifts in basking frequency during the five months of the study with the expectation that basking activity might increase during the months with cooler air (April, September) because of the longer time required for turtles to reach preferred body temperatures. Studies of other species have revealed heightened basking associated with cool weather (*Chrysemys picta:* Ernst 1971, *Trachemys scripta*: Moll and

Legler 1971). However, Bury's (1972) study of *Clemmys marmorata* in Hayfork Creek, California, revealed no relationship between duration of basking and time of year. For each sex, Pearson chi-square contingency table analysis (SAS 1990) was used to identify seasonal trends in proportion of baskers . For tables in which expected frequencies were small (less than five in 25% of the cells or more), a Fisher exact test was used.

Monthly proportions were also used to compare male basking to female basking, month by month. I hypothesized, at least during the nesting season (May-June), that gravid females would bask more than males due to the increased costs of reproduction (Ernst 1986, Schwarzkopf and Brooks 1985). Individual Pearson chi-square tests were used to compare males and females, month by month. For months in which expected frequencies were small, a Fisher exact test was used. Juvenile and adult basking frequencies (e.g. juveniles basking/total juveniles where total includes both captured and escaped) for the entire season (April-September) were also compared (proportion test; Zar 1984). The expectation was that a lower proportion of juveniles would be found basking as a result of smaller body size and higher heating rates (Boyer 1965, Lefevre and Brooks 1995).

Comparison of turtle basking site use to availability

Discriminant analysis (DA) was used to ascertain whether turtle-use perches could be distinguished from potential perches on the basis of the measured habitat characteristics. There was a larger sample of potential perches than used perches because the latter was constrained by the number of turtles sighted basking. This large sample allowed me to select multiple random subsets of potential perches for comparison to the used perches, and thereby ascertain which variables most consistently appeared in the discriminant models. Ten random subsamples with replacement were generated and applied to ten two-group DAs using a stepwise procedure to select variables.

Correlation analysis was used to identify redundancies among variables, especially those known to have a conceptually close relationship such as river flow type and water velocity. If two variables were highly correlated (R >= 0.75 or R <= -0.75) and they both entered the model, the one was excluded that contributed less discriminatory power.

For all DAs, the significance level was set at alpha = 0.10 for entry of variables into the model This moderate significance level allows for more variables to enter a model and, thus, provides better discriminatory power given the small sample size (Costanza and Afifi 1979). A moderate alpha level may also be more appropriate for the detection of ecological trends (Tort 1991). Bartlett's modification of the likelihood ratio test was used to test for heterogeneity among variance-covariance matrices (SAS 1990) setting alpha = 0.05. In cases where the matrices were heterogeneous, quadratic as opposed to linear discriminant functions were generated. A jackknife procedure was used to evaluate the classification success of models (SAS 1990). Cohen's Kappa (Titus et al. 1984) was then computed for each test to compare the classification success to chance. The significance level was set at alpha = 0.05. Standardized structure coefficients are presented to indicate the relative contribution of each variable to the canonical discriminant function (Rencher 1992).

DA was not suitable for examination of the non-continuous variable perch substrate type. Its relationship to perch identity (turtle/random) was examined using a Pearson chi-square contingency table analysis (SAS 1990); the null hypothesis being tested was that substrate types occur in the same proportion among utilized perches as among random perches. In fact, I expected that turtles might prefer certain substrates based on their thermoregulatory properties. Western pond turtles bask on rocks, logs, root masses, banks, emergent vegetation, and tree limbs. Their rates of heating may differ according to substrate type (Boyer 1965, Bury 1972, Holland 1985). In some cases, body temperature is more correlated with substrate temperature than with either air or water temperature (e.g. *C. insculpta*, Farrell and Graham 1991).

Because the initial set of substrate types was large (11 substrates) with consequently small cell counts for some types, the substrates were grouped into three broader categories. "Rock" included boulder, cobble, bedrock, and gravel. "Wood" included logs, treefalls, and small woody debris. "Veg" included live vegetation, root masses, and hummocks. The contingency table was subdivided as necessary into simpler 2x2 tables to ascertain where the significant effects occurred (Zar 1984).

Analysis of lifestage differences in basking site characteristics

Hotelling's t-test (multivariate t; SAS 1990) was used to determine whether characteristics of juvenile perches were different from characteristics of adult perches. Variables with nonnormal distributions were transformed or analyzed individually using Wilcoxon tests. I expected that flow, depth, and perch diameter might differ. Previous research indicated that juveniles of *Clemmys marmorata* (Holland 1991) and other emydids (Congdon et al. 1992) inhabit shallower, more lentic areas than adults. Smaller perches may be occupied by juvenile turtles, provided that there is competition for perches and there is some minimum diameter of perch that can support a turtle of a given body size. The Hotelling's t-test was followed with individual t-tests to ascertain which variables were responsible for the overall difference. The significance level was adjusted to account for multiple t-tests (Bonferroni adjustment, Stevens 1986).

Assessment of underwater habitat use

The underwater habitat-use data were not as easily interpreted because I lacked reference to a dataset describing available underwater habitat. The summary statistics did, nevertheless, provide general information on the characteristics of underwater areas used by western pond turtles. Hotelling's T-test followed by individual t-tests was used to compare underwater capture locales to perch sites with respect to distance from shore, canopy, depth, river flow index (Appendix 4-A), and flow velocity. Hotelling's T-test was also used to ascertain whether underwater habitat of females differed from that of males with respect to the five variables that were measured. I suspected that the different physiological requirements associated with reproduction might segregate males from gravid females underwater. Gravid females might, for example, inhabit warmer, shallower waters with greater risks of predation but higher metabolic potential for egg production (Hammond et al. 1988, Kepenis and McManus 1974).

RESULTS

Ninety-seven turtles were sighted on perches during the study, of which 89 individuals were subsequently captured. Most captures occurred underwater because with only a few exceptions, basking turtles had retreated to the water by the time snorkellers were within several meters of basking sites. Of those captured, 59 were adults and 30 were juveniles. The adults consisted of 27 females and 32 males. Ninety-six turtles that were not sighted on perches were captured underwater. Of these, 88 were adults and 8 were juveniles. The adults consisted of 38 females and 50 males.

Examination of basking intensity

Daily mean air temperature ranged from 8.1 to 26.6 degrees Celcius, while water temperature ranged from 10.4 to 11.9. The regression of air temperature against basking intensity revealed a positive relationship, which was significant at the. 10 level and explained a relatively small percent of the variation ($R^2 = 0.15$, $p = 0.061$). When the ratio of air/water temperature was regressed against proportion of baskers, the relationship was even weaker ($p = 0.096$, R-square = 0.12). Water temperature exceeded air temperature on only a single day in April (yielding a ratio <=1.0), and one-third of the captured turtles were basking on that day. This is only slightly lower than the daily average of 52%. On the three days that yielded no basking turtles, the air/water temperature ratio was not particularly high or low.

From the plot of monthly proportion of turtles basking (Figure 4-1), it appeared

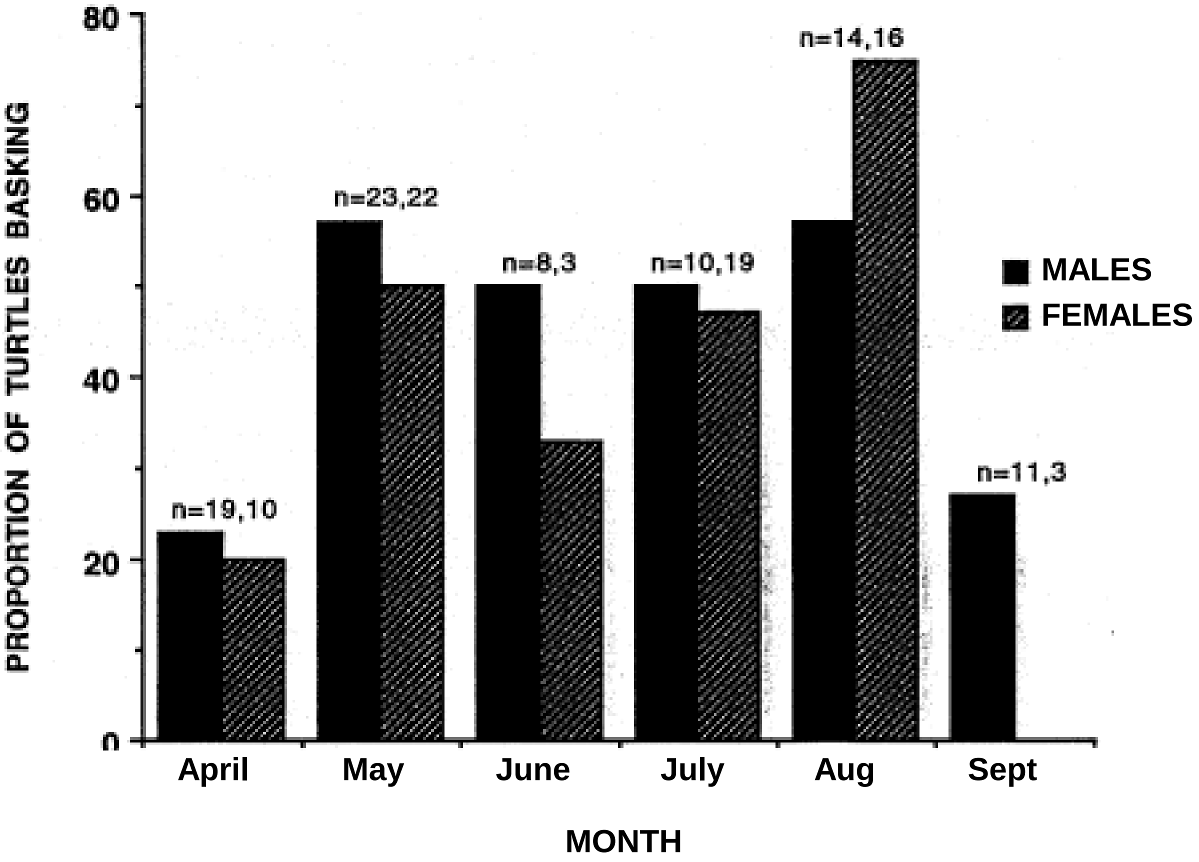


Figure 4-1. Proportion of captured turtles that were sighted basking prior to capture along the mainstem Trinity. n=sample sizes of males, females.

that males might differ from females during the later months. However; the chi-square analyses by month revealed no significant differences between the sexes. The plot also suggested a trend of fewer turtles basking early and late in the season than during the middle months (June-August). This proved not to be true for males (overall Chi-square = 1.144, p = 0.564). For females, there was a slight seasonal trend. The proportion of females basking in April was lower than expected relative to the proportion basking in August (Chi-square = 2.735, p = 0.098).

Assessment of basking frequency by size class revealed that a higher proportion of juveniles were observed basking than adults (q = 6.38, p < .001).

Comparison of turtle basking site use to availability

Data was collected from 164 potential basking sites, which served as the universe from which the 90-observation subsamples were drawn. The correlation analysis revealed no significant correlations between habitat variables, and all measured variables met the assumption of normality (some only after transformation). Thus, all variables were entered into the stepwise process.

The resulting subsample models were all quadratic with the exception of the two that were single-variable. Water depth was the most stable variable, occurring in all ten subsample models (Table 4-1). Turtle perches were in deeper water than potential perches. Perch slope appeared in seven of the models and a flow variable (either river flow type or water velocity) appeared in five. Distance to shore appeared in three models and perch diameter in two. Turtle perches were less sloped, further from shore, smaller in

Table 4-1. Results of ten two-group. discriminant analyses of habitat from 90 occupied basking sites and 90 potential basking sites (subsampled) for western pond turtles on the mainstem of the Trinity River. Model with highest classification success is highlighted.

Model #	Variables entered	Wilk's Lambda	F (df 1,180)	p value	Classifi -cation Success	Cohen's Kappa	p value
1.	depth, canopy, slope, flow ind.	.6408	24.10	.0001	74%	.4889	< .0001
2.	**depth, diam., slope**	**.7173**	**22.98**	**.0001**	**75%**	**.5000**	**< .0001**
3.	depth	.7453	60.15	.0001	73%	.4556	< .0001
4.	depth, slope	.6990	37.67	.0002	73%	.4667	< .0001
5.	depth, slope	.6872	40.06	.0001	73%	.4667	< .0001
6.	depth	.7899	47.34	.0001	72%	.4444	< .0001
7.	depth, velocity, shore distance	.7711	17.42	.0001	66%	.3111	< .0001
8.	depth, slope, velocity, shore, water distance	.6440	19.23	.0001	70%	.4012	< .0001
9.	depth, diam., slope, flow ind.	.7051	19.30	.0001	74%	.4889	.0011
10.	depth, slope, velocity, shore	.7338	15.87	.0001	72%	.4333	< .0001

diameter, and in lower flow areas than potential perches (Table 4-2). The standardized structure coefficients for depth ranged from .7607 to 1.01 and for perch slope from -.4498 to -.2933. The model that included depth, perch slope, and perch diameter had the best classification success (75%, Table 4-1).

The chi-square analysis of substrate type indicated a difference between turtle-used and potential basking sites with respect to the distribution of rock, wood, and live vegetation substrates (Figure 4-2; Chi-square = 35.21, $p < .0001$). Chi-square values from subdivision of the table indicated that turtles were found on woody perches with greater frequency and on rock perches with lesser frequency than predicted by the availability of these substrate types (Chi-square = 0.84, $p = 0.04$).

Analysis of lifestage differences in basking site characteristics

The Hotelling's t-test revealed no overall difference between juvenile and adult basking site characteristics. All of the individual t-tests (and Wilcoxons) were nonsignificant with the exception of the comparison of average water velocity across age class. Juvenile basking sites had significantly lower water velocity below the perch than adult basking sites ($Z = -2.66$, $p = .008$).

Assessment of underwater habitat use

Values of the underwater variables are cited in Table 4-3. Underwater capture locations overall were different from basking site locations (Hotelling's $T^2 = 0.1074$, $p = .0038$), and the difference was mostly attributable to differences in water velocity.

Table 4-2. Values of habitat variables (means and standard deviations) for turtle-occupied basking sites and potential basking sites at the mainstem Trinity River. Note that values of random sites reflect entire sample, which was subsampled for discriminant analysis (Table 4-1).

Habitat Variable	Turtle Sites (n = 90)		Random Sites (n = 163)	
	mean	s.d.	mean	s.d
Flow index (Appendix 2-A)	1.54	0.67	1.68	0.72
Canopy cover (%)	37.80	30.14	33.82	31.11
Slope (degrees)	12.95	11.09	13.61	16.33
Shore distance (m)	2.08	1.41	1.77	1.44
Water depth (m)	1.03	0.55	0.55	0.47
Connectedness (cm)	5.76	6.77	7.14	16.03
Water velocity (m/sec)	0.25	1.19	0.09	0.39
Perch diameter (cm)	13.03	8.39	18.61	22.63
Distance over water (m)	0.25	0.67	0.16	0.23

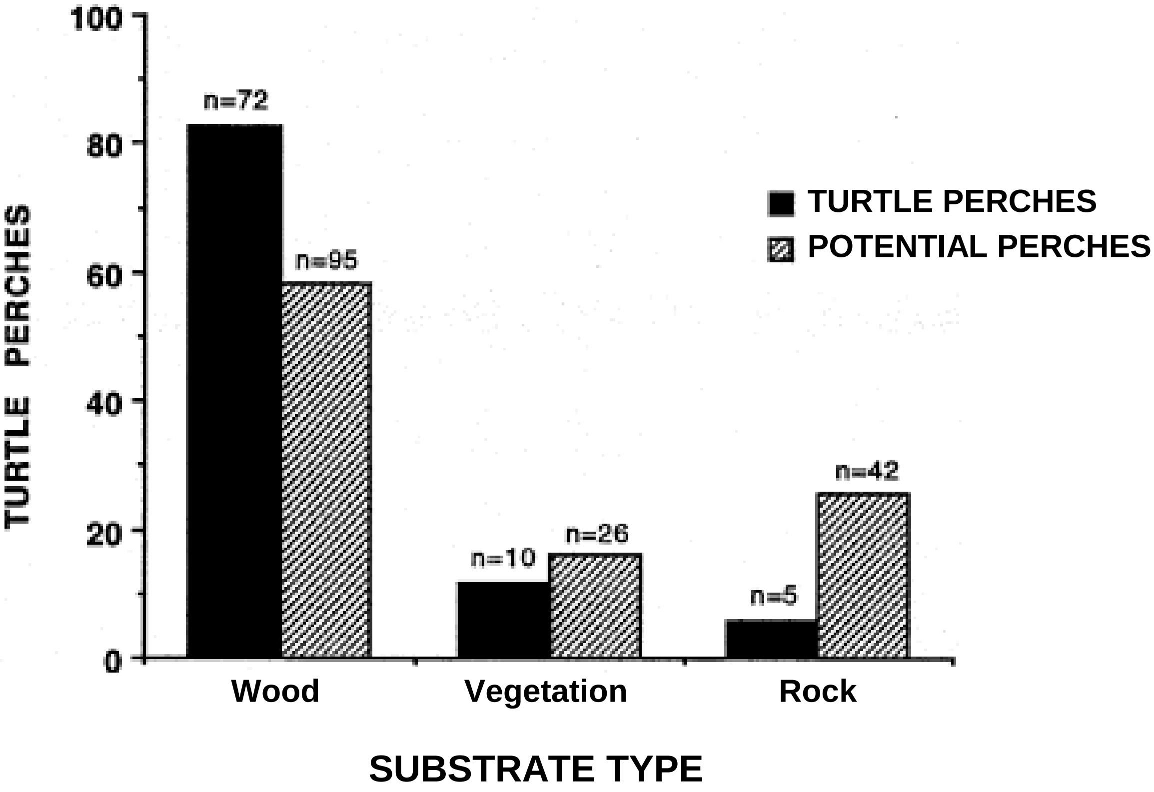


Figure 4-2. Distribution of turtle-use perches and potential perches across substrate types at the mainstem Trinity; n = number of perches

Velocities were significantly lower at underwater capture locales than beneath perch sites (t = 3.13, p = 0.002). The mean flow index for both (approximately 1.5) indicates a condition intermediate between a pool and a glide. A Hotelling's T-test revealed that males did not differ from females with respect to the underwater habitat characteristics that were measured ($T^2 = 0.0462$, p = 0.7946; Table 4-3). None of the individual t-tests comparing males to females were significant either.

DISCUSSION

Examination of basking intensity

The relationship between basking intensity and air temperature was different from my expectation. Higher air temperatures were associated, albeit weakly, with higher proportions of basking turtles. This may be attributable to longer basking bouts per turtle, more frequent basking bouts per turtle, or more individuals engaging in basking. In the context of this study, these effects cannot be separated. The ratio of air temperature/water temperature had a positive association with basking proportion as well. However, the ratio value of 1.0 (air temperature=water temperature) did not emerge as a threshold; turtles engaged in emergent basking on a day for which water temperature exceeded air temperature. It is possible that with more time-specific measurements (instead of daily means), a threshold would emerge. Hourly temperature data are not available for this section of river.

The low r value for both regressions suggests that there is considerable variability

Table 4-3. Habitat characteristics of underwater capture locations for male and female western pond turtles on the mainstem Trinity River and results of t-tests comparing males to females (with Bonferroni adjustment).

Habitat Variables	Males (n = 50)		Females (n=35)		T-tests	
	mean	s.d.	mean	s.d.	T	P-value
Flow type (index) (Appendix 2-A)	1.48	0.61	1.43	0.65	-0.426	4.026
Canopy cover (%)	42.68	30.70	52.05	35.41	1.319	1.146
Shore distance (m)	2.04	1.78	1.69	1.65	-0.782	2.616
Water depth (m)	1.09	0.42	1.06	0.44	-0.385	4.206
Water velocity (m/sec)	0.00	0.06	0.01	0.06	0.738	2.778
Distance to surface (m)	0.69	0.84	0.66	0.77	0.155	5.262

Hotelling's $T^2 = 0.046$ $p = 0.795$

in the proportion of turtles basking that cannot be explained by temperature. High variability in numbers of basking turtles has also been observed in other studies (e.g. Obbard and Brooks 1979), and is probably due to the complex suite of factors influencing basking behavior (Boyer 1965). Factors that warrant further consideration are other physical parameters (e.g. incident solar radiation, wind), individual differences in behavior, and seasonal activity patterns. Bury (1972) found substantial differences between individual *Clemmys marmorata* in the frequency and duration of basking bouts. The examination of monthly shifts revealed relatively less intense basking activity by females during April and relatively more during August. This is consistent with reports of other species showing seasonal shifts in behavior (*Pseudemys concinna:* Buhlmann and Vaughan 1991; *Chelydra serpentina*: Obbard and Brooks 1979). It may result from seasonal changes in metabolic needs and/or activity levels.

It is noteworthy that female basking behavior appeared to be more variable across the months with a peak in August and precipitous decline in September. The peak may reflect a post-nesting (pre-hibernation) boost in physiological processes related to nutrient assimilation. Females that have just returned to the river after nesting may have been mostly on land for as much as a month (Reese and Welsh 1996), during which time they presumably cannot feed (as swallowing is only known to occur underwater, Holland 1991). The apparent September lull may simply reflect a bias from the small sample size (3) of captured females. During September, turtles leave the river and head to terrestrial overwintering sites (Reese and Welsh 1996, Chapter 9). This compares to *Pseudemys concinna* in West Virginia, for which female basking decreased throughout the season

(Buhlmann and Vaughan 1991). Species-specific seasonal patterns of basking most likely, originate from the interaction of life history traits and locale.

Contrary to my prediction, a greater proportion of juveniles was sighted basking than of adults, which may be attributable to longer basking bouts than adults, more frequent basking bouts, or more individuals basking (see above). The first alternative is 11 inconsistent with the known relationship of body size to heat gain in ectotherms. Smaller bodies reach thermal equilibrium more quickly (Boyer 1965, Brattstrom 1965, Spotila and Gates 1975), and should thus require shorter basking times to reach preferred temperatures. Because smaller bodies also cool more quickly, the second alternative of more frequent basking by juveniles could occur as a result of the cold water associated with dam releases. The third alternative (more individuals basking) is consistent with the hypothesis that juveniles have a lower threshold temperature for basking than adults, such that at cool temperatures more juveniles will be basking. It is also possible that other factors override the relationship of body size to thermoregulation; Boyer (1965) found no correlation of time spent on basking sites with body size of emydids. Overriding factors could include learned wariness (with adults tending to exit basking sites more readily than juveniles, Boyer 1965) or different tradeoffs between survival and thermoregulation (with juveniles tending to be more cryptic on basking sites). However, the fact that aerial basking may expose juvenile turtles to a considerable predation risk because of their small body size (Janzen et al. 1992) makes the latter hypothesis unlikely.

Comparison of turtle basking site use to availability

Basking sites used by turtles were distinguishable from potential basking sites primarily in being less sloped and occurring in deeper, slower water. Locomotory limitations imposed by sloped surfaces have been demonstrated for a terrestrial emydid (*Terrapene carolina*, Muegel and Claussen 1994), and may similarly limit the selection of basking sites by *C. marmorata* to those below a certain slope. Water depth and flow emerged as important features in other studies as well (Bury 1972, Chapter 5). Deeper pools in the river are likely to accumulate more underwater cover objects, such as large woody debris, and potentially decrease the risk of predation by aquatic mammals (e.g. otters, minks).

The finding that turtles were not distributed across substrate types in proportion to their availability was not surprising, given that substrates have considerably different properties that pertain to basking. Because of its greater conductivity, rock will transmit heat to a perching turtle more readily than wood (Boyer 1965). However, wood may provide a surface that turtles can scale more easily, facilitating movements on and off the basking site. *Clemmys marmorata* engaged in aerial basking will periodically return to the water to dunk, an apparent cooling mechanism (Bury 1972, Holland 1985). This indicates that they must regulate their behavior to avoid overheating. Rock perches, because they are so radiant, may in some cases be too warm to serve as long-term basking sites. Given that basking serves functions besides heating (e.g. drying, Boyer 1965), wood perches might be preferred in some circumstances.

Analysis of lifestage differences in basking site characteristics

Juvenile and adult perches were more similar than expected with respect to depth and perch diameter. However, juvenile basking sites did occur in areas with significantly lower flow, as substantiated by findings in Chapter 8. Previous research has found that juveniles of other emydids also inhabit more lentic waters than adults (*Trachemys scripta*: Hart 1983, *Graptemys geographica*: Pluto and Bellis 1986). The most likely explanation for this pattern of habitat utilization is that, being poor swimmers (Hammer 1969, Holland 1991, Moll and Legler 1971, Pluto and Bellis 1986), juveniles may have difficulty locomoting in strong currents. Lentic waters offer a situation where juveniles can maneuver more effectively to forage and reach refugia.

Assessment of underwater habitat use

Male and female underwater sites used by *Clemmys marmorata* did not appear to be different. Given that a limited set of characteristics was measured, there may be other features that define sex-related differences in underwater habitat selection such as size of refugia (male and female *C. marmorata* have different shell depths, Holland 1992). The river flow index of underwater locations was similar to that of perch locations, as was the mean depth. I conclude that western pond turtles not only bask over deep, pooled habitats, but also conduct other vital life activities there, which may include foraging and seeking refuge. The difference in water velocities is probably indicative of underwater microhabitat selection, whereby turtles that are captured underwater are often sequestered on the bottom or in refugia with very low flow.

In summary, this study identified several associations between habitat characteristics and basking behavior of *Clemmys marmorata* on the mainstem Trinity River. The association of basking turtles with slower water implies that management efforts for this species should focus on pooled habitats as potential areas for basking site addition and enhancement, particularly if managing for juveniles. Perches of wood (e.g. treefalls) with moderate slopes are likely to be preferred. Juvenile basking appears to be at least as prevalent as adult basking and occurs on perches with similar characteristics. Basking sites may be particularly important to females during the month following oviposition on the mainstem Trinity River.

ACKNOWLEDGEMENTS

I thank the USDI Bureau of Reclamation and Fish and Wildlife Service for providing the funding for and facilitating this project. Special thanks to Jenny Glueck, Sarah Mook, Kris Schimizu, and Randy Wilson for helping to gather the data through diligent field work. Thanks also to Kris Shimizu for her meticulous data entry.

CHAPTER 5

HABITAT USE BY WESTERN POND TURTLES IN AN ALTERED SYSTEM, THE TRINITY RIVER BASIN OF NORTHWESTERN CALIFORNIA

ABSTRACT: Habitat associations of western pond turtles (*Clemmys marmorata*) were examined in a dammed and an undammed tributary of the Trinity River in northwestern California, The dammed tributary was found to have more sedimentation, decreased water temperatures, increased canopy cover, and higher flows, all of which are potentially relevant to turtles. The overall heterogeneity of aquatic habitats was also lower, possibly as a result of the dam. At both the dammed and the undammed site, turtles appeared to be selecting for deep water with low flow velocities and the presence of underwater refugia. On the dammed tributary, turtles were associated with basking structures, which may be particularly important because of the low water temperatures. On the undammed tributary, turtles tended to be in slower-flowing portions of the river with denser canopy cover and higher water temperatures. Given the alterations of channel morphology and flow regimes associated with damming, the implications are that habitat suitability for western pond turtles is decreased. While damming may increase the amount of deep water along shorelines and promote the formation of undercut banks, it eliminates low-flow areas preferred by western pond turtles and lowers water temperatures. Habitat enhancement efforts should focus on restoring natural structural and hydrologic features.

INTRODUCTION

Based on fossil remains, western pond turtles (*Clemmys marmorata*) are likely to have existed in the western United States since at least the late Pliocene (Hay 1908, Holland 1992). During the past two-five million years, this species has faced radical changes in the distribution of suitable habitats (Flint 1957, Levins 1968), the most recent of which are human-induced (Lord and Norton 1990). Some of these changes, such as the modification of the Central Valley of California for agricultural usage, have reduced populations to nonviable levels and thereby caused effective, if not complete, local extirpation. Other changes have been less deleterious, allowing populations to persist with diminished abundances. Few populations, if any, have densities equivalent to their historic counterparts, and age structures of extant populations tend to be adult-biased (Holland 1991).

Current disturbances with potential impacts on western pond turtles include urban development, agricultural development, livestock grazing, gold mining, gravel mining, dams and water diversions, and timber operations. To evaluate the relative severity of these disturbances and develop mitigation measures, we need to understand habitat requirements for this species. Holland (1991) provided descriptions of aquatic and terrestrial habitats utilized by western pond turtles. Bury (1972) analyzed the habitat characteristics of Hayfork Creek, CA, in relation to turtle abundance, providing the only quantitative assessment of habitat associations. His analysis was limited to pools and lacked the multivariate approach necessary to establish context across a range of available habitats. Understanding the spatial context of habitat use promotes more effective management. We need well-delineated ranges of habitat values from which the impacts on this species of proposed alterations can be predicted.

Western pond turtles are generalists, occupying a striking variety of lentic, lotic, and even ephemeral waterways (Stebbins 1985). They appear to have unusual flexibility and breadth in their habitat use. This makes the task of quantifying their requirements particularly difficult by introducing high variability. It also underscores the need for development of habitat models on an area-specific basis. A model developed at one site may not be applicable in another area for this species, particularly if the areas differ substantially in latitude or hydrologic regimes. With these considerations in mind, a study of habitat utilization by western pond turtles in the Trinity River Basin was initiated. I hoped to ascertain which physical features of riverine habitat were associated with turtles on the Trinity River through a multivariate analysis along contrasting tributaries.

In this watershed, the existence of the Lewiston and Trinity dams provided a unique opportunity to examine the effects of habitat modification on pond turtle populations. The mainstem and south forks of the Trinity provide both a dammed and an undammed site, respectively, that are in relatively close proximity and can be compared. Although they differ in some geomorphological features, they are similar in flow volume, channel size, vegetation, and land-use history. Comparing habitat utilization by turtles at these two sites can provide insight into the response of this species to dam related modifications. It also yields contrasting data from which can be inferred which habitat attributes are associated with western pond turtles.

The Trinity River system is also unique in continuing to harbor relatively large populations of turtles. Evaluations of habitat suitability, particularly those that compare habitat at occupied and unoccupied sites, should be conducted in areas that are well-populated by the target species. This minimizes the chance of attributing unoccupied habitat to lack of suitability when its placement at the landscape scale is, in fact, responsible. For example, patches may be unoccupied, despite suitable characteristics, if they are located in an unfavorable portion of the larger landscape (Dunning et al. 1995). Wilson et al. (1991) and Lind et al. (1992) reported there to be large populations of western pond turtles distributed over an extensive area in the mainstem Trinity River.

Damming of the mainstem in 1963 resulted in numerous habitat alterations. These include expansion and encroachment of riparian vegetation in response to the absence of winter scouring flows (Evans 1980). Wilson (1993) found that riparian cover nearly tripled during the 27 years subsequent to dam construction. The established riparian vegetation traps sand and has promoted the development of berms in the riparian corridor. Thus, the river has become channelized, changing to a narrow, trapezoidal shape; shallow, edgewater habitats were replaced by deep, swift waters (Hampton 1995, Trinity River Restoration Program 1994). Also, due to the reduction in winter flows, seasonally flooded marshes have been eliminated. Annual sediment transport is reduced, such that pools have been filled with fine sediments (Hampton 1995, Petts 1984, Williams and Wolman 1984).

The south fork, in contrast, is likely to resemble the mainstem in its predam condition. Wide, shallow-water gravel bars alternate with riffles and deep pools, and mature riparian vegetation occurs in small patches on the outside of each riverbend (California Department of Water Resources 1982). The south fork site may, thus, offer different conditions for western pond turtles than the mainstem. Considering that both shallow edgewaters and deep pools have been attenuated on the mainstem as a result of the dam, it is probably more homogeneous now than it was historically. It follows that, depending n the magnitude of other site differences (unrelated to the dam), the south fork may be more heterogeneous than the mainstem. Habitat use by western pond turtles on the south fork might reflect selection from a larger variety of available habitat. The following questions were addressed:

1. How does the available habitat on the mainstem Trinity River compare to that on the south fork Trinity in terms of mean values and variability?

2. How does utilization of habitat by turtles on the south fork compare to availability of habitat on the south fork?

3. How does utilization of habitat by turtles on the mainstem compare to availability?

4. Given what is determined about utilization, and given what is known about habitat alterations induced by the damming, what can be inferred about the consequences for western pond turtles?

MATERIALS AND METHODS

Study Sites

Data were gathered along the mainstem and south fork of the Trinity River in conjunction with mark-recapture dives conducted during 1993 (Chapter 3). Three study reaches, each approximately three kilometers in length, were examined on each site (Reaches 3,10,11 on the mainstem, Figure 2-1; Reaches 1,3,4 on the south fork, Figure 2-2). This subset of study reaches on the mainstem had been chosen for mark-recapture sampling on the basis of their containing a range of turtle densities. They were also suitable for this habitat study in that a range of densities implies a range of conditions. Indeed, Wilson's (1991) report cites a number of differences between upstream areas (Reach 3) and areas further downstream (Reaches 10 and 11). While Reach 3 is an area of high human settlement and impact, Reaches 10 and 11 are among the least disturbed. By virtue of its being closer to the dams and lacking the influence of tributaries, Reach 3 is more affected by the controlled flows than the two downstream reaches. Specifically, it experiences few scouring flows and little deposition of silt. Reaches 10 and 11 are siltier with less riparian vegetation. While Reach 3 has a wide valley floor, Reaches 10 and 11 are narrower with uplands close to the river. The south fork reaches are all undammed and, consequently, are subject to natural flow regimes and fluvial processes.

Field Methods

Habitat data were collected during two mark-recapture dives that were conducted at the mainstem study site and two at the south fork study site in 1993 (Chapter 3). For every unique captured turtle, i.e. the first time it was captured during the year, habitat characteristics were measured. A floating rectangular quadrat measuring 3 meters by 6 meters and divided into nine subquads (1 x 2 meters) was laid on the water surface with its center over the capture location. The quadrat size was chosen to mirror the natural scale of transition of the habitat variables listed below. Casual examination in the field revealed that a 6-meter stretch of shoreline tended to contain only one or two flow types (Appendix 2-A), but was long enough to accommodate basking logs and other large features.

Within each quadrat, the following features were measured: distance to bank, shoreline vegetation, flow types along a transect across the river, subquad flow types, water velocity, water depth, presence of basking sites, presence of cover objects, degree of bank undercut, water temperature, and canopy cover (Appendix 5-A). Some measured features yielded multiple variables for analysis. For example, because Bury's (1972) results indicated that deep water might be important for western pond turtles, I generated a "maximum depth" variable (maximum value of the nine subquads) in addition to the "mean depth" variable. Because of a suspicion that slow-flowing water might be preferred (Lind et al. 1992), I generated a "minimum flow" variable. Finally, because bank undercuts frequently serve as turtle refugia, and deeper undercuts may be more protective, a "maximum undercut" variable was created in addition to "mean undercut".

For every turtle-capture quadrat characterized, a random quadrat was also characterized, the latter intended to represent the available habitat at each river site. The number of random quadrats was set to equal the number of unique turtle captures within each sampled reach. The placement of each random quadrat was determined by using

APPENDIX 5-A

METHODS OF HABITAT MEASUREMENT

Variable	**Methodology**
Bank Distance	Distance (m) from turtle location to nearest river bank
Shoreline vegetation	Vegetation type immediately adjacent to the shore 1) Unvegetated (more than 2/3 gravel,cobble, sand) 2) Immature (more than 2/3 willow) 3) Mixed (at least 1/3 willow and 1/3 alder) 4) Mature (more than 2/3 alder or cottonwood)
River transect	The proportion of each flow type on a transect line from the turtle location to the opposite bank. These variables were converted to a single index by calculating a weighted combination of the proportions with more weight to faster flow types (Appendix 2-A).
Flow index	The proportion that each flow type occurs in each of the nine subquads (1 x 2 meters). The values for each flow type were averaged across the subquads. These variables were then converted to a flow index as described in Appendix 2-A.
Basking sites	The proportion of the nine subquads that contained basking sites. Basking sites were classified as follows: Small: 0-5 mm diameter Medium: 6-25 mm diameter Large: > 25 mm diameter* Banks: bank that met criterion described below To qualify as a basking site, the object had to make contact with the water, be less than 3 meters above the surface, and have a slope of 70 degrees or less.**

APPENDIX 5-A (continued)

Water flow velocity	Measurement (m/sec) with a Marsh-McBurney flowmeter halfway between the river bottom and river surface. Measured at the center of each subquad.
Water depth	Depth (centimeters) at the center of each subquad.
Underwater cover	The proportion of the nine subquads that contained suitable turtle cover. Suitable cover was defined as any material large enough to hide an adult western pond turtle (rocks, logs, debris). The proportion of subquads containing sand (or other sediment, eg. silt) deep enough to hide a turtle was also noted.
Bank undercut	Depth (cms) of bank undercut in each of the three subquads that are adjacent to the shoreline.
Water temperature	Water temperature (Celcius) above the turtle capture locale measured 10 cm below the surface.
Canopy cover	Measured with a canopy densiometer above the turtle capture locale. Any object blocking sky (vegetation or rock outcrop) was counted against the proportion of "open" on the densiometer. Counts in four perpendicular directions were averaged.

** Medium and large sites were later combined into a single size-weighted index of "large basking sites" calculated as follows : Large b.s. = (1 x medium) + (5 x large) where medium and large respectively are the proportions of each size class described above.*

*** Previous research (Chapter 4) indicated that basking sites utilized by western pond turtles at the mainstem Trinity site had a maximum slope of 70 degrees and were no more than 3 meters above the water. It was assumed that contact with the water was a prerequisite for turtles to access a basking site.*

random numbers to select a survey station, a distance from the station, a direction (upstream or downstream), and a distance from shore. At both study sites, the distance from the station was constrained to 0-100 meters to cover as much area as possible without overlap of downstream measurements from one station and upstream measurements from the next. The distance from shore was constrained to 0-4.0 meters to match the actual area searched for turtles (Chapter 3). High-gradient riffles were excluded from the analysis because they were not swimmable and were, therefore, excluded from the search effort. Random quadrats that landed in riffles were removed and another set of random coordinates generated.

Data Analysis

Comparison of available habitat on the mainstem and south fork

To compare habitat heterogeneity between the mainstem and south fork, the ranges of each measured variables were examined. I predicted that there would be larger ranges of values for the south fork site, particularly for those variables likely to have responded to damming such as mean flow, mean depth, water temperature, and canopy. The respective variabilities were also examined using Principal Component Analysis (SAS Institute 1990). I plotted the first two principal component factors for both the mainstem and south fork sites, as recommended by Johntson et al. (1990). Construction of minimum convex polygons facilitated comparison of the spread of factor values at each site, a larger polygon indicating greater overall variability in habitat.

Hotelling's t-test (SAS 1990), a multivariate statistic that indicates difference between means, was used to determine whether available habitat on the mainstem differed from available habitat on the south fork, the null hypothesis being that the two sites offer the same habitat. To ascertain which variables were responsible for the difference between sites in the multivariate model, individual t-tests (or Wilcoxons, depending on the distribution of each variable) were conducted. The significance level was set at alpha=.05. The alpha was adjusted for multiple tests using the Bonferroni inequality (Stevens 1986). In this case, thirteen variables were tested for differences between sites; thus alpha=.05 was adjusted to alpha=.004.

Comparison of turtle habitat use to availability

For each study site, DA was used to ascertain whether turtle-use quadrats could be distinguished from random quadrats on the basis of the measured habitat characteristics, testing the null hypothesis that turtles use habitat in proportion to its availability (i.e. that they are non-selective). The discriminant analyses were accompanied by the Wilk’s Lambda test statistic, which identifies multivariate differences between means. Although many of the habitat characteristics vary daily and seasonally (e.g. water temperature, flow), concurrent measurement at the turtle capture sites and random sites allowed for a comparison of relative values.

Prior to the DAs, variable reductions occurred. The variable "bank distance" was excluded priori because its values were highly constrained by the sampling protocol. Correlation analysis was used to identify redundancies among variables, especially those known to have a close relationship such as measures of mean and maximum values of a habitat characteristic. If two variables were highly correlated (R <=-0.75 or R >=0.75) and they both entered the model, the one was excluded that contributed less discriminatory power. A stepwise procedure was used to select the subset of original variables most useful for discriminating turtle from random sites. The significance level was set at alpha = 0.10 for entry of variables into the model. A moderate alpha level may be more appropriate for the detection of ecological trends (Tort 1991). Also, this moderate significance level allows for more variables to enter a model and, thus, provides better discriminatory power given the small sample size (Costanza and Afifi 1979).

In the case where variables were nonnormally distributed, even after transformation, a nonparametric discriminant analysis was conducted (kernel method, SAS 1990). Kernel density was estimated using the Epanechnikov kernel, which is optimum in the sense of minimizing the smallest mean integrated square error achievable (Silverman 1986). The smoothing parameter (r) was also chosen to minimize the mean square error, assuming a multivariate normal distribution. Although that distribution cannot be assumed here, this was the best approach to obtaining the optimal r, given computational limitations. Bandwidths were allowed to differ between the two groups (turtle/random). For parametric DAs, Bartlett's modification of the likelihood ratio test (SAS 1990) was used to test for heterogeneity among variance-covariance matrices, setting alpha = 0.05. In cases where the matrices were heterogeneous, quadratic as opposed to linear discriminant functions were generated.

A jackknife procedure was used to evaluate the classification success of the parametric and nonparametric models (SAS 1990). Cohen's Kappa (Titus et al. 1984) was then computed for each test to compare the classification success to chance. The significance level for performance was set at alpha = 0.05. Standardized structure coefficient are presented to indicate the relative contribution of each variable to the canonical discriminant function (Rencher 1992).

DA was not suitable for examination of the non-continuous variable shoreline vegetation.) Its relationship to study site (mainstem/south fork) was examined using a Pearson chi-square contingency table analysis (SAS 1990); the null hypothesis being tested was that the study sites are indistinguishable with respect to the distribution of vegetation types. In fact, I expected the mainstem site to have more mature vegetation as a result of dam induced riparian encroachment as described above. The relationship of vegetation to turtle-use quadrats versus random quadrats at each study site was also examined. The null hypothesis was that sites used by turtles have the same distribution of vegetation types as the overall distribution along the river. In cases where a significant relationship emerged ($p < .05$), contingency tables were then subdivided into simpler 2x2 tables to ascertain where the significant differences in the table occurred (Zar 1984).

RESULTS

Ninety-three turtles were captured on the mainstem and 84 on the south fork during the 1993 season, with the same number of random quadrat measurements taken, respectively, at the two sites. The correlation analysis revealed correlations between two pairs of habitat variables (mean flow and flow index, maximum depth and mean depth), both of which are expected to be highly correlated due to their close relationship. One variable in each of these pairs was excluded by the criteria described in Methods.

Comparison of available habitat on the mainstem and south fork

The ranges of habitat values were found to be greater at the mainstem study site for some variables and greater at the south fork site for others (Table 5-1). Specifically, the mainstem site had a greater range of depths, canopy cover, basking sites, and undercuts. For all four of these variables, the greater range resulted primarily from greater maximum values on the mainstem. The south fork site had a greater range of flow types and water temperatures. The within covariance matrices for the mainstem and south fork random quadrats were found to be significantly different (Chi-square = 78.04, p = .0001), indicating a difference in variability of the habitat values. The principal component analysis of habitat values for the two study sites yielded four significant factors, of which the first two explained 63% of the variance. The two-factor plot (Figure 5-1) revealed that the south fork site was overall more heterogeneous with respect to the habitat characteristics that were measured than the mainstem site.

The south fork was found to differ significantly from the mainstem with respect to mean values of the habitat characteristics that were measured (Hotelling's t = 3.207; F (df 1,167) = 42.49 p = .0001). Note that mean water flow velocity, maximum water depth, and maximum undercut were excluded from the analyses because of their strong correlations to other variables (minimum velocity, mean depth, and mean undercut, respectively). Of the thirteen variables remaining, six of them showed significant

Table 5-1. Range of values of random habitat measurements (Appendix 5-A) from the mainstem (n=93) and south fork (n=84) study sites. Larger ranges are highlighted.

HABITAT FEATURE	MINIMUM VALUE		MAXIMUM VALUE		**RANGE**	
	main	south	main	south	**main**	**south**
River transect (index)	135	120	370	380	235	**260**
Flow type (index)	1.0	1.0	3.8	4.0	2.8	**3.0**
Mean water flow velocity (m/sec)	-17.7	-10.1	110.0	119.4	127.7	**129.5**
Mean water depth (cm)	11.7	2.2	236.1	200.0	**224.4**	197.8
Baskable bank (%)	0.0	0.0	44.0	44.0	44.0	44.0
Underwater cover (%)	0.0	0.0	100.0	100.0	100.0	100.0
Sand cover (%)	0.0	0.0	100.0	100.0	100.0	100.0
Water temperature (*C)	10.0	16.0	18.0	25.0	8.0	**9.0**
Canopy (%)	16.0	16.0	100.0	63.9	**84.0**	47.9
Small bask sites (%)	0.0	0.0	89.0	87.0	**89.0**	87.0
Large bask sites (index)	0.0	0.0	4.3	3.7	**4.3**	3.7
Mean undercut (cm)	0.0	0.0	53.3	23.3	**53.3**	23.3

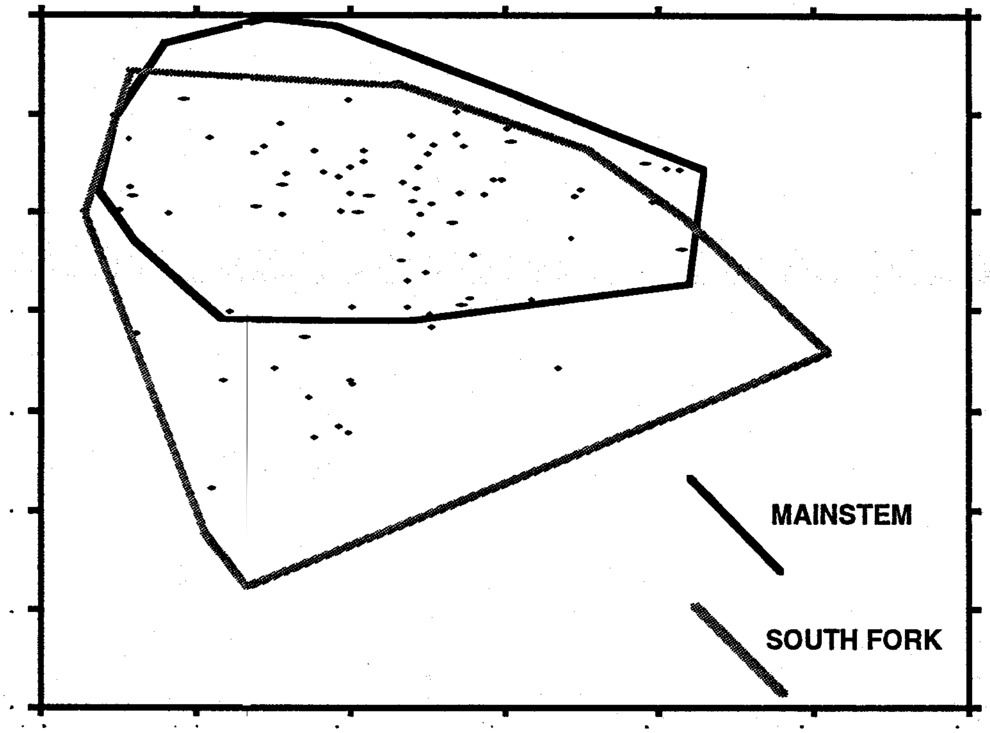


Figure 5-1. Graph of the first two principal components for habitat measurement from mainstem and south fork random quadrats. Polygons represent the minimum convex polygon for each group.

differences between the mainstem and the south fork sites (Table 5-2). There were lower water temperatures, larger bank undercuts, and more canopy at the mainstem site. This site also had deeper water and higher minimum water velocities. There were more small basking objects at the south fork site.

The chi-square analysis of mainstem and south fork random quadrats revealed that shoreline vegetation type is significantly associated with site (Figure 5-2; Chi-sq = 78.73, $p < .0001$). Thus, I rejected the null hypothesis that the sites had identical distributions of vegetation. Chi-square analysis of 2 x 2 tables indicated that the frequencies among the vegetated types were not significantly different; rather, a significant difference occurred between the vegetated and unvegetated (gravel bar) types (e.g. Chi-square = 45.76, $p < .0001$ for table of unvegetated x mixed). The majority of the south fork samples were adjacent to unvegetated gravel bars, while nearly all the mainstem samples were adjacent to riparian vegetation.

Comparison of turtle habitat use to availability on the mainstem

For the mainstem DA, all measured variables met the assumption of normality and were included in the stepwise process. The DA revealed that turtle-use quadrats and random quadrats could be distinguished on the basis of habitat characteristics. The model that emerged was quadratic and was composed of the following variables: small basking sites, flow index, minimum velocity, underwater cover, water depth, and baskable bank (Table 5-3). Specifically, there were more small basking structures and more baskable bank at turtle capture locales than at the random locales. There were lower flow types

Table 5-2. Comparison of available habitat at the south fork and the mainstem Trinity study sites. Means and standard deviations are shown in actual measured units, although some variables were transformed prior to analysis. Significant results (after Bonferroni adjustment) are in boldface.

Habitat Characteristic	Mainstem sites (n=89)		South fork sites (n=84)		Significance test results	
	mean	s.d.	mean	s.d.	T (df),	p-value
River transect (index)	212.6	38.4	201.4	52.5	2.20 (147),	p=0.03
Flow type (index)	1.8	0.6	1.6	0.6	1.90 (175),	p=0.06
Minimum water flow velocity (m/sec)	5.1	18.8	2.1	12.9	4.07 (175),	**p=0.0001**
Mean water depth (cm)	79.8	39.7	53.5	40.8	5.32 (136),	**p=0.0001**
Baskable bank (%)	10.3	15.1	8.8	14.3	0.65 (174),	p=0.52
Underwater cover (%)	27.3	29.0	26.1	30.9	0.52 (175),	p=0.61
Sand cover(%)	23.6	33.5	11.1	23.8	2.84 (169),	p=0.005
Water temperature (*C)	14.2	1.6	18.9	1.8	-17.7(164),	**p=0.0001**
Canopy (%)	56.2	28.6	16.3	15.4	11.2 (127),	**p=0.0001**
Undercut (cm)	7.9	12.0	1.6	4.9	-5.15 **(177),**	**p=0.0001***
Small basking sites (% index)	19.9	21.6	0.2	0.2	-5.82 **(177),**	**p=0.0001***
Large basking sites (% index)	0.2	0.7	0.5	0.8	0.92 (177),	p=0.36

All variables: Hotelling's T = 3.207; F(df 1,167) = 42.49; p = .0001

* Did not meet the assumptions for parametric t-test; reported values are Z-scores for Wilcoxon 2-sample test. Not included in Hotelling's T-test.

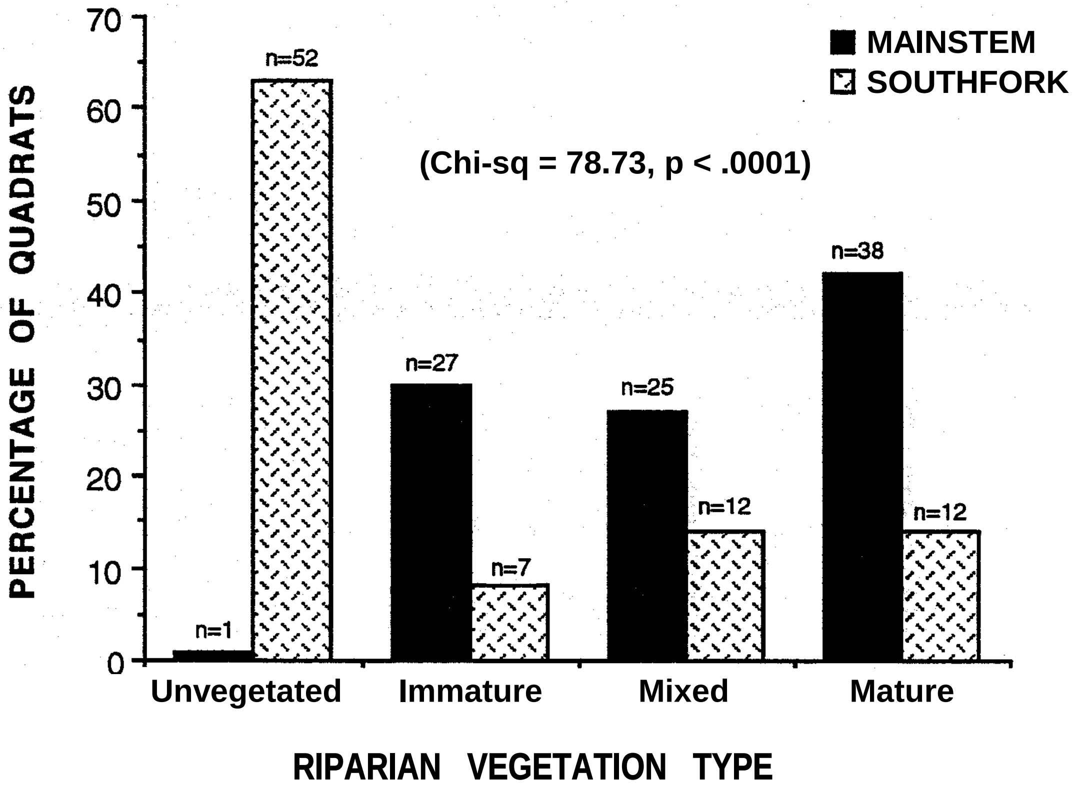


Figure 5-2. Distribution of random habitat quadrats at the mainstem and south fork study sites across shoreline vegetation types; n = number of quadrats

and a lower minimum velocity in turtle quadrats. And, there were more underwater cover objects and deeper water in turtle quadrats than in random quadrats. This model was a highly significant discriminator (Wilk's Lambda F statistic) between turtle capture locales and available habitat along the mainstem. The resubstitution test (Jackknife) classified 80% of the observations correctly, which was significantly greater than chance (Cohens kappa = 0.602, p < .0001; Table 5-3).

The mainstem chi-square analysis revealed that quadrat identity (turtle or random) is significantly associated with shoreline vegetation (Figure 5-3; Chi-square = 6.80, p = 0.03). Chi-square values from subdivision of the table indicated that turtles were found adjacent to immature and mixed assemblages in proportion to the availability of these vegetation types (Chi-square = 0.04, p = 0.84); the mature vegetation type was responsible for the significant difference. Specifically, the random quadrats were most often adjacent to mature riparian vegetation (alder, cottonwood assemblages), while turtle-use quadrats were most often adjacent to immature riparian assemblages (willow dominant). Note that category 1 (unvegetated) was excluded from the analysis because it was uncommon along the reaches and its cell counts for both quadrat types were, consequently, negligible.

Comparison of habitat use to availability on the south fork

For the south fork discriminant analysis, the following variables did not meet the assumption of normality required for the model after transformation: undercut, maximum undercut, small basking sites, and large basking sites. All four had high percentages of

Table 5-3. Two-group stepwise discriminant analysis of available habitat and utilized habitat for western pond turtles at the mainstem Trinity study site. Means and standard deviations are shown in actual measured units, although some variables were transformed prior to analysis. Standardized structure coefficients are presented for those variables that entered the model, which was quadratic in form.

Habitat Characteristic	Turtle sites (n = 93)		Random sites (n = 93)		Standardized Structure Coefficient
	mean	s.d.	mean	s.d.	
River transact (index)	198.3	42.6	212.6	38.4	
Flow type (index)**	1.4	0.4	1.8	0.6	-0.307
Minimum water flow velocity (m/sec)	-1.3	9.2	5.1	18.8	-0.265
Mean water depth (cm)***	88.8	41.2	79.8	39.7	+0.324
Maximum water depth (cm)***	128.5	48.9	110.5	51.3	
Baskable bank (%)	17.1	15.6	10.3	15.1	+0.322
Underwater cover (%)	50.5	31.1	27.3	29.0	+0.293
Sand cover (%)	24.9	35.2	23.6	33.5	
Water temperature (*C)	14.2	1.5	14.2	1.6	
Canopy (%)	66.3	26.7	56.2	28.6	
Small basking sites (% index)	49.6	31.8	19.9	21.6	+0.637
Large basking sites (index)	0.8	1.1	0.2	0.7	
Mean bank undercut (cm)	11.0	16.2	7.9	12.0	
Maximum bank undercut (cm)	20.7	33.0	14.5	20.2	

Wilk's Lambda = 0.597; F(df 1, 185) = 18.68; p = .0001
Jackknife success (%) = 80; Cohen's Kappa = 0.602; p < .0001

** correlated with mean water flow velocity, which was removed from the model
*** correlated pair, of which only mean water depth entered the model

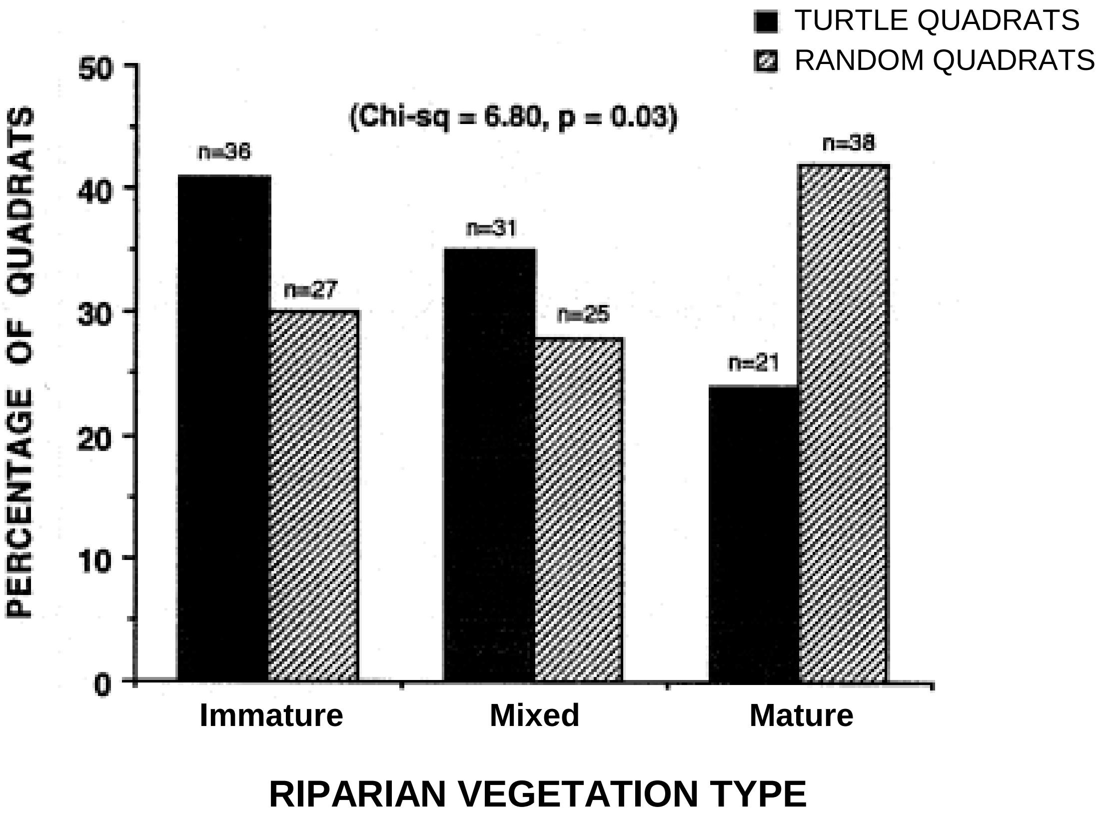


Figure 5-3. Distribution of turtle habitat quadrats and random habitat quadrats across shoreline vegetation types at the mainstem site; n = number of quadrats.

zero values (i.e. undercuts and basking sites were infrequent). A nonparametric discriminant analysis (Epanechnikov kernel, r = 2.38) revealed that turtle-use quadrats and random quadrats could be distinguished on the basis of the following habitat characteristics: river transect, underwater cover, canopy, small basking sites, water temperature, flow index, and maximum depth, and maximum bank undercut (Table 5-4). Specifically, the river transect and the habitat quadrats were composed of slower flow types at turtle locales than at random locales. There were more underwater cover objects, more basking sites, and deeper maximum undercuts in turtle quadrats. Turtles quadrats also had higher water temperatures, deeper water, and more canopy than random quadrats. This model was a highly significant discriminator (Wilks Lambda F statistic) of turtle capture locales and available habitat along the south fork. The resubstitution test (Jackknife) classified 73% of the observations correctly, which was significantly greater than chance (Cohen's kappa = 0.181, $p < .0001$; Table 5-4).

The chi-square analysis of shoreline vegetation on the south fork indicated a difference between turtle-use and random quadrats (Figure 5-4; Chi-square = 8.59, $p = 0.03$). The significant chi-square value was attributable to the unvegetated habitat type (gravel bar) occurring with greater frequency than other types (Chi-square = 8.20, $p < 0.02$). Specifically, turtle-use quadrats were associated less with unvegetated habitat than random quadrats.

Table 5-4. Two-group nonparametric discriminant analysis of available habitat and used habitat for western pond turtles at the south fork Trinity study site. Standardized structure coefficients are presented for those variables that entered the model.

Habitat Characteristic	Turtle sites (n=84)		Random sites (n=84)		Standardized Structure Coefficient
	mean	s.d.	mean	s.d.	
River transect (index)	148.0	45.6	201.4	52.5	-0.318
Flow type (index)**	1.1	0.3	1.6	0.6	-0.311
Average water flow (m/sec)**	2.1	5.6	14.5	20.5	
Minimum water flow (m/sec)	-1.9	4.3	2.1	12.9	
Average water depth (cm)***	109.6	76.5	53.5	40.8	
Maximum water depth (cm)***	161.9	102.9	80.9	51.6	+0.411
Baskable bank (%)	12.7	17.0	8.8	14.3	
Underwater cover (%)	46.5	36.1	26.1	30.9	+0.483
Sand cover (%)	31.4	39.3	11.5	24.2	
Water temperature (*C)	20.2	2.3	18.9	1.8	+0.438
Canopy (%)	27.9	19.8	16.3	15.4	+0.313
Small basking sites (% index)	0.31	1.08	0.20	1.08	+0.182
Large basking sites (% index)	1.10	3.26	0.49	0.83	
Maximum bank undercut (cm)	5.3	14.0	4.1	13.2	+0.194

Wilk's Lambda = 0.545; F(df 1,167) = 22.38; p = .0001
Jackknife success (%) = 73; Cohen's Kappa = 0.464; p < .0001

** correlated pair, of which only flow type entered the model
*** correlated pair, of which only maximum water depth entered the model

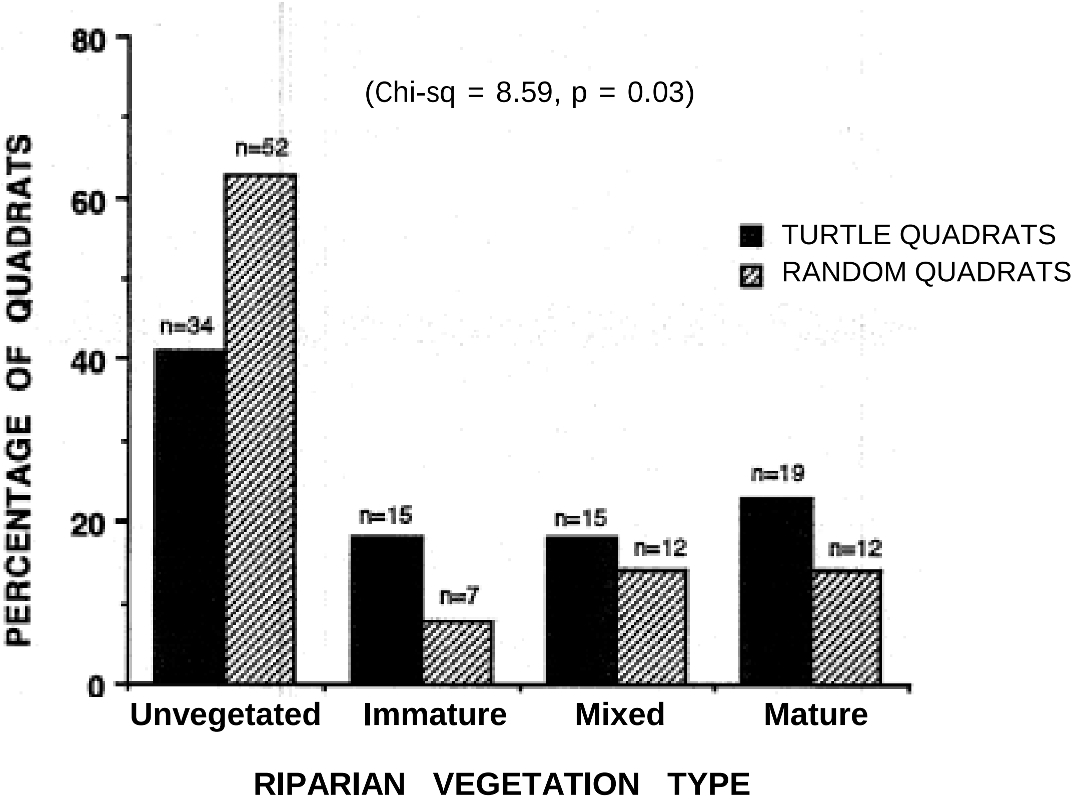


Figure 5-4. Distribution of turtle habitat quadrats and random habitat quadrats across shoreline vegetation types at the south fork site; n = number of quadrats

DISCUSSION

Dams and water diversions on rivers are responsible for fragmenting aquatic habitat directly, by acting as barriers to migration, and indirectly, by creating patches of unsuitable habitat. Such habitat fragmentation can increase the stress on populations of species that are already reduced in number. Impoundments on streams inhabited by the flattened musk turtle in Alabama, for example, created areas of deep lentic waters that were not only unsuitable for this species, but also served to segregate the suitable habitat on either side. Due to increased isolation, these musk turtle populations were then potentially subject to numerous threats including loss of genetic variability, abnormal population structure, stochastic factors, and susceptibility to disease (Dodd 1990). Western pond turtles are contending with similar fragmentation conditions on the Trinity River and in other dammed portions of their range. Previous research shows that significant habitat alterations have occurred downstream of the Lewiston and Trinity dams. Stretches of unsuitable habitat are likely, on a large scale, to reduce the continuity of pond turtle populations.

The analysis of available habitat on the two study sites is consistent with previous accounts of impacts of damming of the mainstem Trinity (Evans 1980, Hampton 1995, Petts 1984, Trinity River Restoration Program 1994, Wilson et al. 1993). Relative to the south fork site, the mainstem has denser shoreline canopy cover, a result in accord with the known encroachment of riparian vegetation onto previously unvegetated gravel bars.

Indeed, the analysis of shoreline vegetation confirmed that random mainstem quadrats are significantly more likely to be vegetated than random south fork quadrats. Vegetation promotes the formation of berms, which are then subject to undercutting; thus, the deeper undercuts on the mainstem channel. The higher minimum flow velocities at the mainstem site are probably attributable to the elimination of slow-flowing edgewater habitats on this fork, as is the deeper water. By definition, a more trapezoidal channel hosts deeper water adjacent to the shoreline. The mainstem water was also found to be cooler; summer water temperatures on the mainstem have decreased substantially from their historical values as a result of artificial flow regimes associated with the dam (U.S. Fish and Wildlife Service 1995). Outflow is released from the base of the reservoir, thereby tapping deep, cold water instead of the warm upper layer. The greater abundance of small basking material on the mainstem is likely to be related to the patches of woody debris that accumulate in the absence of natural flushing flows and the abundance of shoreline vegetation.

The mainstem and south fork sites also differ with respect to habitat heterogeneity. For the former, the ranges of depths, canopy cover, undercuts, and basking sites are all wider, with most of the difference attributable to the high ends. The larger maximum values of these four variables can be explained (see above), as the consequences of decreased water volume and lack of seasonal, flushing flows on the mainstem. The smaller range of flow velocities and temperatures in the mainstem are consistent with the postulated decrease in heterogeneity of aquatic habitats. Specifically, a natural alternation of pools and riffles is more likely to provide a wide variety of flow velocities and temperatures than a straightened, trapezoidal channel. Indeed, overall heterogeneity was higher on the undammed south fork site as hypothesized.

Comparisons of turtle-use quadrats and random quadrats at each study site show patterns of association. On both the mainstem and the south fork, turtle-use quadrats have lower flow velocities, deeper water, and more underwater refugia than are randomly available. These results are consistent with the fact that western pond turtles are relatively poor swimmers (Holland 1991) that rely on crypsis and use of refugia to escape from predators. Use of deep pools with large woody debris, which provides cover, is likely to decrease the chance of turtles being detected by aquatic predators such as otter and mink. These findings underscore the importance of maintaining deep, pooled habitats for this species on the Trinity River. Although deep waters have increased as a result of damming of the mainstem, the trapezoidal shape of the channel promotes high velocities (Hampton 1995) that are likely to have reduced habitat suitability for western pond turtles.

In addition, on both forks of the Trinity, turtles utilized areas that contained more small basking objects and (on the mainstem) more baskable bank than were randomly available. Basking structures are critical for thermoregulation, particularly when water temperatures are low (Boyer 1965, Brattstrom 1965, Lefevre and Brooks 1995). At the south fork, basking structures are more scarce (see above), but may be less critical because of the higher water temperatures. The lower relative contribution of basking sites to the south fork model (standardized structure coefficients) supports this assertion.

At the south fork, the variables canopy cover, maximum undercut, water temperature, and river transect also emerged as discriminators of habitat utilized by turtles. The association of turtles with denser canopies may be attributable to the presence of nearly vertical rock faces on the south fork that were often adjacent to pools and therefore to turtle capture locales (see Appendix 5-A for definition of "canopy"). It is also possible that vegetative canopy is important to western pond turtles, as indicated by the results of the shoreline vegetation analysis; turtle locales are associated, with vegetated banks with, greater frequency than expected from their availability. Areas of denser canopy could provide protection from predators (e.g. raccoons, coyotes, humans), whether it be through decreased accessibility (rock faces), decreased visibility (vegetative barriers), or increased camouflage (dappled shade). The conditions of patchy sunlight generated by vegetative cover may also moderate incidental solar radiation and allow turtles to thermoregulate effectively via small shifts in body position (Holland 1985).

Canopy cover is significantly denser on the mainstem site (see above), which may explain why canopy did not emerge as a variable distinguishing turtle-use quadrats at that site; i.e. it may not be a limiting factor. The results of the shoreline vegetation analysis for the mainstem support this assertion. Nonvegetated shorelines were nearly absent, and turtles were associated more frequently with immature riparian vegetation than with mixed or mature types. It appears that western pond turtles may select a moderate condition between the extremes of unvegetated gravel bars and advanced-stage riparian vegetation.

The significance of water temperature as a variable defining habitat utilization by turtles on the south fork is unclear. The south fork site offers significantly warmer water than the mainstem, yet turtle distribution appears to be related to water temperature on the former and not the latter. I could hypothesize that the scarcity of basking structures on the south fork forces aquatic basking (see Holland 1991) by which turtles are more dependent on warm waters than they might otherwise be. The issue warrants further research. Finally, the emergence of the river transect and undercut variables in the model for the south fork indicate that turtles use lower-velocity sections of the river and areas with deeper bank undercuts, which serve as refugia (Reese, unpublished obs.).

The results of this study serve to clarify aquatic habitat utilization by this cryptic, generalist species. Favorable western pond turtle habitat (Figure 5-5) is characterized by deep, slow-flowing pools with underwater cover and emergent basking sites and/or warm water. Although dams do increase the amount of deep water and promote the formation of undercut banks, they compromise habitat suitability by eliminating slow-flow areas and lowering water temperatures. Given that deep water with refugia is available in a naturally flowing river as part of the dynamic channel morphology, dams are likely to decrease overall habitat suitability for turtles. Some of the effects of altered flow regimes not addressed by this study, such as sedimentation, may prove beneficial in the short-run (e.g. by providing substrate that turtles burrow into for cover; Holland 1994), but detrimental in the longrun (e.g. by filling deepwater pools and crevices with consequent reductions in cover and interstitial invertebrate fauna; Holland 1991, U.S. Fish and Wildlife Service 1995).

Managing land use to promote western pond turtle survival throughout its range has become increasingly important as this species experiences local extirpations and range contractions (Holland 1991). Results of this study suggest that managers should focus on preserving and restoring structural features such as cover objects and basking logs on riverine systems. They should also work to maintain natural flow regimes with

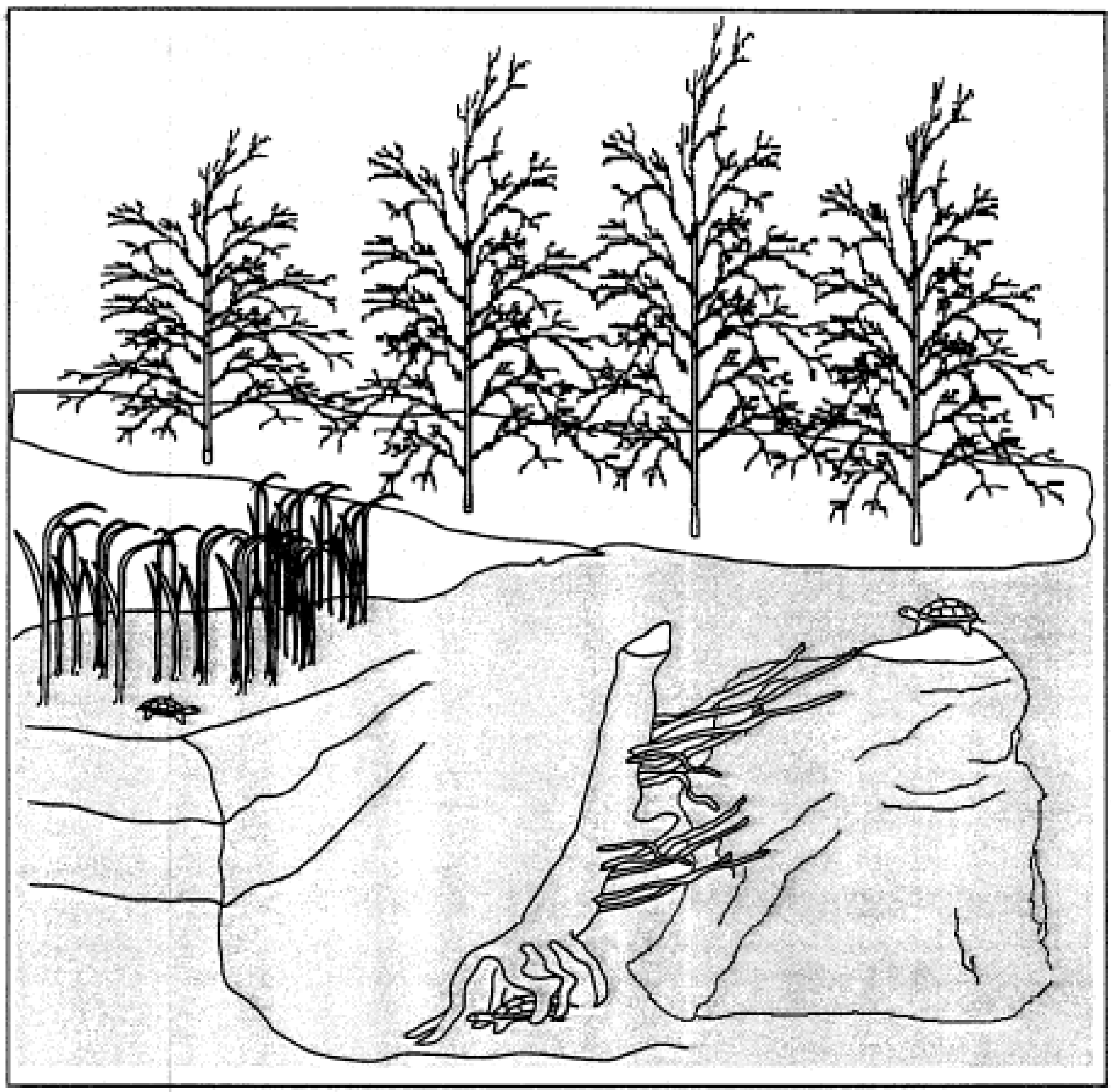


Figure 5-5. depiction of favorable habitat for western pond turtles.

their associated consequences for water temperatures, flow velocities, and depths. Future research should consider the potential of fisheries mitigation measures (e.g. artificial high flows, mechanical manipulations of shorelines) to enhance habitat suitability for western pond turtles on the Trinity River.

ACKNOWLEDGEMENTS

I thank the USDI Bureau of Reclamation and Fish and Wildlife Service for providing the funding for and facilitating this project. Special thanks to all those who gathered the data through diligent field work; these include Don Ashton, Jenny Glueck, Kary Schlick, and Polly Taylor. Thanks also to D. Ashton and K. Schlick for invaluable assistance with data entry and to Jim Baldwin for his statistical advice. Garth Hodgson deserves praise for creating Figure 5-5.

CHAPTER 6

INVESTIGATION OF WESTERN POND TURTLE POPULATIONS IN LEWISTON LAKE

ABSTRACT: Lewiston Lake was formed in the early 1960s by the construction of the Lewiston and Trinity Dams on the mainstem Trinity River: This study aimed to determine whether it currently supports populations of western pond turtles (*Clemmys marmorata*) and provides suitable aquatic and terrestrial habitat. Baited traps were used to survey for turtles during May-August of 1995 in the reservoir as well as adjacent ponds generated by the construction. Logistic regression was employed to predict the proportion of trap sites with turtles based on habitat characteristics. Upland areas adjacent to successful trap locations and within 500 meters of the reservoir were surveyed for nests. A total of 20 turtles were captured in the reservoir and 28 in eight adjacent ponds. All of the reservoir turtles and 93% of the pond turtles were adults. Presence of turtles could be predicted by higher water temperatures and higher densities of boats and humans. Surveys of seven meadows yielded one inactive turtle nest. I conclude that the reservoir is inhabited by a small, adult-biased population of western pond turtles (100-300 individuals) congregated in warmer areas and potentially feeding on fish tossed overboard. The adjacent ponds may be significant for recruitment. Protection of suitable nesting habitat around the lake, eradication of bullfrogs from the ponds, and elevation of lake water temperatures to natural, seasonal levels are recommended.

INTRODUCTION

Construction of the Lewiston and Trinity Dams on the Trinity River in the early 1960s resulted in the formation of Lewiston Lake. Aquatic habitat was converted from a stretch of flowing river to a deep, pooled reservoir with minimal flow and low water temperatures. A number of small ponds were created adjacent to the reservoir incidental to construction operations. Some wildlife species have clearly benefited from the increase in lentic waters, including waterfowl (e.g. wood ducks) and bald eagles, which have established nesting territories near the lake. For other species, such as the western pond turtle, the impact of this large-scale habitat change is unclear.

The western pond turtle (*Clemmys marmorata*) was a candidate for federal listing, primarily because of habitat destruction and alteration throughout its range (Holland 1991, Jennings and Hayes 1994). Juvenile turtles have been particularly vulnerable due to their specialized habitat requirements and small body size. Introduced predators, including bullfrogs (*Rana catesbiana*) and bass (*Micropterus salmoides*), prey upon juvenile turtles, which has spurred declines in recruitment at many localities. Suitable nesting habitat has also become increasingly scarce. Because western pond turtles nest in upland areas from 3-400 meters from waterbodies (Holland 1994), their nesting areas are susceptible to various forms of human impact (e.g. agriculture, urban development). Thus, it is common to encounter adult-biased populations of this species.

Adult western pond turtles inhabit portions of the mainstem Trinity river with relatively low velocities and deep water (Chapter 5). Juvenile turtles are found in shallower, slow edgewater areas with emergent vegetation, as well as in nearby ponds and vernal pools (Holland 1991, Chapter 8). Given these habitat associations, they may have benefited from the creation of the Lewiston reservoir and associated ponds. On the other hand, the unseasonably cold waters of the reservoir may inhibit feeding, metabolism and reproduction of this ectothermic species. The inundation of upland areas may have eliminated historic nesting sites. It may also have flooded overwintering sites, which consist of terrestrial refugia from 15-500 meters from the water course (Holland 1994, Reese and Welsh 1996). Since there is increasing evidence that western pond turtles display both nest-site and overwintering site fidelity, this is a matter of some concern (Holland 1994).

Surveys of Lewiston Lake for western pond turtles (Reese et al. 1994) indicated that they do occur, but in low densities. Turtles were distributed in several small clumps exclusively at the south end of the lake. The majority were associated with a large, instream, cattail/willow marsh. Sample sizes were too small to generate a population estimate using mark-recapture models. The site was revisited in 1995 and additional surveys conducted to increase the sample size of recaptured individuals. The goal was also to gather more information on the surrounding area, including suitability of the adjacent ponds for western pond turtles and availability of potential nesting sites. Because they have higher water temperatures, I suspected that the adjacent ponds might be more suitable for turtles than the reservoir itself.

METHODS AND ANALYSIS

Study Site

Lewiston Lake was formed in the early 1960s by the construction of the Trinity and Lewiston dams in conjunction with the Trinity River Division of the Central Valley Project (Figure 6-1). The primary function of the T.R.D. is to store water from the mainstem Trinity River for regulated diversion to the Central Valley. Lewiston Lake receives water from Clair Engle Lake via the Trinity Dam and releases water downstream into the mainstem Trinity. The Lewiston Dam, located at river mile 111.9, serves to regulate flows to meet temperature requirements for fisheries downstream (USDI 1992). Lewiston Lake has developed into a recreational area as well, with fishing use occurring throughout the year. Its 15-mile perimeter is mostly undeveloped, with the exception of a marina, trailer park, and camping areas associated with recreational fishing.

Surveys

Baited traps were used to capture turtles. The traps, which were constructed for the 1994 surveys (Reese et al. 1994), consisted of a traditional three-hoop design with an inverted funnel opening (Figure 6-2). They were initially baited with punctured tins of sardines in oil. Baits were switched after the third round of trapping to mitigate for potential trap avoidance based on chemical cues; frozen grilse (8-12") salmon from the Trinity River Fish Hatchery (operated by Department of Fish and Game) were used for the remaining two rounds. One fish was tied into the back of each trap. Each trap was anchored to the shore with a line tied to stable vegetation and a portion of the trap

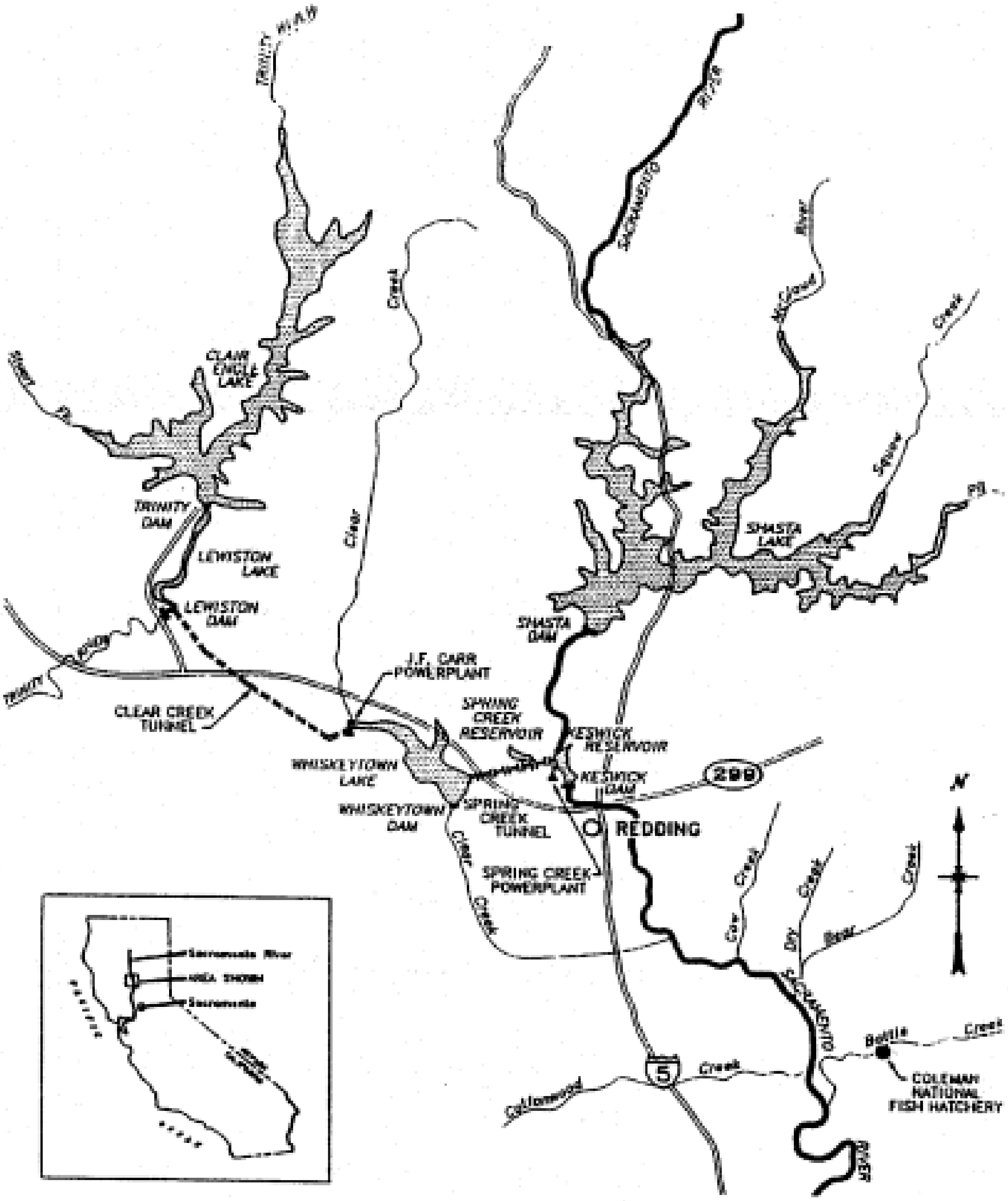


Figure 6-1. Map depicting the location of Lewiston Lake in relation to the Central Valley Project. From USDI Bureau of Reclamation 1992.

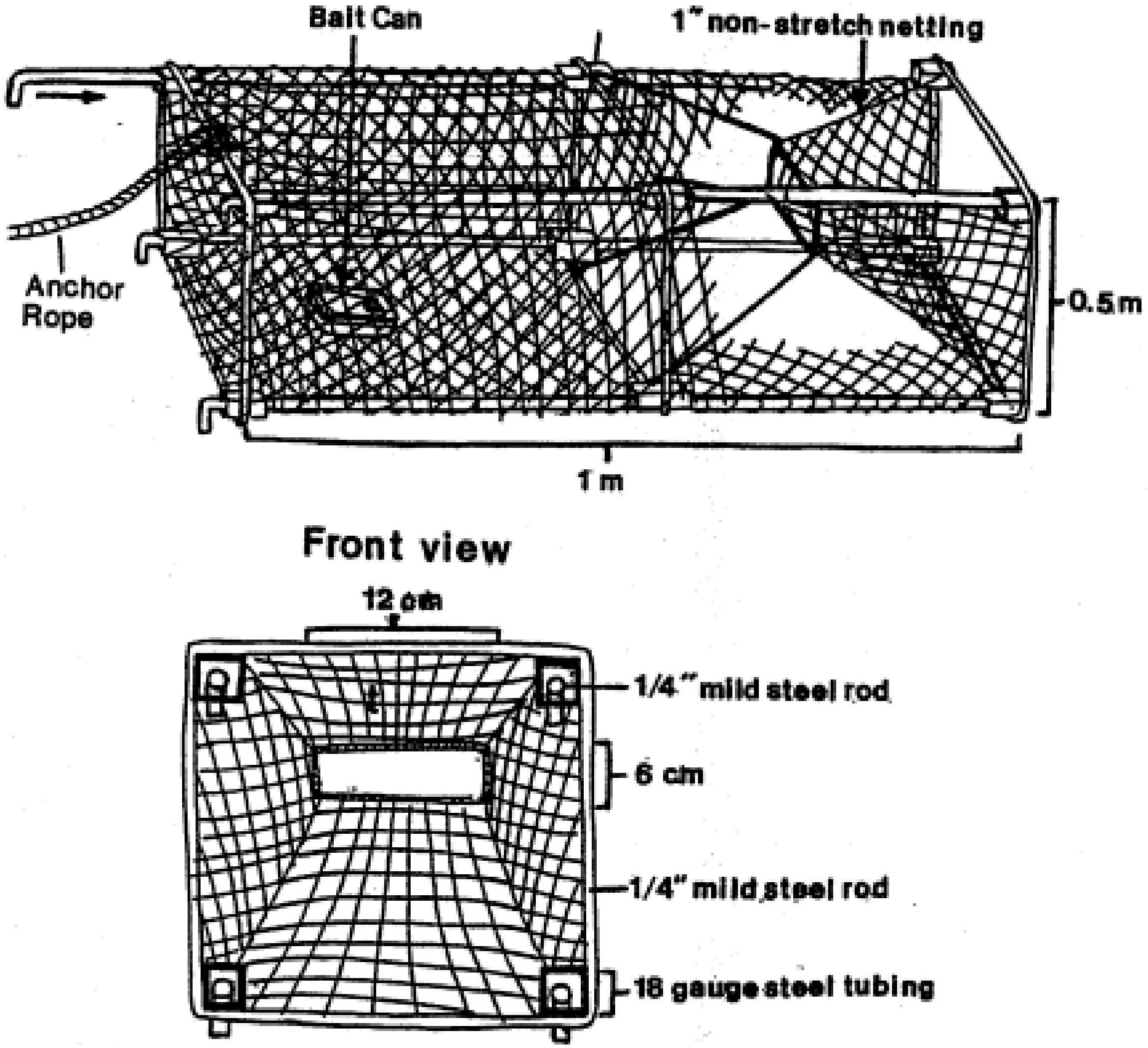
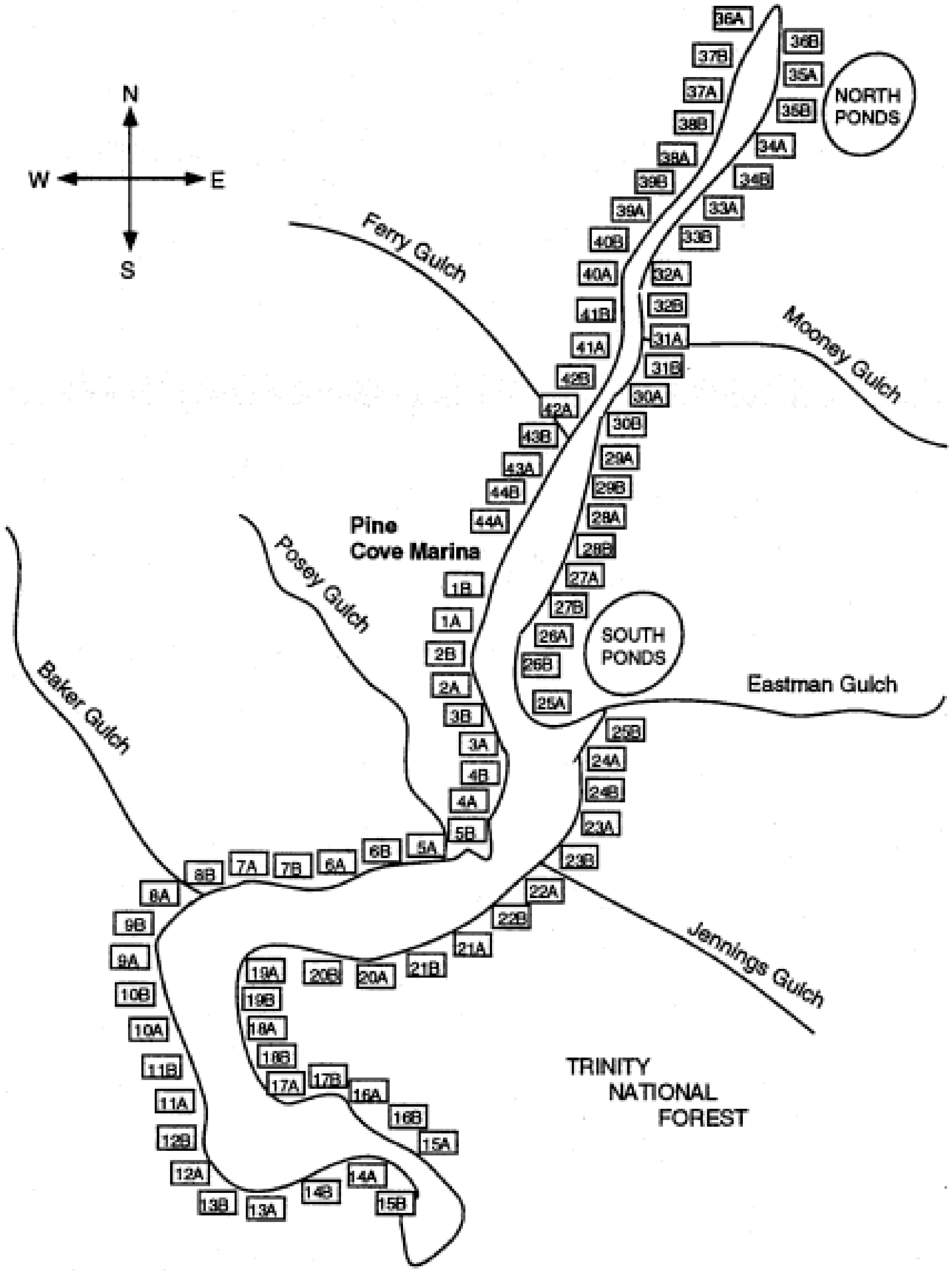


Figure 6-2. Diagram of baited trap used to capture turtles in Lewiston Lake. Drawing from Holland 1991.

emergent so that captured turtles could surface for air. Floats made from sealed milk jugs allowed the traps to rise and fall with changing water levels in the reservoir. Both the trap frame and the floats were painted a dark green color to make them less conspicuous to turtles and humans.

Five trapping sessions were conducted during the active turtle season (May-August); they occurred every three weeks beginning in the last week of May. During each session, a total of 70 traps were deployed with one every 250 meters around the perimeter of the lake (Figure 6-3). Because of a shortage of traps from theft during the previous year, two areas that had yielded no captures or sightings of turtles during 1994 surveys were excluded (traps 20B-23A and traps 40B-44A). Considering that areas harboring turtles in 1994 were far outnumbered by areas without turtles, I felt it was important to retain the former. The large size of the lake prohibited trapping of the entire perimeter simultaneously. Thus, it was trapped in four sections over a period of 4 1/2 days. In each section, traps were set and then checked the following day. Checking entailed removing captured turtles and recording their sex, weight, and maximum carapace length, as well as giving each a unique mark (Chapter 2). All turtles were returned to their capture sites immediately after data collection, which took about 5 minutes per individual.

Thirteen ponds in two general locations were also surveyed with traps during the month of June. These included: 1) five ponds at the north end of lake near the dam and 2) eight ponds in the more southerly Eastman area (Figure 6-3). With the exception of two large ponds at the north end (about 0.6 and 0.9 hectares, respectively), all the ponds were


N
W
E
S
36A
36B
37B
35A
NORTH PONDS
37A
35B
38B
34A
38A
39B
34B
39A
33A
Ferry Gulch
40B
33B
40A
32A
41B
32B
Mooney Gulch
31A
41A
31B
42B
30A
42A
43B
30B
43A
29A
44B
29B
44A
28A
Pine Cove Marina
28B
27A
1B
27B
1A
26A
SOUTH PONDS
Posey Gulch
2B
26B
2A
25A
Eastman Gulch
Baker Gulch
3B
25B
3A
24A
4B
24B
4A
23A
5B
5A
6B
6A
7B
7A
8B
8A
23B
22A
9B
22B
9A
21A
Jennings Gulch
19A
20B
20A
21B
10B
19B
10A
18A
11B
18B
17A
17B
16A
11A
16B
TRINITY NATIONAL FOREST
12B
15A
12A
14A
14B
13B
13A
15B

relatively small (< 0.5 hectares). One trap was set per small pond, while the large ponds received two traps. Additional trap surveys of a subset of southern ponds occurred during mid July. The two largest northern ponds were surveyed again in late July using four traps for each. In contrast to the lake survey, which was structured to permit the use of mark-recapture models (multiple sampling periods with equal sampling efforts), the goal of the pond surveys was to ascertain whether turtles were present or not. During late July, visual surveys of the ponds were also conducted, which consisted of observers sitting in cryptic locations with binoculars and counting turtles.

Aquatic Habitat Analysis

For each trap set in the reservoir, habitat attributes were recorded for the trap location and the surrounding area. These included: water depth, water temperature, water velocity, slope and aspect of the adjacent landform, vegetation at the trap site, vegetation type in the vicinity of the trap site, percent cover of emergent vegetation, presence of basking sites, "coveness" (degree to which adjacent landform is a cove), and "human use" (index of human activity in the area). Appendix 6-A details the measurement procedures. Habitat attributes were recorded at the time of setting the traps. Although habitat attributes were not recorded at the 13 surveyed ponds, simultaneous readings of water temperature in the ponds and the reservoir were taken.

Logistic regression (SAS 1990) was used to develop a model to predict the proportion of sites containing turtles based on the measured habitat characteristics. This technique allows for the explanatory variables to be categorical or continuous and uses

Variable	**Methodology**
Water Depth	Depth (cm) measured at the trap site.
Water Temperature	Temperature (*C) one meter below the water surface at the trap site.
Water Velocity	Velocity (m/sec) at the trap site measured one meter below the water surface.
Landform Slope	Slope of landform adjacent to the trap site.
Emergent Cover	Percent cover of emergent vegetation within a 1-meter radius circle centered on the trap site.
Coveness	The average of three measurements: the distance to the shore from the trap site in three perpendicular directions. Low numbers indicate a cove as opposed to a straight shore.
Basking Sites	The number of basking structures within 1/6 mile on either side of the trap site. Basking structures must be greater than 5 cm in diameter with a slope of less than 70 degrees.*
Humans	The number of humans visible within 1/6 mile on either side of the trap site.
Boats	The number of boats visible within 1/6 mile on either side of the trap site.
Trapsite	Dominant vegetation type (at least 75%) within a 1-meter radius circle centered on the trap site. riparian hardwood conifer mixed
Area	Dominant vegetation type (at least 75%) within a 40 meter radius circle centered on the trap site. riparian hardwood conifer mixed

---

* Characteristics of suitable basking sites for this species gleaned from Reese (Chapter 4)

maximum likelihood to fit a linear logistic regression model. A stepwise procedure was used to select a subset of the original variables that is most useful for predicting the ratio of turtle/no-turtle sites. I set the significance level at alpha = 0.10 for entry of and staying of variables in the model. A moderate alpha level may be more appropriate for the detection of ecological trends (Tort 1991).

Error rates for classification were examined by plotting the frequency of omission and commission errors over all possible thresholds. A threshold refers the critical probability for classification, ranging from zero to one. Omission error in this case consists of erroneously classifying turtle sites as no-turtle sites, while commission error consists of classifying no-turtle sites as turtle sites. Selection of a suitable threshold depends on the management goals; one might want to minimize either one or both types of error. For example, if the critical issue is to identify all sites where turtles might be present, then a threshold should be chosen that minimizes omission error.

Nesting Searches

During late June, upland areas around the reservoir were searched for evidence of western pond turtle nesting during late June. Searching was confined to within a half-kilometer of the reservoir shorelines, as the maximum known nest site distance is 400 meters from its associated waterway (Storer 1930). Because of time constraints, searching was also confined to upland areas adjacent to aquatic locales where turtles were captured (in 1994 or 1995). Prior to actual site visits, aerial photographs were used to identify meadows or other openings that might harbor turtle nests. *Clemmys marmorata* females lay eggs in open areas with a high content of clay and silt in the soil (Holland 1991, 1994). Because active nests are covered with soil and are extremely cryptic, we were not likely to locate them Rather, we were searching for hatched and predated nests that are uncovered and often contain egg-shell fragments. Either because nesting habitat is limited or because of site fidelity, both active and inactive nests often occur in clusters (Holland 1994).

Searching consisted of observers walking the potential nesting areas and noting any nest-like depressions in the ground. When potential nests were found, the following habitat information was recorded at the nest location: distance from edge of clearing, condition (active-i.e. with live eggs or hatchlings, inactive with remnant eggshells, inactive without eggshells), slope and aspect, vegetation type, canopy, soil type, and percent vegetative cover within a one-meter radius circle centered on the nest. Characteristics of the clearings containing potential nest sites were also recorded. These included distance to nearest water, slope and aspect of clearing, size of clearing, soil type, vegetation type within clearing, percent cover of vegetation within clearing, and vegetation type around clearing. Soil type was assessed by laying two perpendicular transects across the meadow and taking soil samples, consisting of 1 pint of soil obtained with a soup can and post hole digger, every 20 meters. Percent cover of vegetation within the clearing was assessed by recording how many meters of rock, bare soil, grasses, forbes, or other substrates the transect lines crossed through.

RESULTS

Surveys

Eight turtles were captured at five traps during the first trapping session (late May), while only one turtle was captured during the second session and three during the third. After the switch in baits to grilse salmon, seven turtles were captured at five traps on the fourth trapping round and one turtle on the fifth. The captured turtles were adults (11 males/9 females) and none of them had been previously marked. The females were not gravid. All twenty turtles were captured in the southern half of the lake (south of Pint Cove Marina). In addition, during the course of the surveys a total of 354 turtles were sighted basking (ranging from 32-82 and averaging 59 turtles per survey), all in the southern half of the lake with the exception of one. It was not possible to ascertain which individuals were sighted repeatedly, as carapace notches are not visible with binoculars.

The low number of captured turtles and absence of recapture prohibited the use of mark-recapture models to estimate population size. However, an approximate estimate can be obtained from the counts of basking turtles. On average, 28% of resident turtles in the mainstem Trinity River are basking at a given time during the active season (Chapter 3). Assuming that a similar ratio applies to turtles in Lewiston Lake, and using the range of basking counts, I estimated that the resident population consists of a minimum of 114 individuals, but may be as large as 293 individuals. From topographic maps, I derived a length measurement of 11,585 meters and an average width of 272 meters for the lake. Given its rectangular shape, this indicates a surface area of approximately 1900 hectares and a density of 0.06-0.15 turtles per hectare.

A total of twenty-eight western pond turtles were captured in eight ponds adjacent to Lewiston Reservoir. Sixteen captures occurred in the southern group of ponds and twelve in the northern group. The captured turtles included 15 males, 11 females, and two juveniles, one of which was a first-year individual and the other a three-year old. None of the females were gravid. Five juveniles were sighted basking in each of two ponds as well. With the caveat that size estimation by eye is difficult, they appeared to be in the 1-3 year-old age classes. Basking adult turtles were also sighted in two of the ponds that did not yield captures; thus, only three of the thirteen ponds surveyed had no captures or sightings of turtles. Simultaneous temperature measurements of the ponds and reservoir revealed that the ponds hold substantially warmer water, at least during the months sampled (mean pond temp = 22.5, mean reservoir temp = 9.4, Table 6-1).

Aquatic Habitat Analysis

Because the total number of turtles captured was low, I used a binary response variable (turtles present or absent), as opposed to an ordinal response variable (number of turtles per trap site) in building the logistic regression model. Turtles were designated as "present" if they were captured or sighted at a particular trap site during any of the five sampling periods. Values of the explanatory habitat variables were averaged across the five periods to obtain more general assessments of site characteristics. A single model was then fit to the data, as opposed to fitting separate models for each sampling period. The variable "basking sites" was excluded because it had the same value ("present") at all trap sites.

Table 6-1. Water temperatures of Lewiston Lake and adjacent ponds during July of 1995.

Pond Site	Temperature (celcius)	Lake Site	Temperature (celcius)
North Pond # 1	28	Lake at trap 24A	14
North Pond # 2	22	Lake at trap 25A	8
North Pond # 3	25	Lake at trap 34A	8
North Pond # 4	22	Lake at trap 36A	7
North Pond # 5	22	Lake at trap 36	10
South Pond # 1	23		
South Pond # 2	18		
South Pond # 3	22		
South Pond # 4	23		
South Pond # 5	20		
MEAN POND TEMP	**22.5**	MEAN LAKE TEMP	**9.4**

The stepwise procedure yielded a model that was composed of the variables water temperature, density of boats, and density of humans (Table 6-2). Specifically, the presence of turtles could be predicted by higher water temperatures and greater human activity. The model was a significant predictor of turtle presence (-2 Log Likelihood = 42.17, p=.0001). Values of the standardized structure coefficients indicated that density of boats had the largest effect, while density of humans had the smallest. Examination of the plot of threshold proportion against classification error rate (Figure 6-4) reveals that minimization of the joint error rates occurs at a threshold of approximately 0.52. Both error rates at this threshold are approximately 0.13. Maximization of model specificity (proportion of turtle sites classified correctly) occurs at a threshold of 0.97, while maximization of model sensitivity (proportion of no-turtle sites classified correctly) occurs at a threshold of 0.16.

Nesting Searches

Six areas, each one in the vicinity of turtle captures, were searched for nests. This included the meadows adjacent to the two groups of ponds, as well as other meadows adjacent to turtle capture locations on the reservoir. One inactive turtle nest was found in the vicinity of the northern ponds (Table 6-3). Eggshell remains provided a positive identification of the nest, which was only two meters from a pond where turtles had been captured. Another potential inactive nest without eggshell fragments was found nearby.

Comparison of characteristics of the meadow containing the active nest with characteristics of the other meadows revealed that the former was closer to water and

Table 6-2. Logistic regression of turtle presence/absence against habitat characteristics at Lewiston Lake traps. Standardized structure coefficients are shown for variables that entered the stepwise model.

Habitat Characteristic	Turtles Present (n = 23)		Turtles Absent (n = 41)		Standardized Coefficient
	mean	s.d.	mean	s.d.	
Water Depth (cm)	58.6	19.1	65.6	21.5	
Water Temp (*C)	**12.7**	2.7	**8.6**	2.2	-1.352
Water Velocity (m/sec)	0.00	0.01	0.03	0.08	
Slope (degrees)	23.1	9.3	21.8	9.0	
Emergent cover (%)	16.2	16.4	21.5	20.2	
Coveness (index)	150	95	216	11 0	
Humans	**1.14**	1.32	**0.88**	0.94	0.819
Boats	**0.67**	0.88	**0.40**	0.42	-1.754
Trapsite riparian	0.61	0.50	0.73	0.45	
Trapsite hardwood	0.21	0.41	0.12	0.33	
Trapsite conifer	0.18	0.39	0.15	0.36	
Trapsite mixture	0.00	0.00	0.00	0.00	
Area riparian	0.26	0.45	0.41	0.54	
Area hardwood	0.21	0.41	0.12	0.33	
Area conifer	0.27	0.45	0.10	0.34	
Area mixture	0.39	0.50	0.34	0.4$	

-2 log likelihood = 42.17 p = .0001

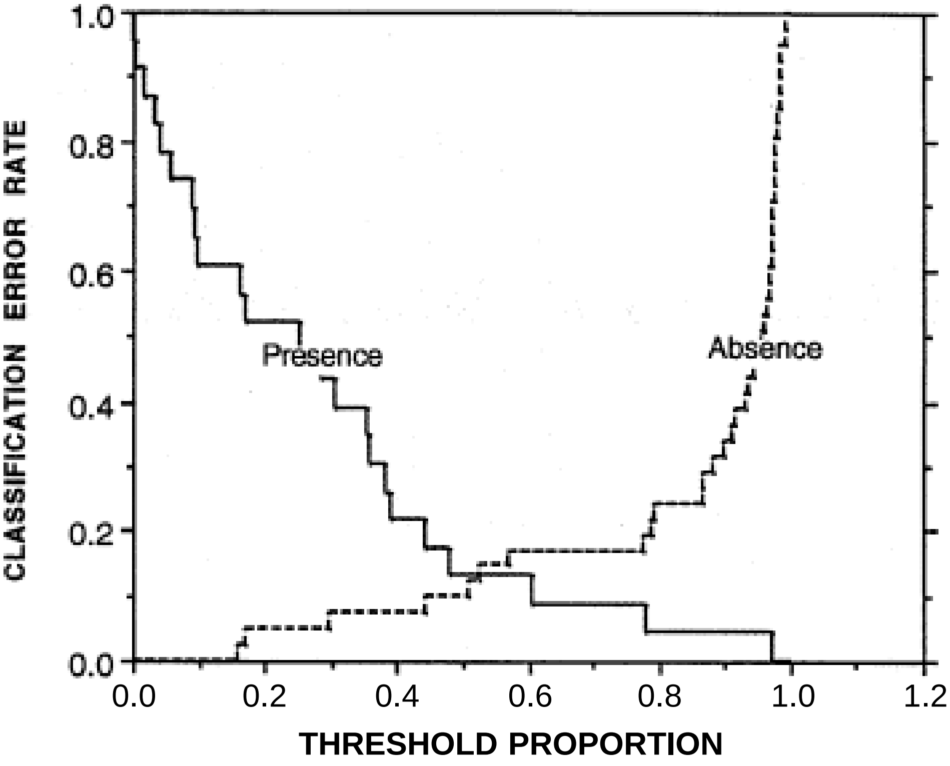


Figure 6-4. Plot of classification error rates across threshold values for logistic regression of turtle presence against habitat characteristics.

Table 6-3. Habitat characteristics of potential nesting areas and nest sites within 500 m of turtle capture locales.

MEADOW I.D.	2	7A	7B	11A	11B	11C	11D
Size (m^2)	576	434.	5796	3075	25	120	270
Distance to nearest water (m)	2	85	12	20	131	145	143
Slope (degrees)	15	0	0	0	10	12	4
Aspect	WNW	-	-	-	SSW	SSW	WNW
Meadow Veg	grass/ willow	grass/ shrub	grass	grass	grass	grass/ shrub	grass
Surrounding Veg	conifer/ hardw./ riparian	conifer dominant	conifer dominant	hardw./ conifer	conifer dominant	hardw./ conifer	conif.
Rock(%)	16	1	3	0	29	1	1
Soil (%)	0	3	12	1	14	11	35
Grass (%)	71	40	53	99	16	83	6
Forbes (%)	0	0	0	0	1	0	0
Duff (%)	6	56	32	0	40	5	58
Wood (%)	7	0	0	0	0	0	0
Mean vegetation height (cm)	27	32	33	48	17	24	34
Number of nests	2	0	0	0	00		0
Distance from edge of clearing (m)	5.5/5.0						
Condition	Inactive						
Microslope	8/25 degrees						
Microaspect	WNW/NW						
Vegetation type	grasses/thistle						
Canopy closure (%)	10/5						
Soil texture	silt loam	loam	loam loam sand fine sandy loam	loam silt loam clay loam	clay loam	loam	loam

consequently bounded by riparian vegetation. It was also more sloped with rocky ground, relatively lush grasses, and no exposed soil. The nests themselves had relatively low canopy and vegetative cover. Examination of the soil samples revealed that the soil was a silt loam. The other six meadows all contained some type of loam soil, with silt loam occurring in portions of two meadows (Table 6-3).

DISCUSSION

The low number of western pond turtles captured in Lewiston Lake is congruent with the 1994 results (Reese et al. 1994) and can be attributed to several factors. First, turtles may become trap shy, as suggested by the declining capture rate after the first sampling period. Trap shy responses have been known to occur during sampling for this species at other locales (Holland, pers. comm.). However, even assuming such responses, turtles that have never been captured should be attracted to the traps. Given the poor capture success coupled with visual sightings at only a few, discrete locations, the density of turtles appears to be low relative to other known populations. For example, turtle populations in pond habitats in the Rogue River drainage in Oregon may be as dense as 500 individuals/hectare (Holland 1994). Estimates from California indicate that, albeit rarely, this species can achieve densities as high as 3700 individuals/hectare (Holland 1991). This study found less than one individual per hectare in Lewiston Lake.

The high capture success in ponds adjacent to the reservoir indicates that they may offer more suitable habitat. It is particularly interesting that turtles were captured in the northern set of ponds, considering that there were no reservoir captures and only a single sighting in this area. Research on habitat utilization in the mainstem Trinity (Chapter 5) indicates that adult western pond turtles inhabit deep, pooled water with abundant basking sites and underwater cover objects. Portions of Lewiston Lake appear to offer such habitat. Juveniles frequently inhabit warmer, more lentic waters such as sloughs and seasonal ponds adjacent to the main channel (Chapter 8). The water temperatures in Lewiston Lake (Table 6-1) are substantially lower than water temperatures of sites used by juvenile or adult turtles along the mainstem Trinity River, ranging from 10-17 degrees Celsius for adults and 12-33 degrees for juveniles (Lind et al. 1994, Chapters 5 & 8). Thus, both age classes of turtles may be seeking thermal refuge in the adjacent ponds.

It is striking also that the ponds contained some juveniles (7% of the captures), whereas the reservoir population appeared to be composed entirely of adults. This suggests that the ponds may be a valuable component of this altered system with respect to western pond turtles, especially given that low juvenile recruitment is of range-wide concern (Holland 1991). However, bullfrogs inhabit at least several of the ponds, indicating a predation risk for hatchling turtles (Moyle 1973, Holland 1991).

The logistic regression model indicated that presence of turtles in the lake can be predicted by higher water temperatures and greater human activity. The association with water temperature is explainable; western pond turtles are ectotherms and have been shown to be associated with warmer waters (Chapter 5). The association with human activity is surprising because turtles are usually cryptic and wary. It is possible that more food is available to turtles where humans are present as a result of fish tossed overboard, lost bait fish, and/or mortalities from propellers. It is also possible that human activity is indicative of some other factor that was not measured. Given that the activity on the lake is mostly related to fishing, humans and turtles may both congregate in high quality fish habitat, e.g. in areas with aggregations of aquatic invertebrates, neither of which were quantified. The logistic regression model, although significant, may not be useful as a predictive model if these associations with the human use variables are surrogates for other, unmeasured associations.

Discovery of the nests indicated that nesting is occurring in at least one location around Lewiston Lake. The habitat characteristics were consistent with characteristics at other locales where this species nests (Goodman 1994, Holland 1991, 1994, Rathbun et al. 1992). Specifically, the site was in a meadow with low canopy cover, a ground cover of grasses, a moderate slope, and soil with a high silt content. It is not surprising that another potential nest was found nearby; western pond turtle nests are often found in clusters (Holland 1994). Nesting site fidelity or limited amounts of suitable habitat are probably responsible for the clustering.

Overall, the results are indicative of a small population of western pond turtles, clustered in the warmer portions of Lewiston Lake, and potentially interacting with populations in adjacent ponds. Although there does appear to be some recruitment of juveniles, it is confined to ponds where there is a risk of bullfrog predation. Suitable nesting habitat is present, but not abundant, around the lake. The meadows in the vicinity mostly contain loamy soils lacking the high clay or silt component that characterizes western pond turtle nesting habitat. Management actions to enhance the potential of

Lewiston Lake to support viable populations of turtles could include: 1) protection of suitable nesting habitat, i.e. meadows with appropriate characteristics within 400 meters of the lake 2) boosting of water temperatures to levels within the range known to be utilized by western pond turtles 3) eradication of bullfrogs in the adjacent ponds, which may require draining them every 1-2 years.

ACKNOWLEDGEMENTS

I thank the USDI Bureau of Reclamation and Fish and Wildlife Service for providing the funding for and facilitating this project. Special thanks to Michelle Gilroy for conducting the field work and Bob Olson for providing logistical support. Don Ashton providing training and guidance during the early phases.

CHAPTER 7

HABITAT QUALITY OF ARTIFICIAL SIDE CHANNELS AND BANK FEATHERED EDGES FOR WESTERN POND TURTLES IN THE TRINITY RIVER

ABSTRACT: Attempts to restore the mainstem Trinity River to its pre-dam condition, particularly with reference to fisheries enhancement, include the construction of side channels and feathered edges. These modifications of the river channel simulate the historic condition of low-velocity waters provided by shallow river margins and a wide, braided channel. This study evaluated the suitability for western pond turtles (*Clemmys marmorata*) of the twenty-eight modifications made to date. Suitability assessments, made during the summer of 1995, consisted of snorkel surveys as well as comparison of habitat characteristics to characteristics known to be associated with this species. A total of 8 adult turtles and 4 juveniles were captured in modified habitats. The results of the habitat characterization indicated that shallow, low-velocity waters with reduced canopy closure distinguish the modified habitats from the surrounding main channel habitat. The feathered edges are also characterized by less sandy substrate and fewer basking sites. Neither modification provided more suitable habitat for juvenile or adult turtles than the main channel in its current condition. Lack of suitability was primarily attributable to the reduced canopy closures and absence of deep waters. Recommendations for enhancing the modified areas relative to western pond turtles include increasing structural complexity by creating pockets of deeper water and adding woody debris.

INTRODUCTION

Ongoing research on habitat associations of the western pond turtle (*Clemmys marmorata*) has shown significant relationships between the distribution of this species and specific riverine habitats (Wilson et al. 1991, Lind et. al. 1992). Western pond turtles are concentrated in slow-flowing areas of rivers, such as edgewater and backwater pools. They are associated with deep water and the presence of woody or rocky debris that provides basking sites and underwater cover (Bury 1972, Holland 1991, Chapter 5). While adult western pond turtles have relatively broad habitat requirements, juveniles appear to be more specialized. They utilize shallow, warm, low-flow areas with emergent vegetation (Holland 1991, Chapter 8). These areas may be essential for their survival, as they are relatively poor swimmers and perhaps cannot forage or navigate effectively in deeper, swifter waters (Holland 1991).

Damming of the mainstem Trinity River (Trinity County, California) in 1963 has resulted in numerous habitat alterations, some of which pertain to the availability of suitable western pond turtle habitat (Chapters 5 & 8). The most significant reduction appears to be in shallow, river margin habitats with rocky substrates. These habitats have been replaced by deeper, swifter waters as the river has become channelized by year-round low flows and encroaching vegetation (Hampton 1995, Trinity River Restoration Program 1994, Wilson 1993). Not only were the historic shallow margin habitats likely to be suitable for western pond turtle hatchlings, but they were critical for fish rearing and overwintering.

For the purpose of fisheries restoration, anthropogenic side channels and bank feathering projects have been initiated to simulate the historic conditions of the river margins (USDI-FWS and TCDTP 1992). To date, a total of nineteen side channels and nine feathered edge projects have been built, with the first side channel constructed in 1981, but the bulk of construction occurring from 1990 through 1993. Side channels are created by excavating a channel of pre-determined length and gradient and then excavating an inlet and outlet through riparian berms (Figure 7-1). Channels often follow high flow conduits on the historic floodplain and have different shapes, widths, and depths depending on restoration objectives (USDI-FWS and TCDTP 1992). Existing side channels range in length from 107-940 meters (350-3085 feet). Bank feathering (to create feathered edges) entails removal of sections of riparian berms and recontouring of the river banks to provide a gradual sloping bank and river margin (Figure 7-2). They are typically constructed at historic point bar locations and cobble-sized rocks are added to both aquatic and terrestrial areas (USDI-FWS and TCDTP 1992). Existing feathered edges range from 120-365 meters (395-1200 feet).

Pilot evaluation of a subset of the side channel and feathered edges (Lind et al. 1995) indicated no evidence that they provide more suitable western pond turtle habitat than the pre-construction river. Suitability was assessed by quantifying habitat characteristics relative to the range of characteristics known to be used by western pond turtles along the mainstem Trinity. Comparison of habitat pre- and post-construction indicated that side channels offered the same amount of suitable habitat and feathered edges offered less suitable habitat than what was available prior to construction.

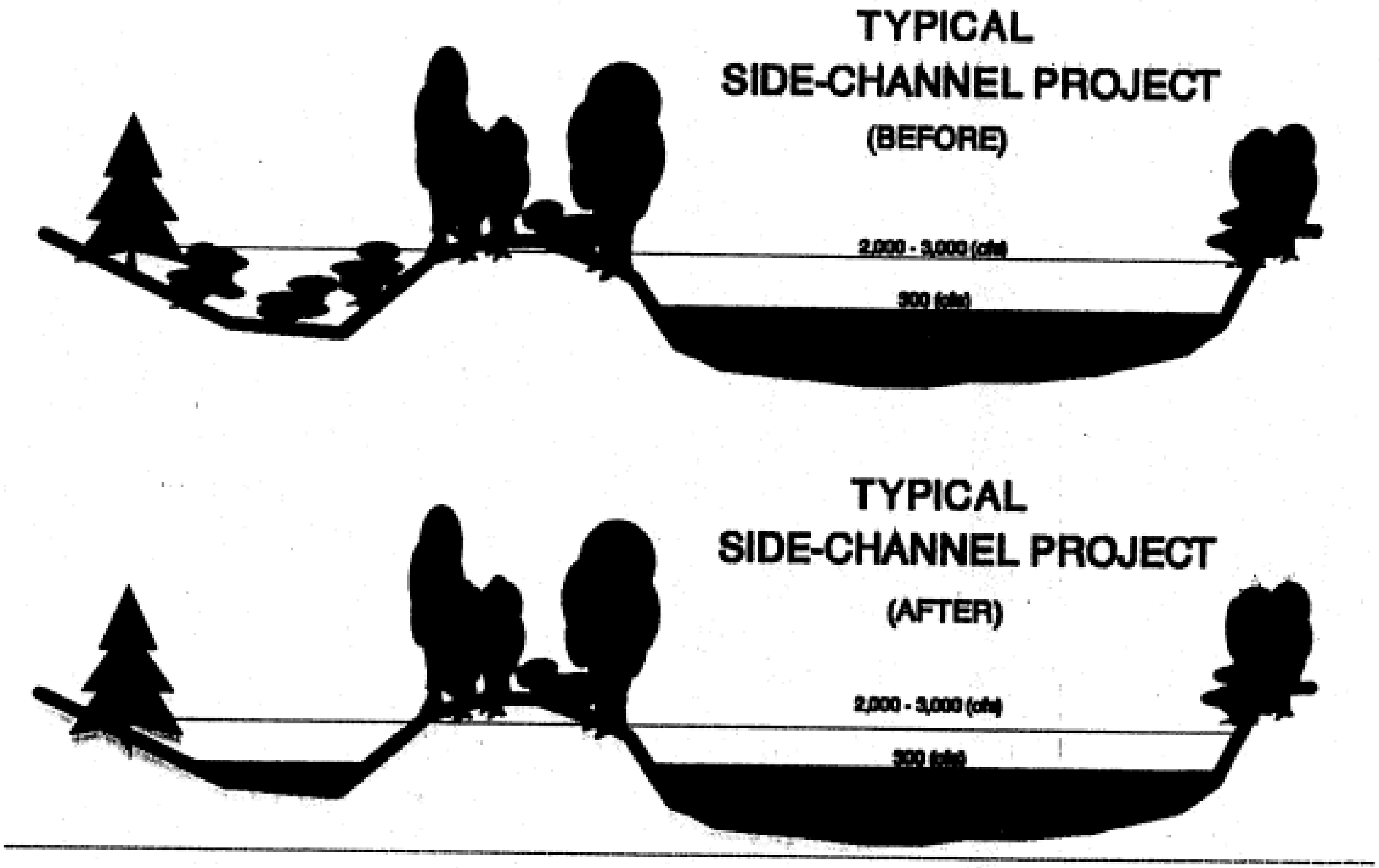


Figure 7-1. Schematic profile of side channel sites before and after construction. Pre-construction channel contains shrubs.

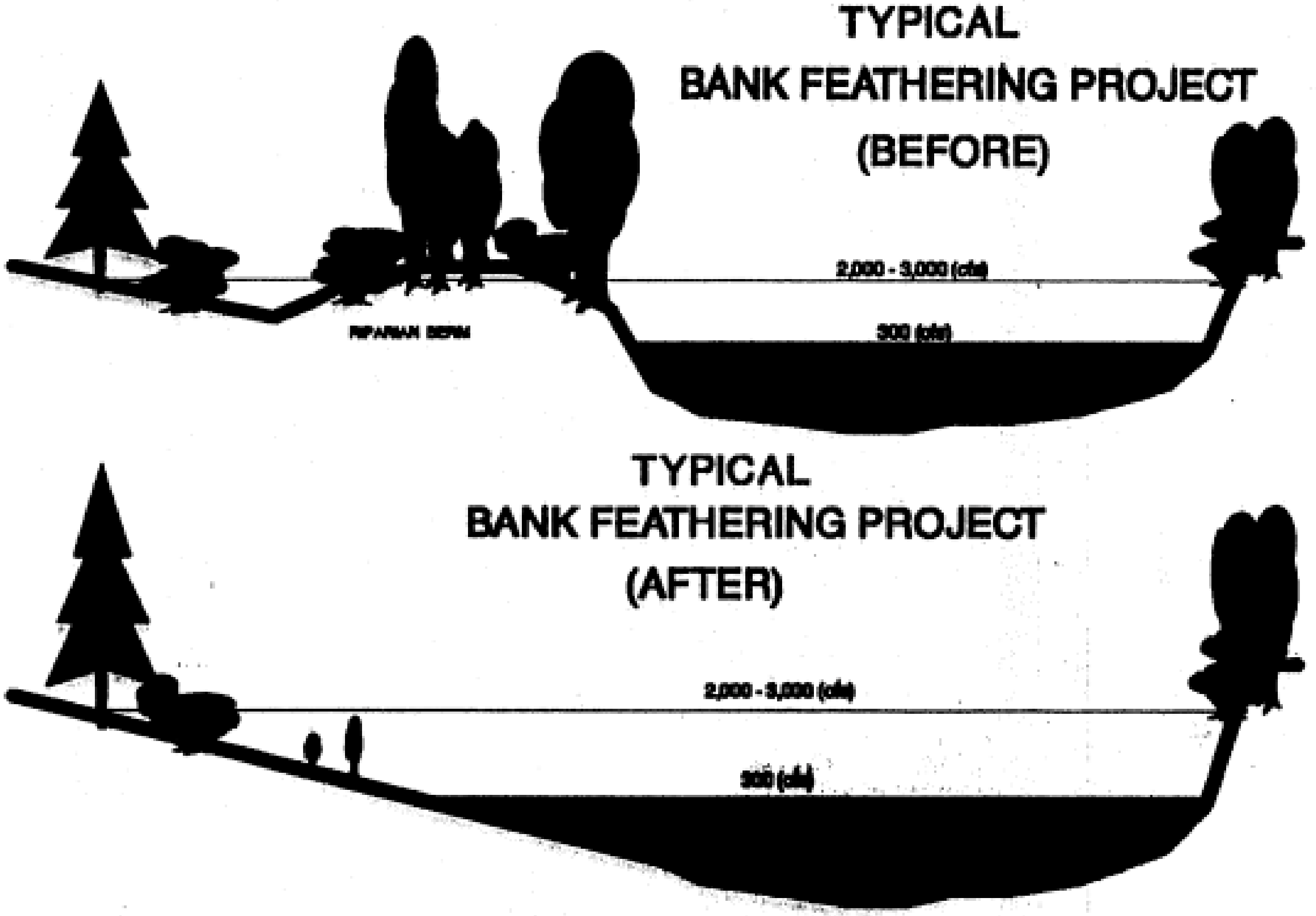


Figure 7-2. Schematic profile of bank feathering sites before and after construction. Pre-construction channel contains shrubs.

However, despite these apparent reductions in habitat quality, several juvenile turtles were captured in the new projects. This inspired the current study, which consists of evaluations of all 28 projects and discriminates between the age classes in classification of habitat as suitable. As discussed above, habitat associations differ between juvenile and adult western pond turtles. While the new projects may not enhance habitat for adult western pond turtles, juveniles may benefit from the increase in shallow edgewaters.

The following questions were addressed: (1) What proportion of the projects are being used by western pond turtles? (2) What characteristics of the project habitat distinguish it from the main channel river habitat? (3) To what extent do the projects provide habitat characteristics that fall within the known range of habitats used by juvenile and adult western pond turtles?

STUDY AREA

The study area encompassed the entire 63 km stretch of the Mainstem Trinity River from below the Lewiston Dam downriver to the confluence with the North Fork Trinity River, Trinity County, California (Figure 7-3). Evans (1980) defined four broad habitat types within the riparian zone: (1) bare rock or gravel bar, (2) willow dominant, (3) willow-alder mix and, (4) mature alder-cottonwood. The width of the riparian zone varies from 5 meters to 50 m. The oldest and most mature riparian areas are closest to the dam because of the controlled flows and lack of flooding. Further downstream, tributary streams contribute variable flows and create periodic flooding, resulting in some younger

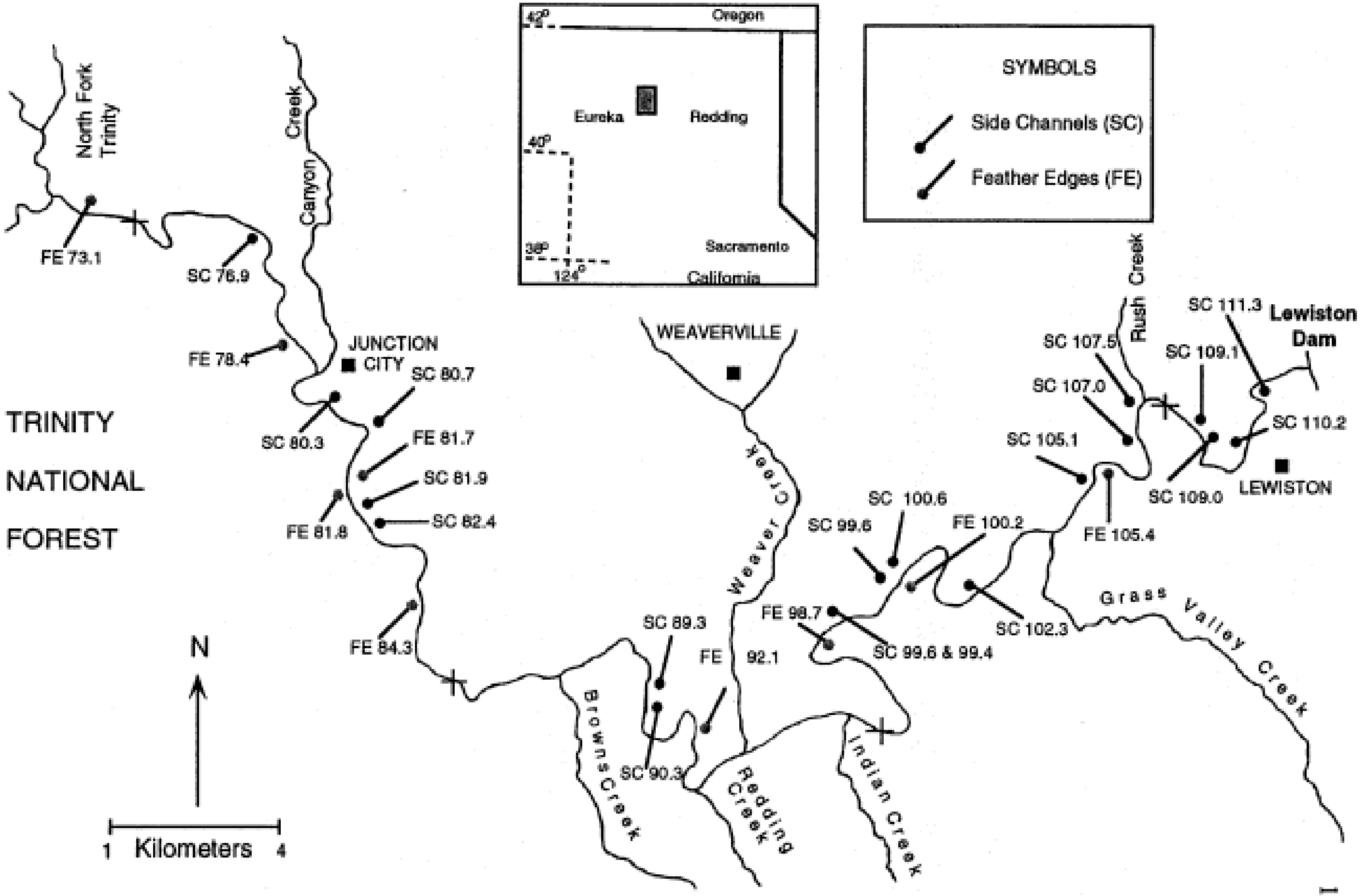


Figure 7-3. Side channel and feathered edge sites sampled on the mainstem Trinity River

riparian vegetation. Mining tailings are extensive along the lower third of the mainstem study area; some with scattered willows, and others barren of vegetation.

METHODS

The evaluations consisted of three parts: 1) surveys for western pond turtles; 2) aquatic habitat comparisons; 3) aquatic habitat evaluations.

Surveys

The entire length of all 19 side channels and 9 feathered edges was surveyed (Figure 7-3) as well as the river adjacent to each project plus an additional 50 meters upstream and 50 meters downstream. Surveying consisted of snorkelers traveling along the designated stretches and searching all underwater areas using the methods described in Chapter 3. In addition to visual scanning, this included manual exploration of bank undercuts, caves, rock crevices, debris piles, and clumps of vegetation. In the main channel, the search area was limited to within 4 meters of the shoreline because that was ascertained to be the maximum distance a diver could scan visually while moving downstream. In addition, beyond four meters the rapid flows often rendered searching impossible. Considering that underwater cover objects are clustered along the shorelines and that western pond turtles are relatively poor swimmers (Holland 1991), it is likely that the search area harbored the majority of turtles.

Aquatic Habitat Comparisons and Evaluations

Aquatic habitat was measured with a protocol that permitted comparison to existing data on turtle habitat utilization collected during 1993 turtle surveys on the mainstem Trinity (Chapter 5). Specifically, a floating rectangular quadrat measuring 3 meters by 6 meters and divided into nine subquads (1 x 2 meters) was laid on the water surface. Within the quadrat, the following features were measured: bank distance, flow type (e.g. riffle, pool), water velocity, water depth, presence of basking sites, presence of cover objects, degree of bank undercut, and canopy cover. A flow index was calculated to derive a weighted average of the proportion of flow types within the quadrat. Flow types were also measured along a transect across the river. Appendix 5-A details the measurement procedures.

Some measured features generated multiple variables for analysis. For example, because Bury's (1972) results indicated that deep water might be important for western pond turtles, I generated a "maximum depth" variable (maximum value of the nine subquads) in addition to the "mean depth" variable. Because I suspected that slow-flowing water might be preferred (Lind et al. 1992), a "minimum flow" variable was generated. Finally, because bank undercuts frequently serve as turtle refugia, and deeper undercuts may be more protective, a "maximum undercut" variable was created in addition to "mean undercut".

Ten floating quadrats were distributed at random along each project and ten were distributed along the adjacent stretch of river on the opposite side. In both cases, random numbers were used to select a distance from the top of the site and a distance from shore.

The distance from the top was constrained to the length of the project such that all quads fell within the project boundaries. The distance from shore was constrained to 0-4.0 meters to match the actual area searched for turtles (see Methods: Surveys). Habitat was also quantified at all turtle capture locales, whether in the river or projects. The floating quadrats were placed with their centers over the capture point.

ANALYSIS

For all analyses, side channel sites were considered separately from feathered edge sites. They are different enough in their attributes that combining them was unwarranted.

Surveys

The survey results provided information on whether colonization of projects by western pond turtles had occurred. For each side channel and feathered edge, the number of captured turtles within the project and the number of captured turtles in the vicinity of the project were tallied. Adults and juveniles were tallied separately.

Aquatic Habitat Comparisons

Discriminant analysis was used to ascertain whether side channel and feathered edge quadrats could be distinguished from main channel quadrats on the basis of measured habitat characteristics. The null hypothesis was that the restoration projects do not provide habitat that is distinct from what already is available in the river. Correlation analysis was used to identify redundancies among variables, especially those known to have a close relationship such as mean and maximum values of a habitat characteristic. If two variables were highly correlated (R <=-0.75 or R >0.75) and they both entered the model, the one was excluded that contributed less discriminatory power.

A stepwise procedure was used to select the subset of original variables most useful for discriminating project from river sites with the significance level set at alpha = 0.10 for entry of variables into the model. A moderate alpha level may be more appropriate for the detection of ecological trends (Tort 1991) and reduces the probability of a type II error. A type II error would entail not discriminating project habitat from river habitat when it is, in fact, different. From a management perspective, this could underrate the value of the channel modifications in providing unique habitat.

For variables that were nonnormally distributed, even after transformation, a nonparametric DA was conducted (kernel method, SAS 1990). Kernel density was estimated using the Epanechnikov kernel, which is optimum in the sense of minimizing the smallest mean integrated square error achievable (Silverman 1986). The smoothing parameter (r) was also chosen to minimize the mean square error, assuming a multivariate normal distribution. Although that distribution cannot be assumed here, this was the best approach to obtaining the optimal r, given computational limitations (Baldwin, pers. comet). Bandwidths were allowed to differ between the two groups (project/river). For parametric DAs, heterogeneity among variance-covariance matrices was tested for using Bartlett's modification of the likelihood ratio test (SAS 1990) setting alpha = 0.05. In cases where the matrices were heterogeneous, quadratic as opposed to linear discriminant functions were generated.

A jackknife procedure was used to evaluate the classification success of the parametric and nonparametric models (SAS 1990). Cohen's Kappa (Titus et al. 1984) was then computed for each test to compare the classification success to chance. The significance level for performance was set at alpha = 0.05.

Aquatic Habitat Evaluations

Values of the aquatic habitat variables were examined in the context of the "known universes" of utilized sites for juvenile and adult turtles in the mainstem Trinity. The known universes for juveniles and adults were each obtained from the following sources: 1993 data on habitat utilization along three stretches of the mainstem Trinity (Chapter 8), 1994 data from the side channel and feathered edge evaluations (Lind et al. 1995), and the 1995 data from turtle captures associated with this study. In each case, habitat was measured with the same protocol as described above (Appendix 7-A). The sample size of juveniles totalled approximately 100 while the sample size of adults totalled approximately 130 with some variability across habitat variables (i.e. not all habitat variables were measured for every captured individual).

For each of these "known universes", I calculated the range of values for all measured habitat variables and then determined the proportion of habitat quadrats whose values fell within these ranges for side channels and feathered edges. For the quadrats that did not qualify as suitable, I examined values of the habitat variables to determine which were most frequently responsible for the lack of suitability. Given that ten floating quadrats were placed along each project and ten in the adjacent river, there were a total of 180 habitat quadrats for side channels with 180 corresponding river quadrats and a total of 90 habitat quadrats for feathered edges with 90 corresponding river quadrats.

RESULTS

Five of the side channels were partially dry due to changes in configuration that occurred in the absence of maintenance (site numbers 76.9, 80.3, 81.9, 82.4, 89.3, Figure 7-3). Specifically, sediment accumulated in the inlets such that water could not enter. Although the entire project lengths were nevertheless searched for turtles, aquatic habitat evaluations were restricted to those parts of each project with water. Thus, the sample size of habitat quadrats for side channels was slightly reduced from the expected figure.

Surveys

A total of 11 turtles, 3 of which were juveniles, were captured in seven of the side channels. Thus, 37% (7/19) of the side channels harbored turtles with a maximum of four turtles in a single side channel. A total of 1 turtle (juvenile) was captured in the feathered edges; this constitutes 12% (1/8) of the feathered edges that harbored turtles. Sixteen adult turtles and two juveniles were captured outside the newly constructed projects, mostly adjacent to side channels. Table 7-1 displays this distribution of turtles near and within projects by project type.

Table 7-1. Number of turtles captured within side channel and feather edge projects and number of turtles captured in the adjacent river during 1995 surveys along the mainstem Trinity. Numbers in parentheses represent number of projects.

	Juveniles	Adults	Total
Side Channels	3 (3)	8 (4)	11 (7)
Feather Edges	1 (1)	0 (0)	1 (1)
Adjacent to Side Channels	2 (2)	14 (8)	16 (10)
Adjacent to Feather Edges	0 (0)	2 (1)	2 (1)

Aquatic Habitat Comparisons

For the discriminant analysis (DA) of side channel and river habitat, all measured variables met the assumption of normality. The DA revealed that side channel quadrats could be distinguished from river quadrats on the basis of habitat characteristics. The model that emerged was quadratic and composed of the following variables: river transect (of flow types), canopy, depth, and flow index (Table 7-2). Specifically, the side channels offered lower flow types than the river. The side channels were also shallower with less canopy cover. This model was a significant discriminator of side channel habitat and main channel habitat (Wilk's Lambda and F statistics). The crossvalidation test was able to classify 76% of the habitat quadrats from the two sample sites correctly, which was significantly greater than chance (Cohen's kappa = 0.612, $p < .0001$).

For the discriminant analysis of feathered edge and river habitat, five variables (sand, undercut, maxcut, canopy, small basking sites) did not meet the assumptions for parametric discriminant analysis, even after transformation. A nonparametric discriminant analysis (Epanechnikov kernel, $r = 3.41$) revealed that feathered edge quadrats could be distinguished from river quadrats on the basis of the following habitat characteristics: canopy, small basking sites, sand, flow index, and depth (Table 7-3). Specifically, the feathered edges had less canopy cover, fewer small basking sites, and less sand than other areas of the river. The feathered edges were also shallower with more flow types. This model was a significant discriminator (Wilk's Lambda and F statistics) of feathered edge habitat and main channel habitat. The crossvalidation test (Jackknife) classified 96% of the quadrats from the two sites correctly, which was

Table 7-2. Two-group stepwise discriminant analysis of side channel habitat and river habitat along the mainstem Trinity. Although some variables were transformed prior to analysis, means and standard deviations are in actual measured units. Standardized structure coefficients are presented for variables that entered the model, which was quadratic.

Habitat Characteristic	Side Channels (n=171) mean	s.d.	Main Channel (n=190) mean	s.d.	Standardized Structure Coefficient
River transect (index)	166.1	48.9	217.3	41.6	
Flow type (index)*	1.6	0.6	1.8	0.6	
Average water flow (m/sec)*	17.7	23.1	32.7	32.5	
Minimum water flow (m/sec)	1.1	14.5	8.8	26.2	
Average water depth (cm)**	342	25.4	52.6	28.5	
Maximum water depth (cm)**	52.4	31.5	77.4	34.6	+0.308
Baskable bank (%)	0.1	0.1	0.1	0.1	
Small basking sites (index)	4.5	9.8	8.2	14.1	
Large basking sites (index)	33.1	60.8	46.0	72.6	
Undercut (m)***	2.3	7.2	6.5	12.9	
Maximum undercut (m)***	4.1	11.6	10.9	19.4	
Underwater cover (%)	14.4	19.9	15.8	18.3	+0.404
Sand cover (%)	1.7	9.1	3.8	13.0	
Canopy (%)	27.7	32.9	57.5	35.0	+0.359

Wilk's Lambda = 0.584; F(df 4,357) = 63.58; p = .0001
Jackknife success (%) = 76; Cohen's Kappa = 0.612; p < .0001

* correlated pair, of which only flow type
** correlated pair, of which only depth entered the model
*** correlated pair, of which neither variable entered the model

Table 7-3. Two-group stepwise discriminant analysis of feather edge habitat and and deviations are shown in actual measured units. Standardized structure coefficients are presented for those variables that entered the model, which was nonparametric (Epanechnikov kernel, r = 3.41).

Habitat Characteristic	Feather Edges (n=89) mean	s.d.	Main Channel (n=89) mean	s.d.	Standardized Structure Coefficient
River transect (index)	200.0	34.7	207.5	30.0	
Flow type (index)*	1.6	0.4	1.7	0.5	-0.316
Average water flow (m/sec)*	22.5	24.0	36.5	31.6	
Minimum water flow (m/sec)	6.4	19.3	9.7	27.0	
Average water depth (cm)**	21.8	18.4	63.9	26.8	+0.684
Maximum water depth (cm)**	35.4	24.2	95.3	28.9	
Baskable bank (%)	0.1	0.2	0.1	0.2	
Small basking sites (index)	3.5	8.2	13.5	17.7	+0.220
Large basking sites (index)	18.2	31.1	37.9	57.8	
Undercut (cm)***	0.1	0.5	7.8	13.5	
Maximum undercut (cm)***	0.1	1.1	13.6	20.9	
Underwater cover (%)	1.5	4.1	20.7	18.2	+0.196
Sand cover (%)	1.0	6.8	7.9	14.6	
Canopy (%)	0.8	1.4	74.9	31.0	+0.846

Wilk's Lambda = 0.169; F(df 5, 157) = 153.9; p = .0001
Jackknife success (%) = 96; Cohen's Kappa = 0.921; p < .0001

* correlated pair, of which only flow type entered the model
** correlated pair, of which only depth entered the model
*** correlated pair, of which neither variable entered the model

significantly greater than chance (Cohen's kappa = 0.921, p < .0001).

Aquatic Habitat Evaluations

The evaluation of project suitability for juvenile western pond turtles revealed that side channels provided proportionally more suitable habitat than the adjacent river (48% of side channel quadrats were suitable, while 41% of river quadrats were suitable; Figure 7-4). Feathered edges, in contrast, provide substantially less suitable habitat for juveniles than the river (18% of feathered edge quadrats were suitable). The relationships between project type and habitat suitability were different for adult western pond turtles. The river provided proportionally the most suitable habitat (60% of river quadrats qualified) with size channels providing less (45%) and feathered edges less still (14%).

Analysis of the factors responsible for lack of suitability reveals trends (Tables 7-4 and 7-5). For both adult and juvenile turtles, the variables whose values most frequently fell outside of the "known universe" were those related to depth, flow, and canopy. Unsuitable side channels lacked areas of deep water, were too fast-flowing, and were too exposed (not enough canopy). For both age classes, unsuitable feathered edges also lacked deep-water areas and were too exposed. For juveniles, they were in addition too fast-flowing. For the samples taken in the river, high flow values were most frequently responsible for a lack of suitability. The much greater suitability of the river for adults than juveniles (60% versus 41% of quadrats qualified) is attributable to the narrower range of flows associated with juveniles.

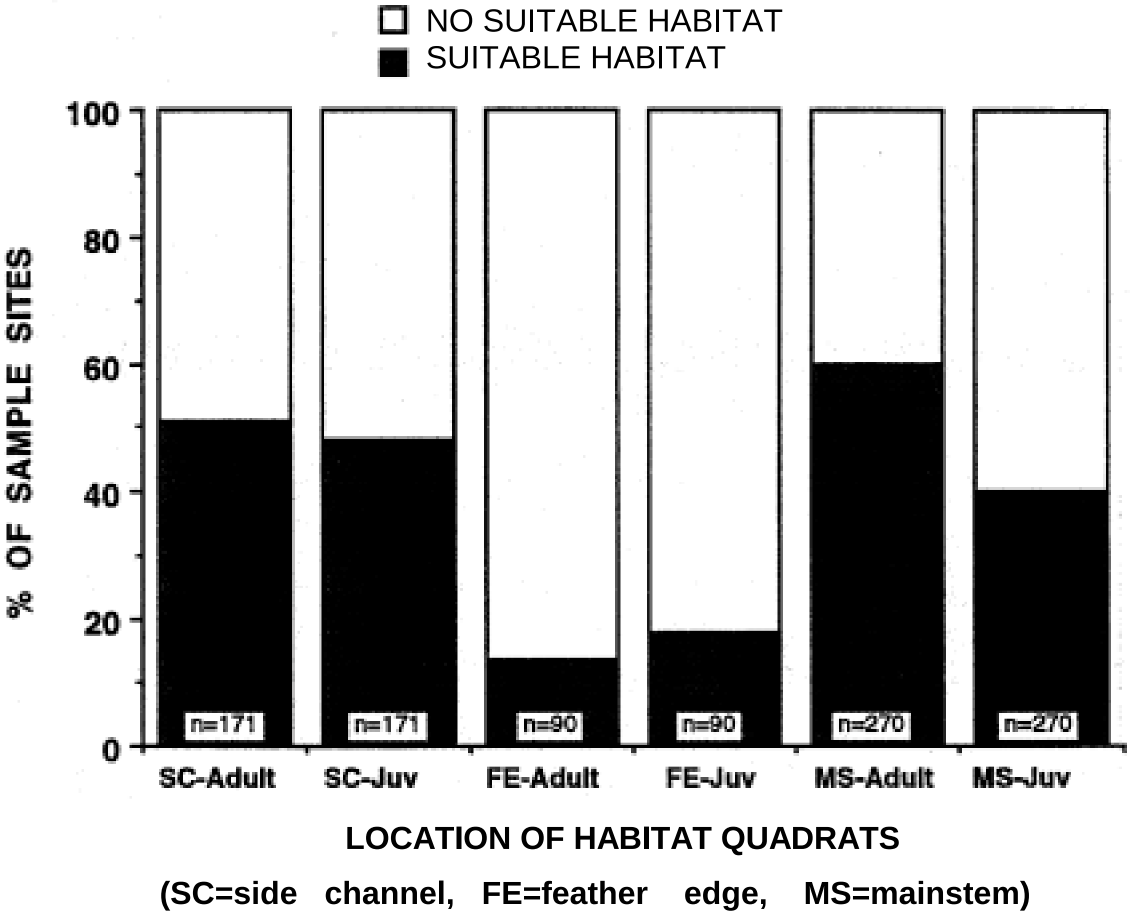


Figure 7-4. Percent of sample sites at side channel and feathered edges with suitable habitat for adult and juvenile western pond turtles.

Table 7-4. Number of habitat quadrats that were NOT suitable for adult western pond turtles in terms of values of each habitat variable.

HABITAT VARIABLE	SUITABLE RANGE	SIDE CHANNELS (n = 171)	FEATHER EDGES (n = 90)	MAIN CHANNEL (n = 280)
River Transect (index)	100 to 250	8	7	55
Flow Type (index)	1.0 to 2.6	13	0	24
Average flow (cm/sec)	-16 to 65	7	6	43
Minimum flow (cm/sec)	-22 to 38	8	8	39
Average depth (cm)	8.8 to 267.8	19	18	5
Maximum depth (cm)	23 to 310	21	33	5
Baskable bank (%)	0 to 67	0	0	0
Small basking sites (index)	0 to 56	0	0	6
Large basking sites (index)	0 to 264	1	0	5
Bank undercut (cm)	0 to 70	0	0	1
Maximum bank undercut (cm)	0 to 185	0	0	0
Underwater cover (%)	0 to 100	0	0	0
Sand cover (%)	0 to 100	0	0	0
Canopy (%)	0 to 68	50	70	16

Table 7-5. Number of habitat quadrats that were NOT suitable for juvenile western pond turtles in terms of values of each habitat variable.

HABITAT VARIABLE	SUITABLE RANGE	SIDE CHANNELS (n = 171)	FEATHER EDGES (n = 90)	MAIN CHANNEL (n = 280)
River Transect (index)	100 to 250	8	7	55
Flow Type (index)	1.0 to 2.0	20	2	49
Average flow (cm/sec)	-10 to 50	19	12	91
Minimum flow (cm/sec)	-15 to 38	10	9	50
Average depth (cm)	0-600	0	0	0
Maximum depth (cm)	13-600	13	9	2
Baskable bank (%)	0 to 44	4	6	10
Small basking sites (index)	0 to 78	0	0	0
Large basking sites (index)	0 to 413	0	0	0
Bank undercut (cm)	0 to 70	0	0	1
Maximum bank undercut (cm)	0 to 100	0	0	0
Underwater cover (%)	0 to 69	3	0	1
Sand cover (%)	0 to 100	0	0	0
Canopy (%)	0.16 to 98	50	65	49

DISCUSSION

The results indicate that side channels and feathered edges are readily distinguishable from the main channel on the basis of habitat characteristics. Both these project types offer shallower, lower-flow microhabitat with less canopy cover than the remaining river. Feathered edges in addition contain less sand and fewer basking sites. These findings are consistent with the objectives of the fish habitat restoration program, namely to simulate the historic conditions of shallow edgewaters with exposed gravel bars. Under natural flow conditions, annual floodwater would create a wide, braided channel with a low concentration of riparian vegetation (Trinity River Restoration Program 1994). This provides salmonids with the lentic conditions conducive to rearing (Heede and Rinne 1990).

However, the results also indicate that neither project type provides substantially more suitable habitat for western pond turtles than the main channel in its current condition. Side channels are slightly more suitable for juveniles than the river as a result of their lower flows, but they are markedly less suitable for adults because of their reduced canopy cover. Feathered edges, because they are shallow and exposed, are considerably less suitable than the river for both age classes, but slightly more suitable for juveniles than adults. Considering the association of adult western pond turtles with deep, pooled habitats (Chapter 5), it is not a surprise that the fish restoration projects would be marginally suitable. Juveniles, which are more apt to inhabit shallows (Holland 1991, Chapter 8) benefit from the increase in lentic waters.

The survey results, although of limited value due to small sample sizes and lack of replication, are consistent with the above findings regarding habitat suitability. A disproportionate number of juveniles are inhabiting the projects considering their abundance relative to adults in the river. They were mostly found in side channels, although this could either be attributed to the fact that side channels outnumber feathered edges or to the fact that side channels provide more suitable habitat. In any case, given that juvenile habitat was found to be much more limited in the river than adult habitat, the fish habitat restoration projects may be more alluring to juveniles. Because western pond turtles demonstrate site philopatry, they may not move quickly into new areas immediately after construction, even if conditions are suitable. Continued monitoring of the projects for colonization is needed.

Analysis of suitable habitat may be the best avenue for determining potential use of these new projects; it transcends temporal variability in actual use of the projects by the target species, which could shape the conclusions from a species survey alone. As side channels and feathered edges change over time, whether maintained or not, periodic evaluation of habitat will be informative. Assessments of habitat suitability can be refined as the known universe of utilized habitat for western pond turtles continues to expand. Coupled with increasingly effective techniques for characterizing habitat, the large sample size of measurements will enhance the validity of habitat models. Data from restored areas can be used to test and improve the models.

The findings of this study indicate ways in which the side channel and feathered edge projects could be modified to enhance habitat for western pond turtles, particularly for juveniles. Although juveniles can be found in very shallow water, there are pockets of deeper water in the vicinity (judging from values of the "maximum depth" variable for juvenile use sites). Thus, some areas of deeper water are recommended in addition to areas of lower flow. This could be achieved by adding more structural complexity. The existing "u-shaped" side channels could be improved by a combination of bank contouring to create lentic and localized dredging to create small, deep pools. Also, woody debris or other large material could be added to create cover, provide basking sites, and form pools. Generating complexity in feathered edges could prove more difficult, as by design these projects are uniformly sloped along their length. To increase suitability of either project type for adult western pond turtles, some vegetative canopy must be restored and/or retained.

ACKNOWLEDGMENTS

I thank the USDI Fish and Wildlife Service and Bureau of Reclamation for facilitating and providing the funding for this project. Ian Gilroy provided background information on existing restoration projects as well as providing Figures 7-1 and 7-2.

CHAPTER 8

MOVEMENTS AND MICROHABITAT USE OF HATCHLING AND JUVENILE WESTERN POND TURTLES IN THE TRINITY RIVER BASIN

ABSTRACT: Little research has been conducted on juvenile western pond turtles (*Clemmys marmorata*), in part because they are scarce and in part because their small body size and crypticity limit the use of certain techniques. Yet, the potentially high susceptibility of this age class to human impacts has made them the focus of discussions about the status of the species. This study gathered information on movements and habitat associations of juvenile *C. marmorata* inhabiting the mainstem and south fork of the Trinity River. Juveniles were captured in warm, slow-water portions of the main river channels as well as in ponds and vernal pools. The proportion of juveniles/adults was higher in the ponded waters than the river. The advent of smaller radiotransmitters made it possible to radiotrack juveniles over a period of several months. Several individuals made overland journeys, which appeared to be associated with overwintering, terrestrial basking, and travel to a vernal pool. The average, linear aquatic home range size (84 m) was substantially larger than Bury's (1972) estimate of 16 meters for juveniles in Hayfork Creek. I conclude that juvenile western pond turtles are associated with warm, lentic waters. In addition to pooled portions of the river, this may include vernal pools, ponds, or other adjacent wetlands. The home ranges of juveniles are smaller than those of adults, but larger than previously recognized, and they include terrestrial components.

INTRODUCTION

The western pond turtle (*Clemmys marmorata*) has declined throughout its range during the last century (Brattstrom 1988, Holland 1991, Federal Register 1992). Early impacts included large-scale commercial exploitation for the restaurant trade; seining ships removed hundreds of thousands of turtles from the shallow lakes of the Central Valley (Holland 1991, Smith 1895). Although commercial exploitation is now minimal, habitat alteration and destruction are continuing to push this species towards extinction. The young age classes appear to be particularly impacted, as evidenced by their near absence in the majority of populations. Several factors may be responsible, including elimination of nesting habitat, introduction of nonnative predators (e.g. bullfrogs) and habitat changes that foster increases in native predators (e.g. raccoons), and reduction in hatchling microhabitats (Holland 1991, Jennings and Hayes 1994).

A 1992 petition for a federal listing for this species (Federal Register 1992) was found to be "not warranted" by the U.S. Fish and Wildlife Service. One argument for declining listing was that young (i.e. small) turtles are difficult to locate, such that existing evidence for recruitment failures was insubstantial. Specifically, it was proposed that in some cases where hatchlings are reported to be absent, they might actually be present but cryptic. Studies of other aquatic turtle species have reported that failure to find juveniles may be attributed not to a real scarcity, but to a failure to search appropriate microhabitats (Kofron and Schreiber 1985, Pappas and Breck 1992); hatchlings may exhibit different habitat selection than adults (Butler and Graham 1995). This underscores the importance of gaining more information on habitat use by hatchling and juvenile western pond turtles. Such information could contribute to refining survey methodology to ensure the detection of hatchlings if they are present. It, alternatively, might confirm that existing survey techniques are adequate for detecting the younger age classes.

Since 1991, western pond turtle populations have been examined in the Trinity River system (Lind et al. 1992). Mark-recapture studies on both the mainstem and south fork have indicated that young turtles are associated with low-flow microhabitats, such as edgepools and backwater pools (Chapter 3, unpublished observations). Other aquatic turtles hatchlings are associated with low-flow portions of rivers and streams (*Trachemys scripta*: Moll and Legler 1971, Hart 1983). Holland (1991) reported that *Clemmys marmorata* hatchlings use shallow water with abundant emergent vegetation. Juveniles of other aquatic species are also associated with shallow waters (*Graptemys geographica:* Pluto and Bellis 1986, *Clemmys insculpta:* Brewster and Brewster 1991, *Chelydra serpentina* and *Chrysemys picta:* Congdon et al. 1992, *Emydoidea blandingii:* Pappas and Brecke 1992). Habitat requirements of young pond turtles may, thus, overlap with those of fish fry such that habitat improvements for one will benefit the other. Through this study, I hoped to further clarify the significance of these lentic microhabitats for young western pond turtles.

Shallow, edgewater habitats are particularly vulnerable to alterations in flow and have, thus, been impacted by the construction of the Lewiston/Trinity Dams on the mainstem Trinity. River margins have become straighter, deeper, and faster-flowing as the river becomes more channelized (Hampton 1995, Trinity River Restoration Program

1994). A tremendous expansion and encroachment of riparian vegetation has occurred in response to the diversion of historic flow volumes (Evans 1980). Seasonally flooded marshy areas that were filled by meanders have been largely eliminated (Wilson et al. 1991). All of these changes could have an impact on young western pond turtles, depending on the degree to which they require these microhabitats.

With these information needs in mind, I initiated a study of hatchling and juvenile habitat use. The study consisted of two parts: 1) capturing juveniles and recording the habitat characteristics of the capture locales 2) radiotracking juveniles and recording their movements and habitat associations. Monitoring of radioed adults over the last two years revealed that terrestrial journeys are frequent and can occur over long distances (up to 500 m; Chapter 9, Reese and Welsh 1996). There is currently no information on overland travel by hatchlings and juveniles except those few instances noted by Holland (1994). The intent of this study was to describe their relationship with both the aquatic and terrestrial landscapes.

METHODS

Field Methods

Juvenile Searches

The search for juveniles of an appropriate size for telemetry began in May of 1994. For logistical reasons, the search areas were defined as a reach of the mainstem Trinity (Reach 11, Figure 2-1), a reach of the south fork Trinity (Reach 1, Figure 2-2), and various seasonal and permanent ponds in the vicinity of these reaches. Each river reach was approximately 3 kilometers in length and had already been judged to be accessible on foot for the purpose of monitoring radioed adult turtles (Chapter 9). Searching consisted of snorkeling both banks of the main channels up to 4.0 meters from the shoreline (outside of which the high flow prohibits searching and is likely to prohibit utilization by juvenile turtles). Search effort was concentrated in areas where juveniles had been spotted or captured previously during mark-recapture dives (Chapter 3).

The adjacent ponds and vernal pools were included as additional lentic areas that might harbor juveniles. These ponds were searched in their entirety (as opposed to the shoreline-based search described above). Snorkelers continued to look for turtles until capture rates tapered off to less than one individual per half-hour. In addition, for ponds with high turbidity and consequently low snorkeling success, baited traps were employed. All individuals in these ponds, regardless of size, were measured. I, thus, incidentally obtained information on size structure of turtle populations in a few isolated systems for which capture rates were high. Specifically, the following were sampled: a mainstem pond consisting of a mining crevice with year-round water, a south fork pond containing year-round water that is seasonally connected to the river, and a south fork vernal pool consisting of a seasonally dry pond sitting on a high terrace above the river.

Radiotelemetry

I consulted with AVM Instrument Company (Livermore, CA) about what type of radios to use, considering the tradeoff of weight and lifespan and hoping to track newly hatched turtles, which weigh 1-5 grams. The smallest radio available (weight 0.71 grams) would constitute close to 15% of the body weight of a large hatchling. Tests conducted with radios temporarily affixed to a large hatchling demonstrated that even a 10% radio/hatchling ratio hampered locomotion (unpublished observations). Additionally, these tiny radios have a lifespan of only 7 days. Considering what is known about activity levels of turtles, a week's worth of monitoring is not likely to yield much information.

Consequently, two types of radiotransmitters that weighed more but had longer lifespans were assembled (AVM Instrument Company, Livermore, CA). The first design, with a lifespan of approximately 80 days, was light enough (2.8 grams) and small enough (9 x 15 x 20 mm) to be carried by first-year juveniles. The second design, with a lifespan of approximately 140 days, was light enough (2.84 grams) and small enough (9 x 10 x 23 mm) to be carried by second year juveniles. Thus, short-term tracking of hatchlings was opted against in favor of longer-term monitoring of the next two largest age classes. It was knows from previous years of mark-recapture study (Chapter 3) that juvenile turtles are difficult to find in this study area. Restricting the search to first-year individuals posed the risk of not obtaining the desired sample of 10 individuals. Thus, having these two types of radio would increase the chances of finding ten suitable juveniles to monitor.

Seven juveniles that were suitable for radiotelemetry (i.e. 1-2 year olds) were captured at the south fork site and four suitable juveniles at the mainstem. In order to preserve independence, no two juveniles from the same locale were radioed. Unique locales were defined as bounded bodies of water (ponds, vernal pools) or portions of the river that were at least 50 meters apart.

Each radioed turtle was located once per week. Locations were made as accurately as possible given that the juveniles were usually underwater. In most cases trackers succeeded in spotting the individuals; for cases in which they were not visible, locations were obtained by triangulation. The base range of both types of radio was 300-400 meters (range of unattached radio on flat ground) with a pulse rate of 75/minute, a current drain of 30 microamps, and a 12 cm antennae. Actual range was substantially less after the muting effects of radio installation and topography. When unable to obtain a signal, the person operating the receiver travelled to the location where the juvenile was last found and then searched in increasingly larger concentric circles up to a minimum of 100 meters away. For juveniles that continued to be missing, the entire study reach was searched.

Habitat Measurements

For terrestrial locations of juveniles, the following information was recorded: vegetation type and canopy cover immediately over the turtle locale, vegetation type in the vicinity, microslope, macroslope, aspect, and cover if the turtle was buried. For aquatic locations of juveniles, the following information was recorded: flow type (Appendix 2-A), canopy cover immediately over the turtle locale, water depth, water temperature, and water flow. If the juvenile occurred in a body of water other than the river, the temperature of that site was measured as well as the temperature of the closest river site. Appendix 8-A details the terrestrial and aquatic measurement procedures.

APPENDIX 8-A

METHODS OF HABITAT MEASUREMENT

Variable	Methodology
Microvegetation	Description of vegetation falling in vertical cyclinder with 1 meter radius around turtle locale (aquatic or terrestrial)
Macrovegetation	Vegetation type within 40 meters radius around turtle locale 1) Gravel/cobble bar (unvegetated) 2) Willow dominant (at least 2/3 willow) 3) Willow/alder mix (at least 1/3 of each) 4) Mature alder/cottonwood 5) Douglas fir dominant (at least 2/3 fir) 6) Other conifer dominant (at least 2/3 conifers) 7) Hardwood dominant (at least 2/3 hardwoods) 8) Mixed conifer/hardwood (at least 1/3 of each)
Microslope/aspect	Slope and aspect of ground immediately at turtle locale (terrestrial only)
Macroslope/aspect	Slope and aspect of landform between turtle locale and river (terrestrial only)
Cover	Covering material if turtle is partly or fully buried (e.g. leaf duff, needles, soil, woody debris)
Canopy cover	Measured with a canopy densiometer above turtle capture locale. Any object blocking sky, whether vegetation or rock outcrop was counted against the proportion of "open" in the densiometer. Counts in four perpendicular directions were averaged.
Water depth	Depth (cms) of water at turtle capture locale (aquatic only)
Water flow	Flow (m/sec) of water at turtle capture locale. Measured with Marsh-McBurney flowmeter bulb held halfway between the bottom and the surface (aquatic only)
Water temp	Temperature (*C) of water at turtle capture locale. Measured 10 cm below the water surface (aquatic only)

Habitat measurements were made for all juveniles captured during initial searches, even those that were not subsequently radioed. These included older juveniles or juveniles captured in a locale where a radioed juvenile already existed. Habitat measurements were designed to be comparable to riverine habitat data gathered during the macrohabitat study (Chapter 5).

Data Analysis

Juvenile Searches

As described above, various ponds that were isolated from the main river channels were searched. One pond on the mainstem Trinity and two on the south fork yielded enough turtles to permit comparison of juvenile/adult ratios. For each river site, I compared the pond(s) to each other as well as to the river channel with respect to age structure of turtle populations. Information on size structures within the river channels was obtained from the 1993 mark-recapture dives (Chapter 3). For this analysis, the two seasonal dives were combined and repeat turtle observations discarded to generate a juvenile/adult ratio for each site. The south fork comparisons were made using Pearson chi-square contingency analysis (SAS Institute 1990). If significant differences were found, a Tukey-type proportion test (Zar 1984) was used to determine specifically which proportions were different. The mainstem comparison was made with Fisher's Exact Test (SAS Institute 1990) because the data did not meet the requirement for the Pearson chi-square that fewer than 20% of the cells have expected values of less than five.

Habitat Measurements

The aquatic habitat data for all juveniles captured during the course of this study were compiled into a single habitat database. Multiple records of the same individual were considered to be independent if they were separated by at least a week. For each river site, the juvenile habitat data were then compared with data on habitat availability in the river, the latter consisting of the data for random locales from the 1993 macrohabitat study (Chapter 5). Discriminant analysis ("DA", SAS Institute 1990) was used to ascertain whether juvenile use sites could be distinguished from the random sites on the basis of habitat characteristics. This analysis was restricted to consideration of the continuous variables (flow, depth, temperature, canopy).

Large samples of available habitat observations (97 for each river site), and smaller samples of turtle observations (47 and 19 respectively for the south fork and mainstem) were obtained. The large sample permitted selection of multiple random subsets of available habitat for comparison to the used habitat, from which it could be ascertained which variables consistently appeared in discriminant models. Ten random subsamples with replacement were generated and used in ten two-group DAs. Variables were selected with a stepwise procedure. For all discriminant analyses, the significance level was set at alpha = 0.10 for entry of variables into the model. This moderate significance level allows for more variables to enter a model and, thus, provides better potential discriminatory power given the small sample size (Costanza and Afifi 1979). A moderate alpha level may also be more appropriate for the detection of ecological trends (Toft 1991).

For each run, I tested for heterogeneity among variance-covariance matrices using Bartlett's modification of the likelihood ratio test (SAS 1990) setting alpha = 0.05. In cases where the matrices were heterogenous, quadratic as opposed to linear discriminant functions were generated. The discriminatory potential of the ten subsample models was compared by considering the values of the F statistic and Wilk’s lambda. A jackknife procedure was used to evaluate the classification success of each subsample model (SAS 1990). Cohen's Kappa (Titus et al. 1984) was computed for each test to compare the classification success to chance. Acceptable performance was set at alpha = 0.05.

Radiotelemetry

My analysis of the radiotelemetry data was descriptive due to the limitations of small sample sizes, nonconcurrent monitoring periods, and repeat observations of the same individuals. For each individual, a trajectory was described relative to established river stations and the following parameters were calculated:

1. Maximum extent of aquatic travel, defined as the shortest distance between the two furthest aquatic locations. This can also be viewed as a "linear home range" (Moll and Legler 1971; Bury 1972) that expresses the maximum points of each turtle range on a linear scale. In a river or stream environment, the width of the waterway is likely to constitute a minor distance in the movements of turtles compared to the upstream and downstream distances.

2. Maximum aquatic travel per week, defined as the longest distance travelled between two consecutive telemetry locations.

3. Mean aquatic travel per week, defined as the average distance travelled between consecutive weekly locations.

4. Terrestrial travel, described as the maximum distance from the watercourse achieved during a terrestrial journey.

RESULTS

Juvenile Search

At the south fork site, 69 juveniles were captured or sighted during the course of the study, of which 46 were unique (i.e. first captures). Of these, 92% were captured in the river, while the other 8% were captured in ponds and vernal pools. Of those captured in the river, 86% were caught in slow-water habitats (including backwater pools, side channels, and edgewater pools; see Appendix 2-A). Examination of the 1993 macrohabitat data reveals that these slow-water habitats constitute approximately 44% of available riverine sites. At the mainstem site, 28 juveniles were captured during the course of the study, of which 18 were unique. Of these, 72% were captured in the river and the other 28% in ponds and vernal pools. Of those captured in the river, 77% were caught in the same slow-water habitats listed above. The macrohabitat data for this site reveals that these slow-water habitats constitute approximately 27% of available riverine sites.

For the south fork site, juvenile/adult ratio was significantly associated with habitat type (vernal pool vs pond vs river, Figure 8-1). The proportion of juveniles was highest in the pond and lowest in the river. Comparisons of proportions revealed that the

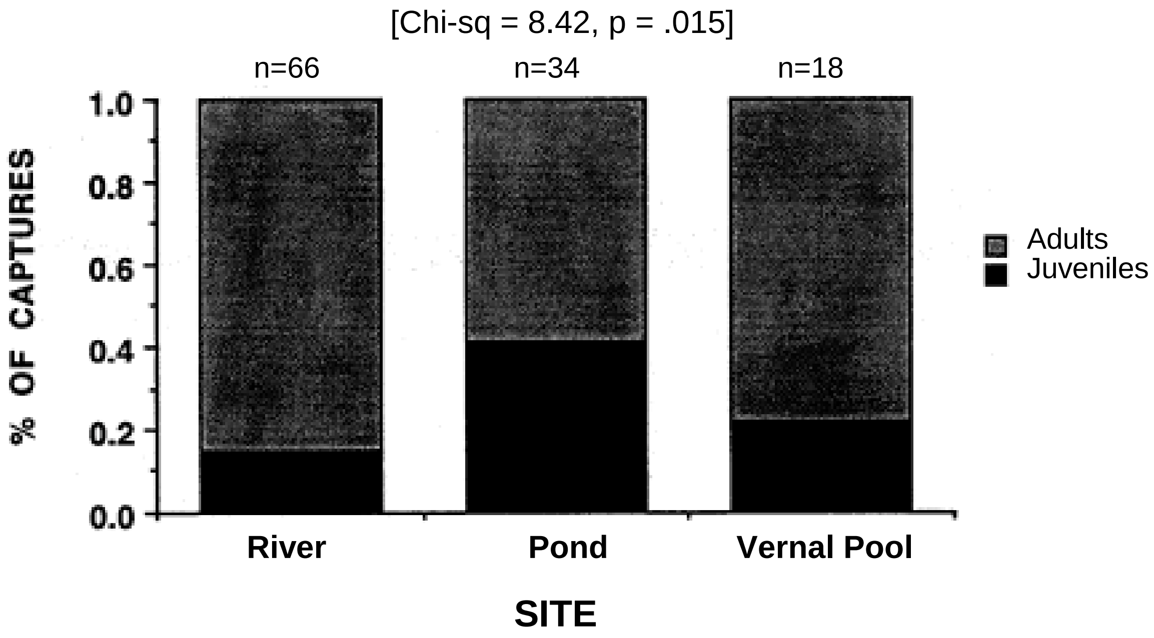


Figure 8-1. Proportion of juvenile and adult turtles inhabiting sites at the south fork Trinity River; n = total captures.

difference in proportion of juveniles between the pond and river was significant ($q = 3.94$, $p < 0.02$) while the other differences were not. For the mainstem site, juvenile/adult ratio was also significantly higher in the pond than the river (Fisher's Exact Test $p = 0.045$; Figure 8-2).

Habitat Measurements

Forty-seven habitat records for juveniles on the south fork site and nineteen habitat records for juveniles on the mainstem site were obtained. (Note that for some juveniles captured incidentally, no habitat data was obtained). Table 8-1 shows values of the habitat variables for juvenile and random samples at each study site.

For the south fork, the discriminant analysis of juvenile habitat and available riverine habitat produced a set of subsample models in which water temperature was the most stable variable Table 8-2). Whereas canopy cover appeared in seven of the ten models and flow occurred in three of the models, water temperature occurred in all ten. Models with temperature and canopy had the best classification success. The standardized structure coefficient for water temperature ranged from .9141 to 1.00, while the coefficient for canopy ranged from .2632 to .4823.

Because the juvenile data were being compared to available riverine habitat measured during the previous study season and because water temperature can vary from one year to the next, the discriminant analysis was followed with a less problematic univariate assessment. Specifically, I compared the water temperatures of 1994 juvenile capture sites to water temperatures measured simultaneously at the nearest riverine sites.

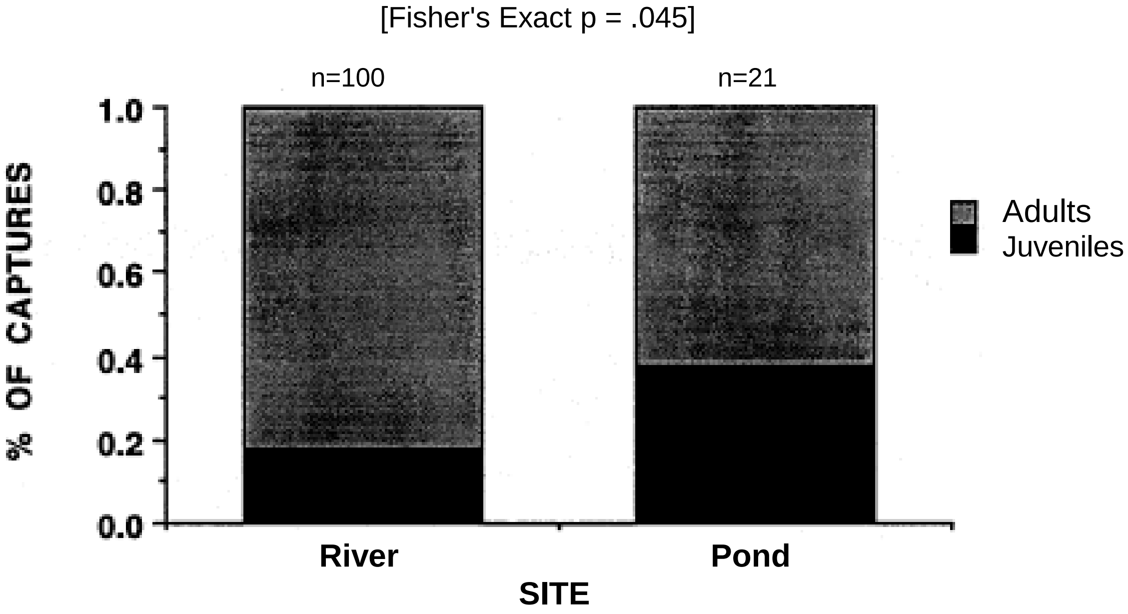


Figure 8-2. Proportion of juvenile and adult turtles inhabiting sites at the mainstem Trinity River; n = total captures.

Table 8-1. Values of habitat variables (means and standard deviations) for juvenile-occupied sites and random riverine sites sampled at the south fork and mainstem of the Trinity River. Note that values for random sites reflect the entire sample, which was subsampled for discriminant analysis (Tables 8-2 and 8-3).

Habitat Variable	SOUTH FORK Juvenile Sites (n = 47)		SOUTH FORK Random Sites (n=84)		MAINSTEM Juvenile Sites (n=19)		MAINSTEM Random Sites (n=93)	
	mean	s.d.	mean	s.d.	mean	s.d.	mean	s.d.
Canopy (%)	25.73	23.20	17.70	15.86	35.59	32.62	20.72	16.08
Depth (cm)	62.25	92.62	52.93	47.93	45.58	48.03	51.15	45.35
Flow (m/sec)	3.16	7.06	8.23	12.64	2.53	6.93	10.92	16.80
Temperature (°C)	22.23	2.76	18.98	1.78	18.62	6.00	18.90	1.81

Table 8-2. Results of ten two-group discriminant analyses of habitat from 47 occupied sites and 84 random riverine sites (subsampled) for western pond turtles on the south fork of the Trinity River.

Model #	Variables entered	Wilk's Lambda	F	p value	Classification Success	Cohen's Kappa	p value
1.	temp, canopy	.5388	38.95	.0001	84%	.6809	< .0001
2.	temp, canopy	.5961	30.83	.0001	86%	.7234	< .0001
3.	temp, flow	.6589	23.56	.0001	74%	.4255	< .0001
4.	temp, canopy	.6352	26.13	.0002	78%	.5532	.0063
5.	temp, canopy	.6162	28.34	.0001	84%	.6809	< .0001
6.	temperature	.6410	51.52	.0001	82%	.6383	< .0001
7.	temp, flow canopy	.5565	23.91	.0001	85%	.7234	< .0001
8.	temperature	.6054	59.97	.0001	83%	.6596	< .0001
9.	temp, flow canopy	.5826	21.50	.0001	83%	.6596	.0011
10.	temp, canopy	.6052	29.68	.0001	82%	.6383	< .0001

(see Field Protocol for methods). A paired-comparisons t-test (SAS, 1991) revealed water temperatures to be significantly higher at the juvenile sites than the river habitat sites (T = -2.82, p = .015).

For the mainstem site, the discriminant analysis of juvenile habitat and riverine habitat produced models that included canopy, flow, and/or depth. However, none of these variables were particularly stable. Of the ten subsample models, seven included canopy, six included flow, and four included depth. Table 8-3 shows the range of F values, Wilks Lambdas, and classification results for the subsample models. Overall, classification results were poor.

Radiotelemetry

The results of the radiotelemetry analysis are shown in Table 8-4. There was limited success in following individuals for the entire intended monitoring time; many of them simply could not be relocated during the period when their radios should still have been operative. This difficulty was at least in part due to radio failures. In two cases, juveniles were spotted carrying radios that emitted no signals, and in another case a juvenile was incidentally captured with a silent radio. The short range of the radios (transmission distance) is likely also to have contributed to the low relocation success.

Thus, individuals were monitored for varying lengths of time, making comparison of their movements difficult. I report the maximum extent (maximum distance between aquatic sightings for each juvenile), which was averaged 84 meters. The maximum weekly travel (maximum distance between two consecutive sightings) was found to

Table 8-3. Results of ten two-group discriminant analyses of habitat from 19 occupied sites and 93 random riverine sites (subsampled) for western pond turtles o the mainstem of the Trinity River.

Model #	Variables entered	Wilk's Lambda	F	p value	Classifi -cation Success	Cohen's Kappa	p value
1.	canopy	.8665	5.55	.0241	66%	.2475	.0354
2.	flow	.8726	5.26	.0278	79%	.1358	.1586
3.	canopy, depth	.8307	3.57	.0390	65%	.3043	.0113
4.	canopy, depth flow	.7194	4.42	.0099	68%	.1683	.1096
5.	none						
6.	flow	.8461	6.55	.0148	79%	.1544	.1341
7.	canopy, flow	.7197	6.82	.0032	74%	.1949	.0704
8.	canopy, depth flow	.6732	5.50	.0034	84%	.3715	.0031
9.	canopy, depth	.8023	4.31	.0212	74%	.2271	.1335
10.	canopy, flow	.8109	4.08	.0255	71 %	.0738	.2982

Table 8-4. Table of radiotelemetered juveniles. MAXIMUM EXTENT refers to the maximum distance between all aquatic sightings. MAXIMUM WEEKLY TRAVEL refers to maximum distance between two consecutive sightings. MEAN WEEKLY TRAVEL refers to mean distance between two consecutive sightings.

Juvenile Capture Locale	Start Date (1994)	Weeks of Moni--toring	Maximum Extent (meters)	Maximum Weekly Travel (m)	Mean Weekly Travel (m)	Land Distance
Mainstem	6-16	10	within crevice pond		--	0
Mainstem	6-29	8.1	175	62.5	26.9	0
Mainstem	4-28	12.3	129	30	15.2	22
Mainstem	4-28	4.9	20	20	8	0
Southfork	9-2	10.1	15	15	8	60
Southfork	5-6	5.6	within vernal pool		--	suspected
Southfork	7-7	6.6	124	54	32	0
Southfork	8-22	4.4	80	50	32.7	0
Southfork	6-17	7.7	21	21	17.4	0
Southfork	8-3	6.3	54	27	22.2	1.9
Southfork	6-17	4.7	141	141	82.5	0
		MEAN	84.3	46.7	19.9	

average 47 meters, and the mean weekly travel (mean distance between two consecutive sightings) averaged 20 meters.

Three of the juveniles made journeys overland during their monitoring periods. The first reported (Table 8-4) was a journey from a vernal pool where the turtle was originally captured to the main river channel. The second entailed travel to a high spot just beyond the riparian zone, where the juvenile still remained buried under duff into the winter when its radio ran out of power. The third was a brief visit to a riparian berm adjacent to the river. The "suspected" journey reported is associated with an individual who was captured in a vernal pool inhabited seasonally by two radioed adults. These adults made round trip journeys between the vernal pool and the river. The disappearance of the radioed juvenile was coincident with the departure of the radioed adults from the vernal pool, suggesting that the juvenile may have also travelled to the river, after which we were unable to locate it.

DISCUSSION

The higher ratio of juveniles/adults in ponds than in the main river channels may be attributable to better hatchling or juvenile survival at the two ponds, selection of these sites by migratory juveniles, or increased capture success in ponded habitats. The latter hypothesis is unlikely, given that the ponds had more dense vegetation and other types of cover than the river channel (Reese, unpublished observations). It is conceivable that ponds enhance the survival of young turtles by providing more navigable waters and a more concentrated food supply than the river channel. It is also possible that juvenile western pond turtles are selecting these lacustrine habitats; preliminary evidence from other radiotelemetry studies (Chapter 9) suggests that adult western pond turtles make round-trip journeys of nearly a half-kilometer between riverine sites and adjacent ponds. Replicated sampling of riverine ponds over multiple seasons and years would help to clarify their significance to different life stages of the western pond turtle.

The discriminant analyses from the south fork site indicate that the areas utilized by juveniles are distinguished by warmer water than what would be available if the river was used randomly without regard to microhabitat. The analysis of concurrent temperatures confirms that the nonriverine habitats occupied by juveniles in 1994 provided significantly warmer water than the closest riverine sites. These two results are likely related to the tendency of low-flow habitats to warm via solar radiation, whether they be lentic portions of the river or adjacent ponds and vernal pools. For both the south fork and the mainstem, low-flow riverine habitats were occupied by juveniles with greater frequency than would be predicted by their availability if use is random. However, the fact that the continuous flow variable did not emerge as significant in the discriminant analysis is paradoxical. It appears (Table 8-2) that although flow was lower at the juvenile sites, the sample size was not large enough to compensate for the high variability in flow.

The discriminant analysis from the mainstem was characterized by ineffective separation of juvenile and random sites and inconsistency across the subset models in terms of which variables were included. Examination of the values of the habitat variables (Table 8-2) indicates that the poor discriminatory ability can be explained by less difference between juvenile and random sites than was found at the south fork. This may be attributable to the lower variability in habitat at the mainstem as a result of the dam (Chapter 5) and consequently smaller potential for selection by juveniles. Further research is warranted.

The estimate of juvenile home range sizes is likely to be conservative, considering the limited duration of monitoring. It is nevertheless considerably larger than that of Bury (1972), who calculated maximum linear extent of juvenile movements in Hayfork Creek (Trinity County, CA) from recapture data. Over the duration of the summer months (May-September), he found that juveniles in Hayfork Creek had an average maximum movement of only 16 meters, compared to my estimate of 84 meters. This disparity in estimates could result from a difference in the distribution of resources at the two study sites. Hayfork Creek is narrower such that food resources and basking sites; which tend to cluster along the shorelines, are more concentrated. However, while the home range size of fishes may be inversely related to food availability (largemouth bass: Savitz at al. 1983), home range size of the turtle *Chelydra serpentina* is independent of local productivity (Brown et al. 1994). The smaller home range sizes of juveniles in Hayfork Creek could also be explained by Bury's (1972) use of mark-recapture methods to define home rang; mark-recapture techniques may yield much smaller home ranges than radiotelemetry techniques by virtue of gaining fewer locations per individual (Schubauer et al.1990).

Bury's (1972) research indicated that juveniles move substantially smaller distances than mature males or females. The results presented here concur; the mean weekly aquatic travel of juveniles (19.9 meters, Table 8-4) is much smaller than the mean of 117 meters travelled per week by radiotelemetered adult western pond turtles on the mainstem Trinity site (Reese, unpublished results). Further research should focus on clarifying the role of habitat and individual variability in the aquatic movements of western pond turtle juveniles.

Overland journeys have been documented for adults of this species by numerous other studies (Holland 1994, Rathbun et al. 1993, Reese and Welsh 1996). Information on terrestrial movements of juveniles is scarce. The movements reported here can be categorized respectively as movement within a home range that includes multiple bodies of water, movement to an overwintering locale, and movement to a terrestrial basking site. All of these movements are consistent with the types of movements that have been made by adult western pond turtles (Chapter 9, Table 9-1).

Terrestrial movements undoubtedly pose a high predation risk for individuals of this species, as they are preyed upon by bears, coyotes, raccoons, feral dogs, and humans (Holland 1991). Whether terrestrial movements are adaptive is unclear, but a number of potential values can be postulated: Overwintering at terrestrial sites, also observed in adult *Clemmys marmorata* (Chapter 9), may provide a refuge from hazardous high flows and promote dormancy during a time of year when food supplies are scarce. Visits to terrestrial spots with duff cover may allow turtles to be cryptic while basking, such that heating and drying of the integument can occur over a longer period than would be possible on an exposed basking site (see Chapter 4).

There are several potential explanations for visits to vernal pools by juvenile turtles. By virtue of their annual drying, vernal pools are less likely to harbor bullfrogs and rarely harbor bass. Small western pond turtles may, therefore, gain a refuge from aquatic predators. Indeed, a vernal pool in Sonoma County was found to contain an extremely juvenile-biased population relative to populations in adjacent artificial ponds with bullfrogs and bass (Reese, unpublished results from Santa Rosa site, Chapter 9). However, the relatively recent invasion of bullfrogs in California and their low density in the Trinity River study site argues against a predator-avoidance explanation for visits to vernal pools in this case. Alternatively, vernal pools provide a warm microclimate with a rich ephemeral supply of invertebrate prey such that feeding and growth are enhanced. Hatchlings of *Emydoidea blandingii* travel to vernal pools before proceeding to permanent wetlands, presumably to take advantage of such resources (Butler and Graham 1995).

Overall, the results affirmed the thesis that slow-water habitats play a significant role in the life cycle of juvenile *Clemmys marmorata*. Juveniles inhabit low-flow portions of the river as well as adjacent ponds, and sometimes travel back and forth between the two. Microhabitat selection by juveniles may be guided by thermal preferences, the distribution of food resources, swimming abilities, and/or predator avoidance (Congdon et al. 1992). The role of thermal preference in habitat utilization was not separable from flow in the context of this study. The distribution of food resources might explain the higher proportion of juveniles in ponds, where aquatic invertebrates are concentrated. Swimming abilities may also be relevant, in that western pond turtles are relatively poor swimmers (Holland 1991); aquatic turtles, in general, lower their energy expenditure by avoiding areas of heavy current (Brewster and Brewster 1991). Predator avoidance is not implicated as a factor guiding habitat selection here because the majority of native predators of western pond turtles are terrestrial (Holland 1991), such that juveniles augment their risk by inhabiting low-flow waters and travelling overland.

Because of small sample sizes and the absence of replication, these conclusions should be viewed as preliminary and suggestive of further research. This study has provided pilot information on movements and habitat utilization by juvenile *Clemmys marmorata*, but also highlights the need for extensive research on this life stage. Juveniles of this species appear to have smaller home ranges and potentially different microhabitat requirements than adults. Surveys for juveniles along rivers should include examination of vernal pools, ponds, oxbows, and other adjacent wetland habitats. Attention to slow-flowing microhabitats will contribute to the development of sound management practices for maintenance of suitable juvenile habitat.

ACKNOWLEDGEMENTS

I thank the U.S. Forest Service Fish Habitat Relationships Program for providing funding for this research. Thanks also to the U.S. Bureau of Reclamation and Fish and Wildlife Service for providing funding and facilitating this project. Special thanks to Don Ashton, Josh Metz, Kari Sadowski, Kary Schlick, Polly Taylor, and Cindy Walker for conducting the field work. D. Ashton, J. Metz, K. Schlick, and P. Taylor assisted with radiotransmitter attachment and testing. Max Taylor deserves credit for his hatchling and juvenile spotting abilities.

CHAPTER 9

USE OF THE TERRESTRIAL AND AQUATIC LANDSCAPE BY WESTERN POND TURTLES: A COMPARISON OF THREE LOCALES

ABSTRACT: Radiotelemetry was used to track western pond turtles (*Clemmys marmorata*) at three study sites in California: the mainstem and south fork Trinity Rivers in Trinity County and a set of agricultural ponds in Santa Rosa, Sonoma County. Six males and six females at each site were monitored weekly for movements and habitat use. The timing, duration, distance, and behavior associated with terrestrial excursions were assessed. Aquatic home ranges were described as minimum convex polygons using global positioning satellite data in a geographic information system. Terrestriality was common throughout the year and most prolonged during the winter. It appeared to have a variety of functions whose prevalence varied by site; including nesting, overwintering, estivating, basking, and seasonal shifts in aquatic habitat. While on land, turtles frequently burrowed under layers of leaf and needle duff. Although overwintering locales were not characterized by a particular set of attributes, individuals showed site philopatry from year to year. At the riverine sites, females initiated overwintering journeys earlier than males, but travelled similar distances away from the watercourse (which averaged 167 m for all individuals at the mainstem and 150 m at the south fork). Males had larger aquatic home ranges than females. I conclude that western pond turtles have a complex semi-terrestrial life history that requires a site-specific approach to management.

INTRODUCTION

The western pond turtle, *Clemmys marmorata*, is the only aquatic turtle native to California, with the exception of *Kinosternon sonoriense,* whose range included a small portion of the southeast corner of the state prior to extirpation (Jennings and Hayes 1994). Western pond turtles have an extensive range (western Washington south to northwest Baja California, Stebbins 1985) and appear to fill a variety of aquatic niches. They are found in ponds, rivers, vernal pools, ephemeral creeks, and estuaries. This contrasts with the turtle fauna of the eastern U.S., comprising more than twenty species occupying a variety of specialized niches. Despite the fact that western pond turtles are widespread habitat generalists, they are declining in numbers (Holland 1991). *C. marmorata* was a candidate for a federal listing (Federal Register 1993). It retains legal status as "Endangered" in Washington State, "Sensitive-Critical" in Oregon, and "Species of Special Concern" in California.

Understanding their utilization of the landscape is essential for developing management plans for this species. Western pond turtles move considerable distances within watercourses (up to several miles, Holland 1991). Although the average aquatic home range sizes are only on the order of several hundred meters, individuals make sporadic, long-distance aquatic journeys (Holland 1994). Another member of the genus *Clemmys* (*C. insculpta*) inhabiting creeks also has elongated aquatic home ranges (Strang 1983). All other members of the genus are semi-terrestrial. *C. insculpta* journeys into alder thickets, grasslands, and corn fields to feed (Kaufmann 1992), while *C. gutatta* estivates in terrestrial habitats (Lovich 1988, Ward 1976). *C. muhlenbergii* can be found in riparian vegetation (Chase et al. 1989). Recent genetic evidence (Bickham et al. 1996) indicated that *C. marmorata* may, in fact, be more closely related to *Emydoidea blandingii* than to its current congeners. Since early on (Pritchard 1979), *E. blandingii* has also been described as semi-aquatic, being found on land as frequently as in the water.

Observations of western pond turtles during 1991-1995 have indicated that they have terrestrial proclivities as well. They nest on land, a feature common to nearly all aquatic turtles. Previous research (Holland 1991, 1994, Rathbun et al. 1992, Reese and Welsh 1996, Storer 1930) indicated that nesting sites for this species may be as far as 400 meters from a watercourse. At some locales, they overwinter on land, also at sites as far as 400 meters from a watercourse (Holland 1994, Reese and Welsh 1996). Hatchlings in the northern part of the range often overwinter in the nest prior to travelling to the watercourse (Holland 1994, Reese and Welsh 1996). Finally, western pond turtles conduct other movements overland that do not appear to be associated with nesting or overwintering and are more difficult to explain. Some consist of movements as far as 5 km between adjacent drainages (Holland 1994).

These types of journeys are consistent with what is known about landscape utilization by other species of aquatic turtles (see Gibbons 1970, 1986). Gibbons et al. (1990) distinguished between "intrapopulational" and "extrapopulational" movements of turtles, the former consisting of movements within the aquatic home range (e.g. for feeding, basking) and the latter consisting of departures, whether they be excursions onto land or long-distance aquatic excursions. This study examines both intrapopulational and extrapopulational movements of western pond turtles, with a focus on the latter. My goal is to clarify the spatial and temporal relationship of this species with its landscape. The Trinity River sites provide a comparison of landscape utilization on a dammed and an undammed section of river. The Santa Rosa site provides the additional comparison of a system of discrete ponds to continuous riverine habitats.

Through these comparisons, I hoped to identify general characteristics of western pond turtle movements that apply across all sites. I also hoped to reveal site-specific differences and gain insight into the factors that shape the timing, duration, and distance of journeys. Some *priori* expectations guided my study design:

1. I expected males to have larger aquatic home ranges than females. Bury's (1972) research reported males home ranges to be 2.93 times larger.
2. I hypothesized that turtles would move overland less frequently at the Trinity River sites than the Santa Rosa site, simply because the continuous aquatic system at the former offers the opportunity for extensive travel without leaving the watercourse. The terrestrial environment is likely to be more dangerous than the aquatic one, considering the prevalence of terrestrial predators on this species (bears, coyotes, raccoons, feral dogs, humans; Holland 1991). It follows that, given the choice with all other factors being equal, turtles might journey through watercourses.
3. I expected to find differences among the sites in the relative frequency of different types of overland movements. Movements to escape unsuitable conditions are most likely to occur at the Santa Rosa site, where the habitat is most altered. Overwintering movements are more likely to occur at the Trinity sites, where the winter climate is harsher in terms of

low water and air temperatures, fast water flow, and abundant precipitation.

METHODS

Study Sites

Western pond turtle movements were examined at three study sites:

1) Reach 11 of the mainstem Trinity River in Trinity County, California (Figure 2-1). This study area consists of a stretch of river that is approximately 2.8 kilometers in length. It runs between Douglas City and Junction City in a section of river with relatively low human densities.

2) Reach 1 of the south fork Trinity River in Humboldt County, California (Figure 2-2). This study area consists of a stretch of river that is approximately 3.8 kilometers in length. It runs between Surprise Creek and Todd Ranch on a sparsely populated section of river.

3) A set of agricultural ponds on private lands just northeast of Santa Rosa, California (Figure 9-1). With the exception of a vernal pool, they consist of portions of creeks that have been artificially ponded by small dams. They are surrounded by agricultural lands including vineyards and cattle pastures. The upland habitat in this area can be characterized as coastal oak woodland (Mayer and Laudenslayer 1988).

Logistical considerations, such as obtaining access from owners and finding areas to launch kayacs, guided selection of the specific study areas.

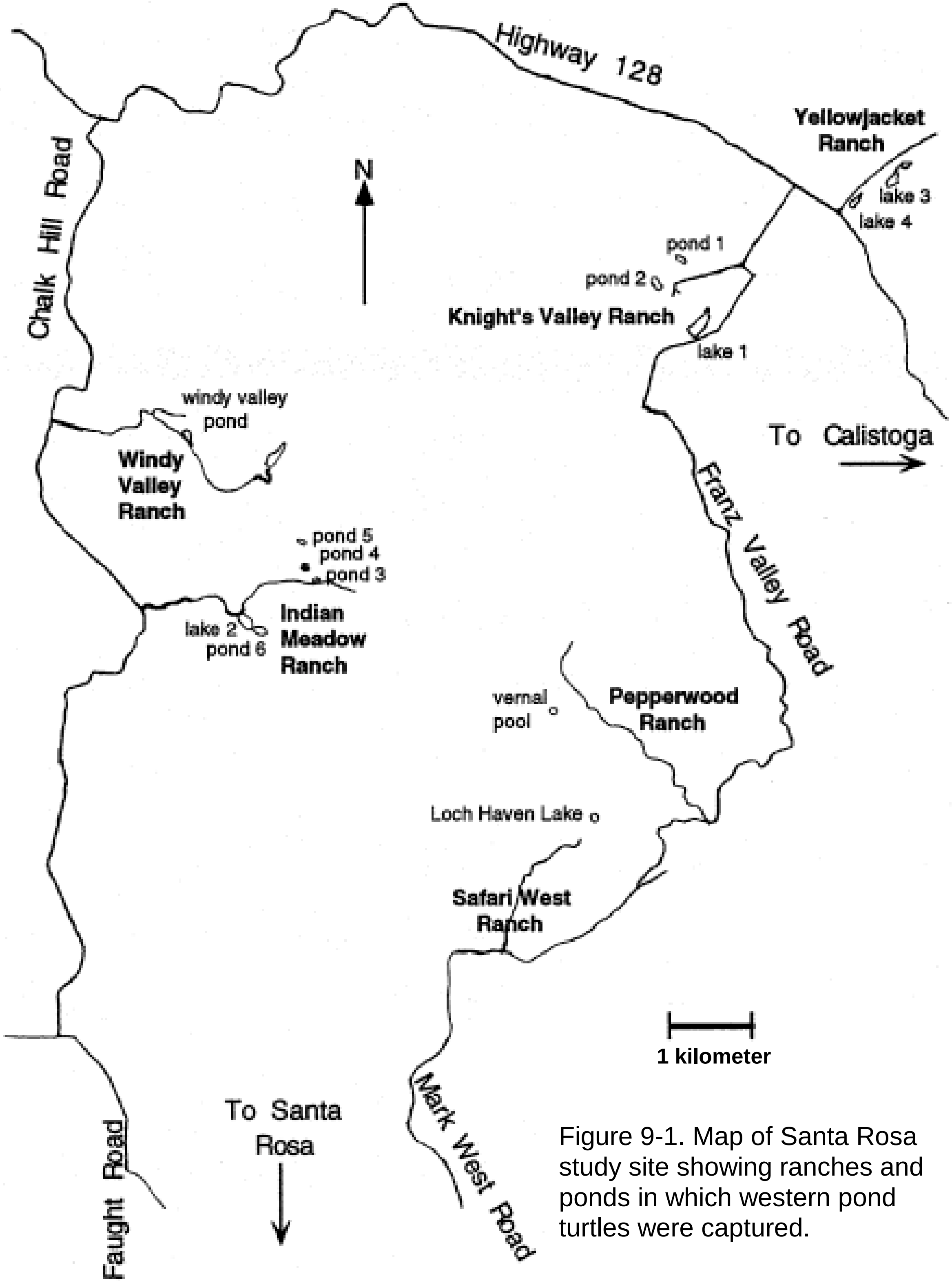


Figure 9-1. Map of Santa Rosa study site showing ranches and ponds in which western pond turtles were captured.

Field Methods

Radiotelemetry was initiated at the mainstem Trinity site and the Santa Rosa site in May of 1992 and continued at the mainstem until December of 1994 and at Santa Rosa until May of 1994. Twelve turtles (six males/six females) were radioed at each site. The south fork radiotelemetry was initiated later (September of 1993) and continued through December of 1994. Six turtles (3 males/3 females) were monitored. At each site, I set up the constraint that males and females be paired in terms of spatial locations to avoid interpreting differences in behavior that are really due to spatial location as sex differences. At the riverine sites, a male and female had to be within 50 meters of each other to constitute a "pair", while at the Santa Rosa site they had to occupy the same pond. I also required that the riverine pairs be separated from each other by at least 300 m to minimize the degree of home range overlap, while keeping the study area to a manageable size for hiking to turtle locations. Each Santa Rosa pair was in a separate pond. If a turtle died during the course of the study, it was replaced by another individual of the same sex from the same aquatic location.

In addition to the sets of radioed turtles described above, seven gravid females at the mainstem Trinity site provided some movement data (see Reese and Welsh 1996). They carried short term radios during 1992 and 1993 for the purpose of monitoring nesting behavior. Appendix 9-A shows the duration of monitoring for all radioed turtles at each of the three sites.

Turtles were fitted with custom-made, single stage radiotransmitters that have a base range of approximately 2 km with a 30 cm antennae (AVM Instrument Company,

APPENDIX 9-A. MONITORING DATES FOR RADIOED TURTLES

Turtle #	Sex	Start Date	End Date	Telemetry Program*
335a	F	5-1-92	7-15-92	Mainstem nesting control
415a	F	5-15-92	8-12-92	Mainstem nesting
377a	F	6-5-92	7-10-92	Mainstem nesting
544	F	6-5-92	7-3-92	Mainstem nesting
395	F	6-9-92	7-10-92	Mainstem nesting
456	F	6-9-92	8-30-92	Mainstem nesting
713	F	6-27-92	7-10-92	Mainstem nesting
248	F	6-28-92	7-10-92	Mainstem nesting
415b	F	7-24-93	8-10-93	Mainstem nesting
528	M	5-15-92	died 11-93	Mainstem perennial
678	M	5-15-92	lost 5-21-94	Mainstem perennial
725	M	5-15-92	12-9-94	Mainstem perennial
335b	M	7-17-92	5-7-94	Mainstem perennial
560	M	8-24-92	12-9-94	Mainstem perennial
377b	M	9-10-92	12-9-94	Mainstem perennial
868	F	5-15-92	4-29-94	Mainstem perennial study
749	F	6-5-92	12-9-94	Mainstem nesting/perennial
949	F	6-5-92	died 12-92	Mainstem nesting/perennial
215	F	6-6-92	8-1-93	Mainstem nesting/perennial
698	F	6-9-92	12-9-94	Mainstem nesting/perennial
773	F	8-24-92	12-9-94	Mainstem nesting/perennial
924	F	6-25-93	lost 4-14-94	Mainstem perennial study (replaced 949)
797	F	7-13-93	12-9-94	Mainstem nesting/perennial (replaced 215)
950	M	9-17-93	12-3-94	South Fork perennial
219	M	9-24-93	12-3-94	South Fork perennial
972	M	9-24-93	12-3-94	South Fork perennial
825	F	9-17-93	12-3-94	South Fork perennial
848	F	9-24-93	12-3-94	South Fork perennial
900	F	9-24-93	12-3-94	South Fork perennial
411	M	5-18-92	3-18-93	Santa Rosa temporary
038	M	5-20-92	lost 2-13-94	Santa Rosa perennial
359	M	5-20-92	lost 3-20-94	Santa Rosa perennial
118	M	5-24-92	died 8-92	Santa Rosa perennial
087	M	5-27-92	lost 9-24-93	Santa Rosa perennial
459	M	5-28-92	5-15-94	Santa Rosa perennial
313	M	8-20-92	5-15-94	Santa Rosa perennial
287	M	8-31-92	lost 3-18-94	Santa Rosa perennial (replaced 118)

APPENDIX 9-A (continued)

176	F	5-18-92	lost 1-23-93	Santa Rosa temporary
777	F	5-18-92	5-15-94	Santa Rosa perennial
262	F	5-19-92	lost 3-13-94	Santa Rosa perennial
509	F	5-20-92	5-15-94	Santa Rosa perennial
889	F	5-21-92	lost 3-18-94	Santa Rosa perennial
676	F	5-27-92	lost 2-13-94	Santa Rosa perennial
209	F	8-20-92	5-15-94	Santa Rosa perennial

* "Perennial" refers to the long-term monitoring described in Methods that entailed weekly locations of males and females during every month for several years.

"Nesting" refers to short-term monitoring of females that was conducted exclusively during the nesting season (summer) and entailed multiple locations per day (described in Reese and Welsh 1996).

Livermore, CA). The 10-gram radios (4.2 cm long, 3.3 cm side, 1.0 cm deep) were affixed to the carapace using PC-7 epoxy with the whip antennae attached to the marginals (Belzer and Reese 1996). The BR 30/32 batteries were predicted to last about twelve months with a pulse rate of 85/minute. The radioed individuals were checked weekly on a random day to avoid the pitfalls of systematic telemetry monitoring. A systematic schedule could, for example, bias the results towards particular cyclical behaviors.

Checking consisted of locating the turtle visually or sonically, recording its position and, if possible, recording its behavior. Turtles were disturbed only to the extent necessary to establish their locations. For example, if a turtle was buried in a terrestrial locale, it was sometimes necessary to feel through leaf and needle duff for its carapace. For aquatic locales, triangulation was used to locate the turtle as precisely as possible and its position was recorded relative to flagged shoreline landmarks. The following data were recorded for all terrestrial locations: shortest distance to the watercourse, slope, aspect, canopy cover, and habitat type.

Short distances were measured by walking the shortest path to the terrestrial point with a walk-chain. Longer distances, for which a walk-chain was impractical, were measured by observers walking the shortest route back to the watercourse, counting their paces, and multiplying by a known meter/pace ratio derived from walking on measuring tapes. Because the high potential for error of these measurements, I decided retrospectively to employ global positioning satellite systems to obtain more precise estimates. Overwintering locations at the south fork and mainstem site was revisited with a GPS (global positioning system) receiver. A Trimble Pathfinder Basic 3-channel receiver was used to record 300 Universal Transverse Mercator (UTM) positions at each turtle location. The elevation mask was set at 15 degrees, the signal-to-noise ratio at 6, the PDOP (position dilution of precision) at 8, and the collection mode at 3D. I made no attempt to select particular constellations of satellites. The steep terrain and dense canopy made it difficult to get the requisite four satellites into view, so it was sometimes necessary to elevate an external antennae on a 20-foot extension pole. I was not able to revisit Santa Rosa locations due to time constraints and lack of access to appropriate equipment.

Data Analysis

Although telemetry data were collected from all three study areas, many of the analyses focus exclusively on the mainstem Trinity site or the two Trinity River sites. The reasons for this are twofold: 1) The mainstem site yielded the largest volume of data. While the south fork site was monitored for less time, the Santa Rosa site was almost entirely monitored by high school volunteers and interns, which yielded more incidences of missing or ambiguous data. 2) The mainstem and south fork sites had GPS data as well as GIS maps associated with them, which1acilitated certain analyses. The mainstem map, made by Wilson (1993) included the river contour at the study site. It was mapped from 1989 ortho-photographs ("spatially corrected") taken during an August flight at a scale of 1:6000. The south fork map was made by Metz (1995) during the course of this study by digitizing the river contour (both shorelines) from ortho-photographs taken during a 1989 flight at a scale of 1:24000. Resources were not available to make a GIS map for the Santa Rosa ponds.

I. Terrestrial Movements

A. Overview

To assess the prevalence of terrestrial journeys, I calculated the proportion of radioed turtles that spent time on land during each month for each study site. Calculations were made separately for males and females, as well as for the combined set. A single location on land at least one meter from the watercourse was considered sufficient. The following assumptions were made: the first day on which an individual was found on land was the first day it occurred there and the last day on which an individual was found on land was assumed to be the last day it occurred there. This generated a conservative estimate of terrestriality in that the turtles were checked once per week and could have made land journeys during the intervals between checks, initiated land journeys prior to a check, or continued land journeys beyond a check. If a turtle was missing for two or more subsequent checks within a month and was not found on land during the remaining time, it was excluded from the analysis for that month. Thus, a missing turtle was not assumed to have remained in the watercourse; missing turtles may, in fact, have had a high probability of being on land somewhere.

For each radioed turtle at each site, I also summarized the total number of terrestrial journeys made, the timing and duration of each journey, the distance travelled, and the apparent destination. These parameters were then used to deduce the "purpose" of the journey (e.g. nesting, overwintering). Since turtles were only located once per week, and were occasionally missing, I used the following procedure to calculate durations: the start of the journey was set as the median day between the last location in the water and the first location on land, while the end of the journey was set as the median day between the last location on land and the first location in the water. Duration was calculated as the number of calendar days that the turtle was in transit from one location to another. With the exception of the overwintering distances for the Trinity River sites (which were calculated from GPS readings using a GIS as described in Methods: Overwintering: Distance), the reported distances are field estimations (see Field Methods).

B. Overwintering: Behavior

In addition to analyzing the variability in timing and duration of overwintering journeys, I analyzed the variability in movements while on land in the context of the behaviors associated with them. Prior to overwintering, western pond turtles may make a number of discrete changes in position on land, during which they bury themselves under duff. Eventually, they occupy a single location for several months or more for the duration of the winter. Upon leaving the overwintering locale in the spring, they may make several stops again before reaching the watercourse (Holland 1994, Reese and Welsh 1996). For each turtle, the number of unique land locations visited before "settling" at an overwintering spot was calculated, as was the number of unique stops on the return journey to the watercourse. After ascertaining that the data were normally distributed, I used an ANOVA to assess the effects of sex and site on the total number of stops, including the overwintering locale. This was followed up with t-tests to identify individual effects.

C. Overwintering: Timing

Several analyses were conducted to interpret the timing of overwintering. Data from the Santa Rosa site were excluded from these analyses because of the small sample size of overwintering journeys (the majority of turtles remained in the ponds for the winter; see RESULTS). For the Trinity River sites, the overwintering journey was divided into three phases: travel from the river to the overwintering locale, overwintering at that locale, and travel back to the river. This generated four timing variables for analysis: time of departure from the river ('DEPART'), time of reaching locale ('SETTLE'), time of leaving locale ('LEAVE'), and time of returning to the river ('RETURN'). In order to convert these date variables into continuous values for analysis, DEPART and SETTLE were expressed as the number of days since August 15th, while LEAVE and RETURN were expressed as the number of days since February 1st. Because of the interdependence of timing and duration, examination of the timing variables also provided information on duration. For each timing variable, some proportion of the observations were missing due to turtles that were not monitored or were lost during that period (Appendix 9-A); thus, sample sizes differ among analyses.

For all four timing variables, I used paired t-tests to search for annual patterns after ascertaining that the variables were normally distributed. Specifically, I compared departure and settling times for turtles from one year to departure times for the same individuals the next year. Data were available to compare mainstem 1992 vs. 1993, mainstem 1993 vs. 1994, and south fork 1992 vs. 1994. For the variables LEAVE and RETURN, I was limited to analysis of patterns at the mainstem site, as it was the only site at which values of the variables were available for two subsequent years (1993 and 1994). The effects of sex (male/female) and site (main/south) were examined for all four overwintering variables. Since there were multiple dependent variables, MANOVA was used. The analysis was restricted to the 1993-4 overwintering period, as it was the only one for which data on all four variables at both sites were available.

The overall duration of overwintering journeys was also examined, although there was some redundancy with the previous analyses since the duration is fixed by the values of DEPART and RETURN. Thus, in part, the analysis of duration served a corroboratory function. In order to ascertain whether there was consistency among individuals in the durations of their overwintering journeys from year to year, Spearman rank correlation coefficients (Rho) were computed. This analysis was restricted to the mainstem Trinity site, where data on duration existed for both the 1992-3 and 1993-4 winters. ANOVA was employed to examine the effects of sex and site on duration, using data from 1993-4.

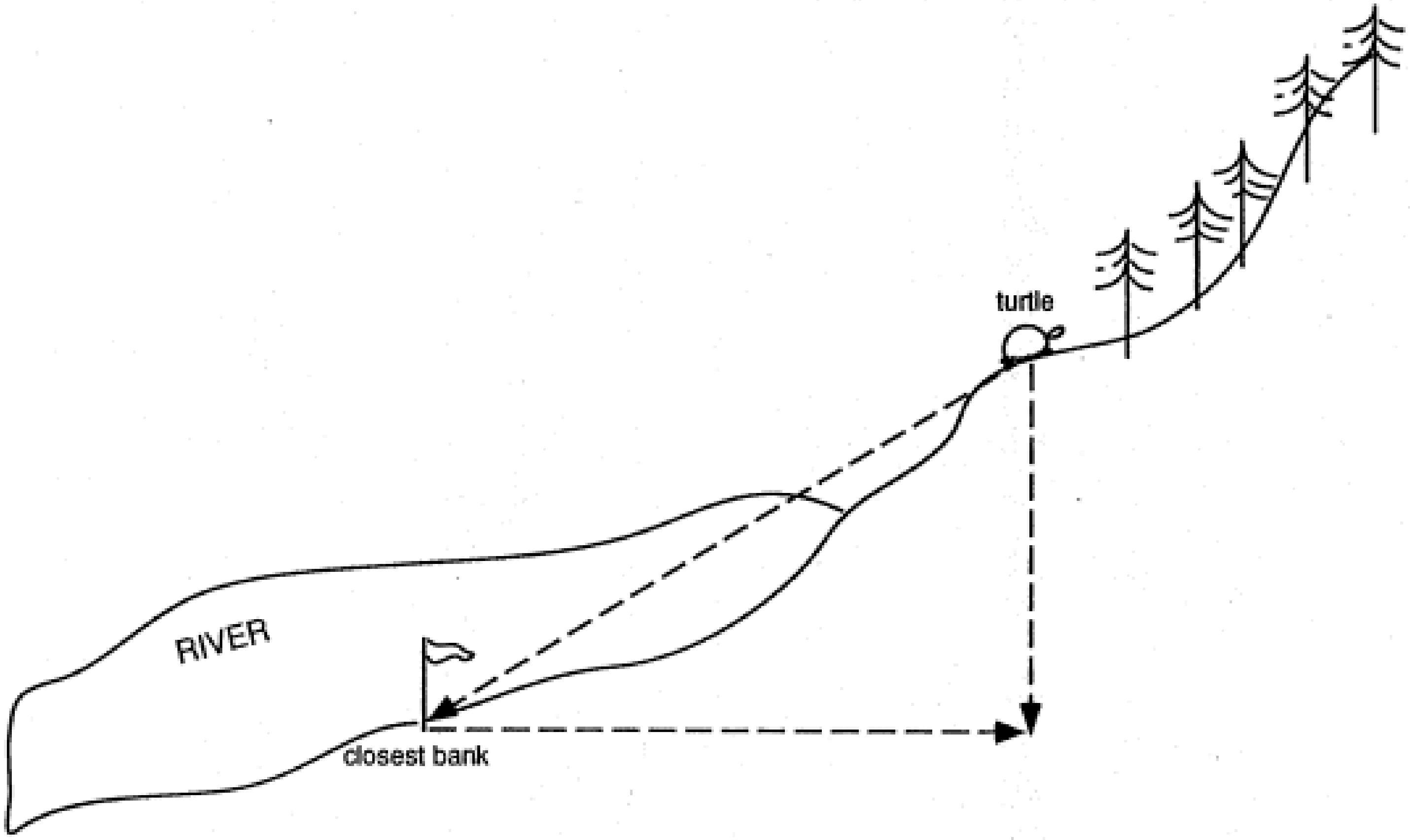
D. Overwintering: Distance

Post-processing of the GPS data on overwintering locales was conducted at the Redwood Sciences Laboratory. The files were downloaded into Pfinder (Trimble Navigation Systems, Version 2.3, 1992) and differentially corrected using base files from the Eureka, California base station. This station is approximately 30 miles from the south fork study site and 60 miles from the mainstem study site. Corrected files were viewed and retained only if the spread of points was less than 20 meters. On the basis of these criteria, approximately one-third of the files were rejected and had to be recollected in the field. Acceptable files were converted to GIS format and a geographic mean taken before export to ARCINFO (Version 7.0, Environmental Systems Research Institute, Inc., Redlands, CA). The mean coordinates for overwintering locales at each site were turned into a coverage. The mainstem means were overlaid, using a UTM projection, on Wilson's (1993) coverage of the river corridor, while the south fork means were overlaid on Metz's (1995) coverage.

The resulting GIS maps were used to compare the locations of overwintering locales from year to year at the mainstem and south fork sites. For each turtle that had carried a radio for more than one winter, the distances between successive overwintering points were measured. Distances to the watercourse were also evaluated. In drawing a GIS trajectory between points, it was assumed that the radioed turtle took the shortest path possible. This also held true for the Santa Rosa site, where distances were obtained in the field by walking the shortest line from a pond to an overwintering point with a walk-chain (see Field Methods).

While field measures incorporate the topography of the landscape, measurements in the GIS from a "bird's eye view" do not. In a landscape with such steep terrain as the Trinity River basin, distances that take elevation into account may be substantially longer than horizontal distances between points identified solely by UTM coordinates. Hence, for all distance calculations at the Trinity sites, a 30-meter DEM (Digital Elevation Model) overlaid in the GIS was used to ascertain the elevation of each overwintering point and of the closest river bank points. Distances were calculated as shown in Appendix 9-B. Each distance was described as the hypotenuse of a triangle with the higher elevation point

Appendix 9-B. Illustration of technique to measure distances of turtle overwintering points from the river and from other overwintering points in the GIS map using information on elevation. Distance is represented by the hypotenuse of the right triangle.



forming one corner and the lower elevation point forming another corner (the third corner being the perpendicular formed by the junction of a vertical line from the high point and a horizontal line from the low point). This technique takes overall slope of the landscape between the target points into account, although it ignores smaller-scale changes of slope between them. Thus, the distances are still likely to be somewhat foreshortened.

Distances to overwintering points on the mainstem Trinity during the 1992-1993 winter were compared to distances during the 1993-1994 winter using a paired t-test. This was the only study site for which there was enough data to make this comparison. An ANOVA was used to assess the effects of site and sex on overwintering distances at the two Trinity River study sites using data from 1993-1994. I also searched for a correlation between distance travelled and duration of overwintering. Assuming that turtles travel at similar rates, the longer overwintering periods of some individuals could simply reflect the time it takes to travel to further overwintering locales.

II. Aquatic Movements

Schubauer et al. (1990) defined the aquatic home range of a turtle as the subset that excludes the terrestrial portions. I estimated aquatic home range sizes by identifying the maximum upstream and maximum downstream locations of radioed turtles at each of the two riverine study sites. To facilitate comparison to estimates from Bury (1972) at Hayfork Creek, I calculated the length of linear aquatic home ranges, ignoring the width component of the river. The telemetry data was supplemented with mark-recapture data from 1991-1993 (Chapter 3), which included incidental captures of turtles that were currently radioed, subsequently radioed, or previously radioed. Schubauer et al. (1990) compared home range estimates for *T. scripta* derived from telemetry and derived from mark-recapture and concluded that the best estimates of home range size are obtained from a combination of telemetry and mark-recapture methods. An ANOVA was used to assess the effects of sex and site on linear, aquatic home range size.

RESULTS

I. Terrestrial movements

A. Overview

Terrestrial journeys were most common during the winter at all three sites. The distribution of terrestriality at the mainstem Trinity site appears unimodal compared to the distribution at the Santa Rosa site, which is relatively flat (Figure 9-2). The south fork distribution is very similar to the mainstem one with the peak of terrestriality during the winter months at both sites (Figure 9-3). All three distributions indicate a high level of terrestriality with some nonzero proportion of males and females on land during nearly every month of the year. Examination of the mainstem distribution by sex indicates that the winter peak results from journeys onto land by both sexes, whereas summer journeys are more common among females (Figure 9-4). Review of the individual journeys (Table 9-1) confirms that both sexes overwinter on land, while gravid females make multiple journeys onto land during the summer. The flatness of the Santa Rosa histogram results from only a fraction of the turtles (31-36 %) travelling onto land each winter, and the others remaining in the ponds. Of those that remained in the ponds, some were stationary

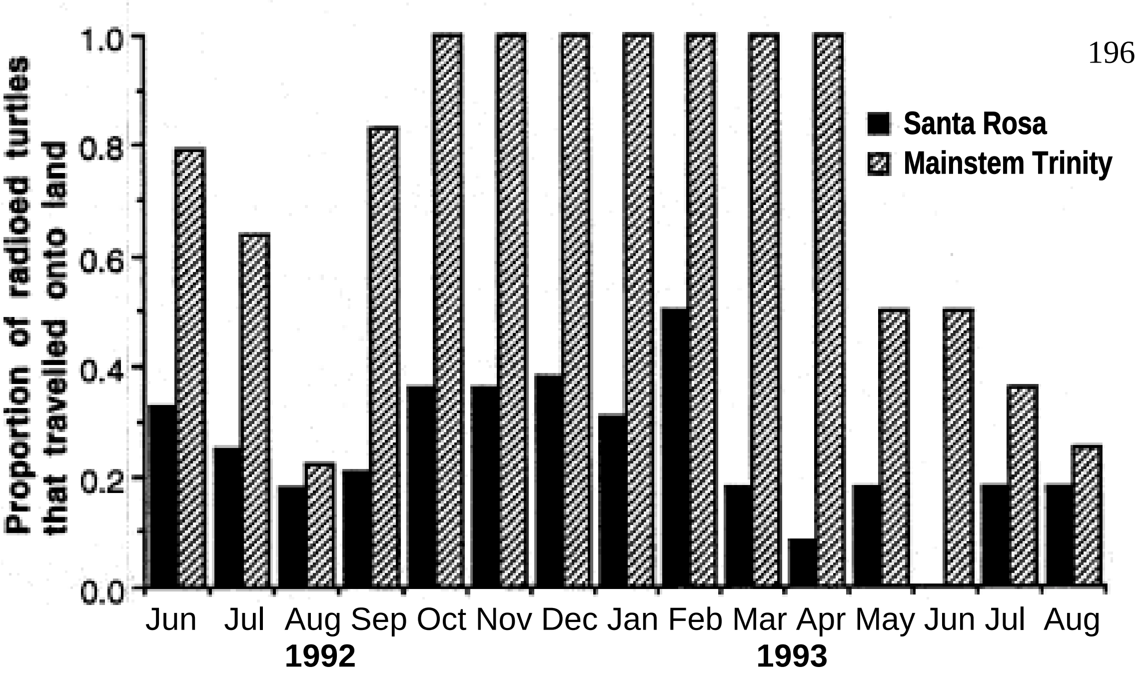


Figure 9-2. Comparison of mainstem Trinity River site and Santa Rosa site with respect to what proportion of turtles made journeys onto land during 1992-3.

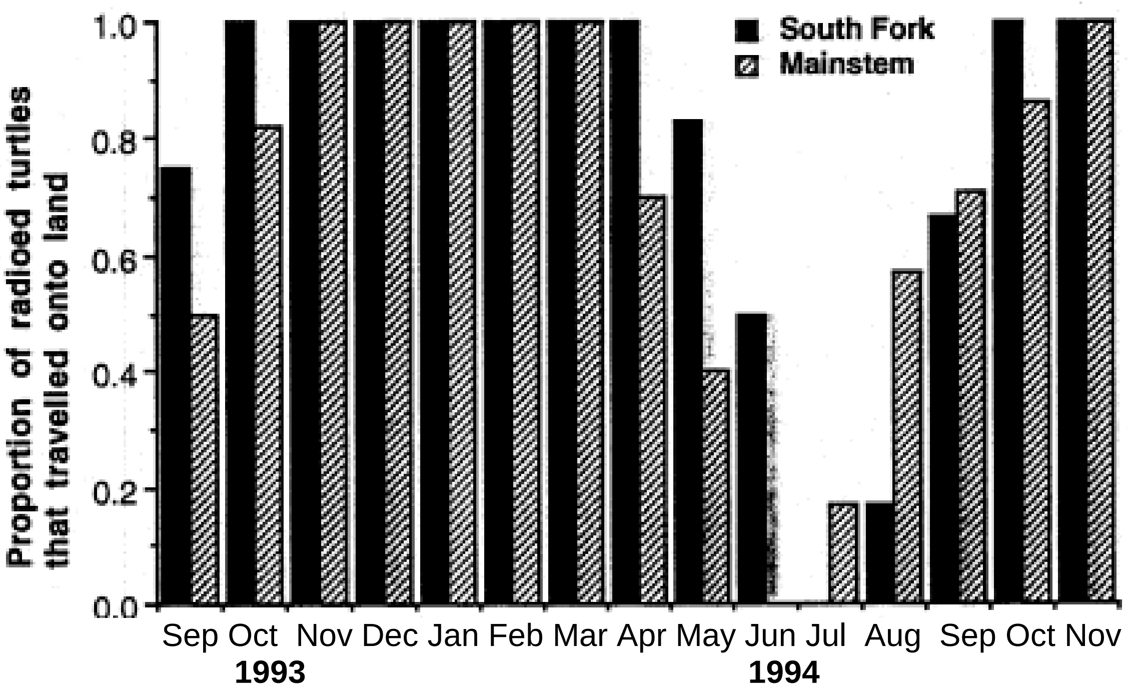


Figure 9-3. Comparison of south fork and mainstem Trinity River sites with respect to what proportion of turtles made journeys onto land during 1993-4.

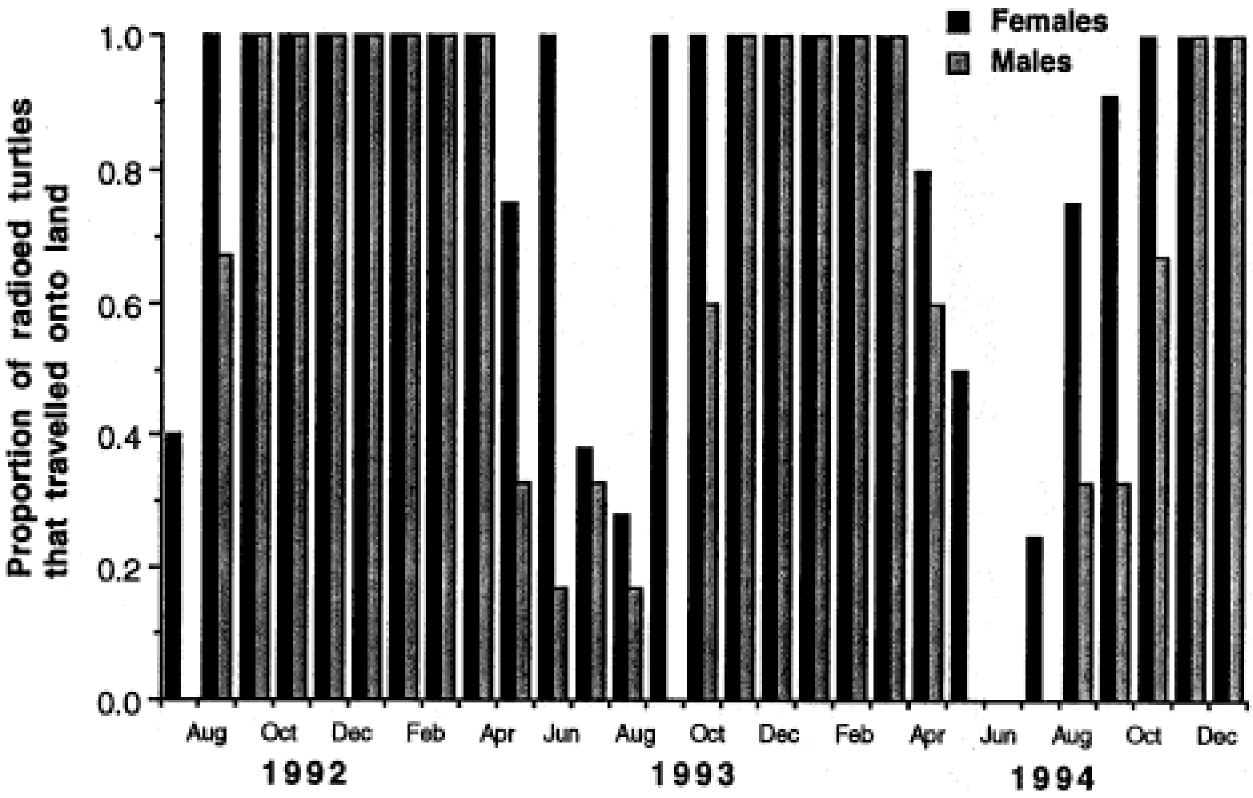


Figure 9-4. Proportion of radioed males and females on the mainstem Trinity River that made journeys onto land during each month.

Table 9-1. List of journeys onto land by radioed turtles at the mainstem Trinity site, the south fork Trinity site, and the Santa Rosa site. Start dates were estimated as the median date between weekly sightings. Duration refers to the number of days on land; if the destination was a pond, then this reflects the duration of overland travel to the pond, not including days spent in the pond. Durations with <= signs indicate that the turtle was only located at the start and end of that interval of time, such that the reported figure is the maximum number of days it could have been on land. * Indicates a one-way journey, as opposed to a round-trip. All reported distances are one-way; thus, figures for round-trips must be doubled to yield total distance travelled. Unless otherwise stated, journeys are from the waterbody of original capture.

Turtle	Site	Visit Start Date	Duration (days)	Distance (m)	"Function"
335a (f)	Main	5-17-92	<=7	86	??
415a (f)	Main	5-15-92	15	30	Gravid
		6-6-92	1	3	Gravid
		6-8-92	6	54	Gravid
		6-17-92	3	73	Gravid
377a (f)	Main	6-7-92	1	30	Gravid
		6-9-92	1	42	Gravid
		6-12-92	1	83	Gravid
		6-14-92	1	83	Gravid
		6-18-92	1/8	15	Gravid
		6-19-92	1	135	Gravid
		6-22-92	1	86	Gravid
		6-24-92	1	92	Gravid
		6-26-92	1/2	88	??
		6-28-92	4	50	??
544 (f)	Main	6-12-92	7	125	Gravid
		6-19-92	1/3	*60	Travel to pond1
		6-20-92	1	*72	Gravid
		6-21-92	1	*132	Travel back to river
		6-30-92	4	130	??
395 (f)	Main	6-18-92	1	30	Gravid
		6-21-92	1/6	23	Gravid
		6-23-92	2/3	47	Gravid
		6-27-92	3/4	40	Gravid
		6-28-92	12	254	Gravid

Table 9-1 (continued)

456 (f)	Main	6-20-92	1	47	Gravid
		6-23-92	1	91	Gravid
		6-26-92	2	81	Gravid
713 (f)	Main	6-27-92	1	50	Gravid
		7-1-92	1 3/4	120	Gravid
		7-8-92	3	124	??
248 (f)	Main	6-28-92	1	30	Gravid
		6-29-92	7/12	145	Gravid
415b (f)	Main	7-25-93	1	110	Gravid
		7-27-93	1	45	Gravid
		8-1-93	10+	7	??
528 (m)	Main	9-4-92	43	*65	Travel to pond1
		10-26-92	115	*46	Overwintering
		2-27-93	74	*65	Travel back to pond1
		6-1-93	<=22	10	??
		11-4-93	36+	139	Overwintering
678 (m)	Main	11-4-92	163	228	Overwintering
		10-19-93	170	208	Overwintering
725 (m)	Main	10-5-92	209	94	Overwintering
		7-24-93	<=5	10	??
		11-9-93	150	117	Overwintering
		11-1-94	159+	39	Overwintering
335b (m)	Main	9-4-92	251	44	Overwintering
		9-26-93	186+	67	Overwintering
560 (m)	Main	8-24-92	1+	20	??
		9-4-92	35	20	??
		10-9-92	49	*65	Travel to pond1
		11-18-92	154	*358	Overwintering
		5-4-93	6	423	Travel back to river
		9-16-93	197	423	Overwintering
		10-28-94	43+	423	Overwintering
377b (m)	Main	9-16-92	186	*140	Overwintering
		3-22-93	36	*60	Travel to vernal pool
		4-21-93	<=6	*60	Travel back to river
		7-20-93	28	18	??
		11-1-93	157	125	Overwintering
		10-7-94	63+	80	Overwintering

Table 9-1 (continued)

868 (f)	Main	7-1-92	<=21	12	??
		9-15-92	184	210	Overwintering
		9-5-93	222+	470	Overwintering
749 (f)	Main	6-8-92	2	120	Gravid
		6-14-92	4	60	Gravid
		6-21-92	1/6	44	Gravid
		6-23-92	1	44	Gravid
		6-27-92	1	15	??
		9-4-92	208	*80	Overwintering
		4-1-93	23	*60	Travel to vernal pool
		4-24-93	29	*80	Travel back to river
		5-29-93	17	37	??
		9-5-93	240	45	Overwintering
		8-13-94	<=19	35	??
		8-28-94	228+	65	Overwintering
949 (f)	Main	6-8-92	11	158	Gravid
		6-19-92	1/8	31	Gravid
		8-12-92	<=52	42	??
		9-4-92	76	78	Died while overwintering
215 (f)	Main	6-10-92	7	*65	Travel to pond1
		6-17-92	2 1/2	*344	Gravid
		6-19-92	2 1/2	*344	Travel to pond1
		6-22-92	2 1/2	*93	Gravid
		6-24-92	1/2	*120	Travel back to river
		9-4-92	176	*161	Overwintering
		3-10-93	22	*112	Travel to pond1
		5-4-93	<=6	*65	Travel back to river
		6-1-93	25	*65	Travel to pond1
		6-26-93	7	*46	Gravid
		7-3-93	<=3	*70	Travel back to river
		8-1-93	1+	*9	??
698 (f)	Main	6-23-92	3	35	Gravid
		6-29-92	2	37	Gravid
		8-12-92	<=15	27	??
		9-11-92	285	401	Overwintering
		9-5-93	237	54	Overwintering
		7-19-94	33	45	Gravid
		9-8-94	17	5	??
		10-7-94	188+	47	Overwintering

Table 9-1 (continued)

773 (f)		9-4-92	239	192	Overwintering
		6-15-93	18	30	Visit to pond2
		9-5-93	193	*200	Overwintering
		5-3-93	65	*175	Travel to pond2
		5-16-93	13	*30	Travel back to river
		8-13-93	<=12	1	??
		9-17-94	20	25	??
		10-25-94	46+	199	Overwinter
924 (f)	Main	9-15-93	198+	132	Overwintering
797 (f)	Main	7-13-93	1/12	10	Gravid
		7-15-93	3	25	Gravid
		7-20-93	1	77	Gravid
		7-21-93	2	103	False nesting dig
		7-23-93	1	20	Gravid
		7-24-93	3/4	66	False nesting dig
		7-25-93	2	100	False nesting dig
		7-28-93	1/9	50	False nesting dig
		8-27-93	223	212	Overwintering
		5-7-94	<=14	116	??
		9-17-94	84+	142	Overwintering
825 (m)	South	10-18-93	217	176	Overwintering
		9-28-94	67+	202	Overwintering
219 (m)	South	10-7-93	<=12	*65	Travel to pond1
		12-25-93	127	*36	Overwintering
		5-1-93	<=10	*36	Travel back to pond1
		6-17-94	<=6	*65	To river from pond1
		9-20-94	<=8	*65	To pond1 from river
		11-3-94	30+	*93	Overwintering
972 (m)	South	10-13-93	137	*128	Overwintering
		2-27-94	<=7	*410	Travel to vernal pool
		5-25-94	<=12	*215	From vernal pool to river
		10-30-94	34+	*126	Overwintering
950 (f)	South	10-4-93	14	*65	??
		10-18-93	<=10	*100	Travel to pond1
		12-25-93	66	*174	Overwintering
		3-1-94	<=16	*174	Travel back to pond 1
		4-15-94	<=6	*65	Travel to river
		9-23-94	<=15	*65	Travel to pond1
		11-3-94	30	*195	Overwintering

Table 9-1 (continued)

848(f)	South	9-24-93	234	*129	Overwintering
		5-16-94	<=20	*510	Travel to vernal pool
		6-10-94	<=8	*215	Travel back to river
		8-27-94	98+	77	Overwintering
900(f)	South	9-24-93	185	*160	Overwintering
		3-28-94	<=6	*222	Travel to pond1
		9-6-94	88	*144	Overwintering
411 (m)	SR	No terrestrial journeys			
038(m)	SR	5-27-92	<=11	*300	From pond1 to pond2
		2-21-93	<=4	*300	From pond2 to pond1
		5-30-93	<=66	*300	From pond1 to pond2
359(m)	SR	6-16-92	29	80	??
		7-20-92	223	88	Aestivation/hibernation
		7-10-93	207	55	Aestivation/hibernation
118(m)	SR	No terrestrial journeys			
087(m)	SR	9-17-92	<=15	*825	From pond3 to lake2
		10-19-92	<1	*825	From lake2 to pond3
		10-30-92	4	27	??
		2-12-93	7	*175	From pond3 to pond4
		3-11-93	<=17	*325	From pond4 to pond5
		3-21-93	<=17	*325	From pond5 to pond4
		6-30-93	<=58	*925	From pond4 to pond6
459(m)	SR	2-28-92	9	*375	From lake3 to lake4
		4-8-92	<=34	*375	From lake4 to lake3
313(m)	SR	No terrestrial journeys			
287(m)	SR	12-16-93	57	160	Overwintering
176(f)	SR	5-18-92	?	65	Gravid
		6-6-92	<=17	*550	From lake1 to pond2
		7-6-92	<=8	*550	From pond2 to lake1
		10-25-92	84+	80	Overwintering
777(f)	SR	5-26-92	<=3	*375	From lake4 to lake5
262(f)	SR	10-10-92	116	235	Overwintering
		3-8-93	<=11	*175	From pond4 to pond3
		11-2-93	122+	*200	Overwintering

Table 9-1 (continued)

509(f)	SR	6-11=92	270	97	Aestivation/hibernation
		7-10-93	20	73	??
		8-7-93	217	112	Aestivation/hibernation
889(f)	SR	12-11-92	<=12	70	??
676(f)	SR	6-4-92	<=14	*550	From pond1 to lake1
209(f)	SR	No terrestrial journeys			

during the winter months, while others were mobile (Figure 9-5).

Some journeys reported in Table 9-1 are clearly associated with nesting (those made by gravid females) or overwintering (those ending at overwintering sites). Other journeys consist of round-trip travel between the river and adjacent ponds at the Trinity sites (e.g. turtles 215, 773) or between sets of ponds at the Santa Rosa site (e.g. turtles 038, 087, 459, 176). A single Santa Rosa male visited eight ponds during the course of the study. Round trip journeys to ponds at the Trinity sites were often interrupted by forays to dry terrestrial sites, which were associated with nesting (e.g. turtle 215) or overwintering (e.g. turtle 528, 219, 950). In numerous cases, Trinity journeys consist of a one-way triangle among the river, a pond, and a dry terrestrial location (e.g. turtles 544, 560, 377b, 749, 215, 773, 972, 848). A seasonal pattern of journeys was often apparent, such as the occupation of one aquatic habitat during the summer and another during the winter (e.g. turtles 335b, 038).

The function of some journeys (indicated by "??") was not immediately identifiable. For example, several mainstem Trinity males travelled short distances onto land during the summer (turtles 528, 725, 377b). Several mainstem Trinity females made journeys onto land in late summer after oviposition (turtles 377a, 544, 713, 415b). Numerous fall journeys occurred at the Trinity sites prior to the actual inception of overwintering (turtles 560, 949, 698, 773, 950). Mysterious spring journeys occurred as well (turtles 749, 797). The Santa Rosa site is distinguished by the prolonged journeys (approximately eight months in 1992-3 and seven months in 1993-4) initiated each summer by one pair of radioed turtles (turtles 359, 509). These journeys, judging from their timing, were at least

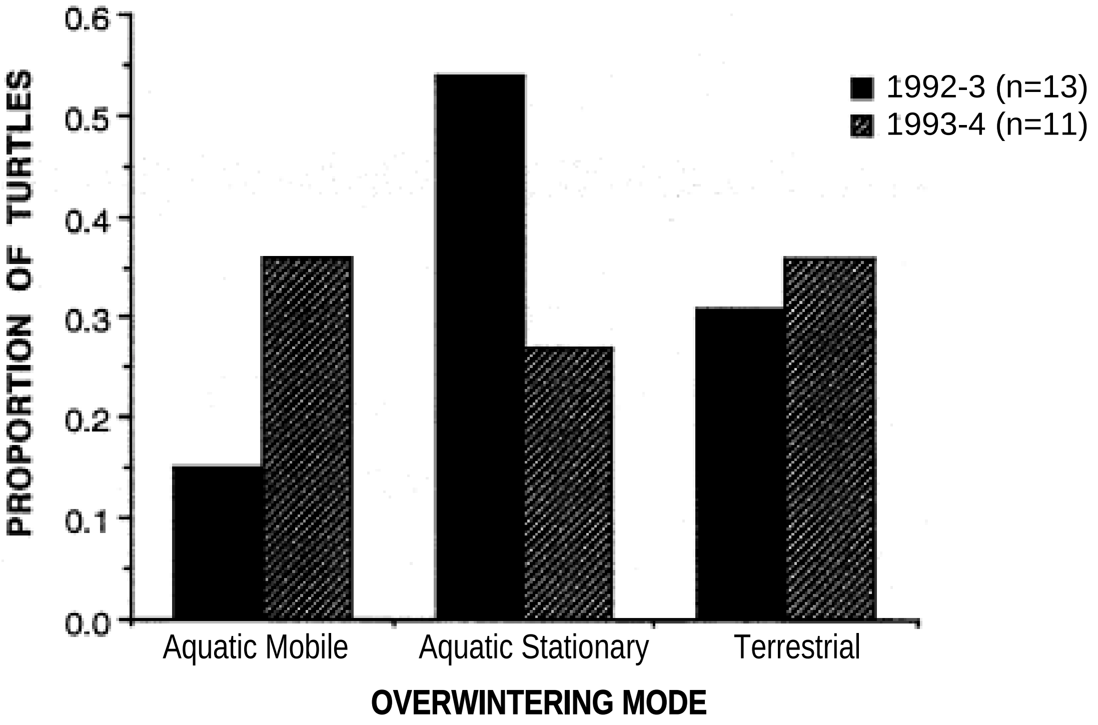


Figure 9-5. Overwintering modes of radioed turtles in ponds at the Santa Rosa study site during 1992-3 and 1993-4 winters (n=sample size).

at their inception motivated by aestivation; this pair inhabits a natural, vernal pool that dries up annually during the summer. The Santa Rosa site is also unique in having individuals (both males and females) that made no terrestrial journeys during their monitoring periods.

B. Overwintering: Behavior

Several different overwintering behaviors were apparent in the study populations. The Santa Rosa populations showed a mixed winter strategy (see above). All turtles in the Trinity, populations left the watercourse for the winter. While the majority travelled onto land, a couple travelled to other bodies of water (Table 9-2). Without exception, those that travelled onto land buried themselves fully under leaf or needle duff (Reese and Welsh 1996). This was true also for turtles from Santa Rosa ponds that overwintered terrestrially. With the exception of one individual from the Santa Rosa site, the behaviors of individual turtles were consistent from year to year with respect to whether their overwintering sites were aquatic or terrestrial.

Habitat at overwintering sites included conifer-dominant, hardwood-dominant, and mixed conifer-hardwood types. The slopes varied as well from flat to as much as 55 degrees. Aspect spanned the compass, although west-facing slopes were used frequently at the south fork and Santa Rosa sites, while east-facing slopes were more frequent at the mainstem. Canopy cover varied, but the majority of overwintering sites had canopies of fifty percent or greater.

The analysis (ANOVA) of the variability in movements of overwintering turtles

Table 9-2. Overwintering habitat of western pond turtles during the 1992-1994 winters.

Site	Turtle	1992 Habitat	1993 Habitat	1994 Habitat	1992 Slope	1993 Slope	1994 Slope	1992 Aspect	1993 Aspect	1994 Aspect	1992 Canopy	1993 Canopy	1994 Canopy
Main	528	3	-	-	0	-	-	none	-	-	70	-	-
	678	4	4	-	0	4	-	none	SW	-	80	78	-
	725	4	4	3	20	12	15	E	E	N	15	85	40
	335b	6	6	-	slough	slough	-	-	-	-	-	-	-
	560	4	4	4	lake	lake	-	-	-	-	-	-	-
	377b	5	5	4	14	45	7	NE	NE	NE	50	99	87
Main	868	4	4	-	5	35	-	N	NW	-	75	89	-
	749	5	5	5	0	18	5	none	NE	E	75	97	95
	949	3	-	-	5	-	-	E	-	-	50	-	-
	215	5	-	-	10	-	-	E	-	-	90	-	-
	698	1	1	1	25	15	15	NE	NW	NE	75	88	94
	773	3	3	5	15	55	45	NE	E	E	50	92	81
	924	-	1	-	-	0	-	-	none	-	-	85	-
	797	-	5	5	-	0	8	-	none	E	-	93	67
South	950	-	5	3	-	23	9	-	SW	W	-	86	45
	219	-	3	5	-	45	17	-	W	W	-	82	94
	972	-	5	5	-	20	18	-	W	W	-	73	88
South	825	-	5	3	-	23	16	-	NW	NW	-	72	75
	848	-	3	5	-	23	22	-	NW	W	-	43	90
	900	-	5	3	-	30	20	-	W	W	-	67	75
S.R.	359	-	3	3	-	20	17	-	NW	NW	-	42	88
	262	3	3	-	5	10	-	NW	NW	-	6	82	-
	509	3	3	-	15	15	-	NW	NW	-	38	25	-

Habitat:

1. Doug Fir Dominant: Composed of at least 75% Doug firs
2. Alder/willow mix with neither comprising more than 75%
3. Hardwood Dominant: Composed of at least 75% hardwoods
4. Conifer Dominant: Conifer mix with no species > 75%
5. Mixed hardwoods with neither > 75%

while on land indicated a significant effect of sex on the number of terrestrial stops made, but no effect of site (Table 9-3). The sex effect was investigated further by pooling across sites and using t-tests to compare sexes with respect to preoverwintering stops, postoverwintering stops, and overall stops. Females made more preoverwintering and more postoverwintering stops than males (preoverwinter T = 2.28, p = .044, postoverwinter T = 2.94, p = .024, Figure 9-6). Females made an average of 9.1 stops before reaching the river, while males made an average of 4.5 stops.

C. Overwintering: Timing

Paired t-tests examining the effects of year on the timing of overwintering behavior indicated no significant differences between years in departure, settling, leave, or return times (Table 9-4.). The analysis of sex and site effects (MANOVA) on the timing of overwintering revealed trends (Table 9-5, Figure 9-7). The only main effect was the effect of sex on departure time from the river. For both departure time and settling time, there was a significant interaction of sex and site. More detailed examination using t-tests revealed that females departed earlier than males for overwintering at the mainstem Trinity (T = -3.08, p = .052), while departure appeared to be synchronous at the south fork Trinity (T = -0.06, p = .953). Males at the south fork site settled later than females (T = -3.43, p =.027). There was no effect of sex or site on the time at which turtles left their overwintering sites or returned to the river.

Analysis of the duration of overwintering journeys by mainstem turtles did not

Table 9-3. Analysis of the effects of site and sex on the number of terrestrial stops made by overwintering turtles on the mainstem and south fork Trinity during 1993-4.

						F-statistic	**P-value**
Site	Main		South			1.84	0.208
Sex	Female	Male	Female	Male		12.77	0.006
Mean # stops	8.0	4.0	11.0	5.0	**Interaction**	0.38	0.553

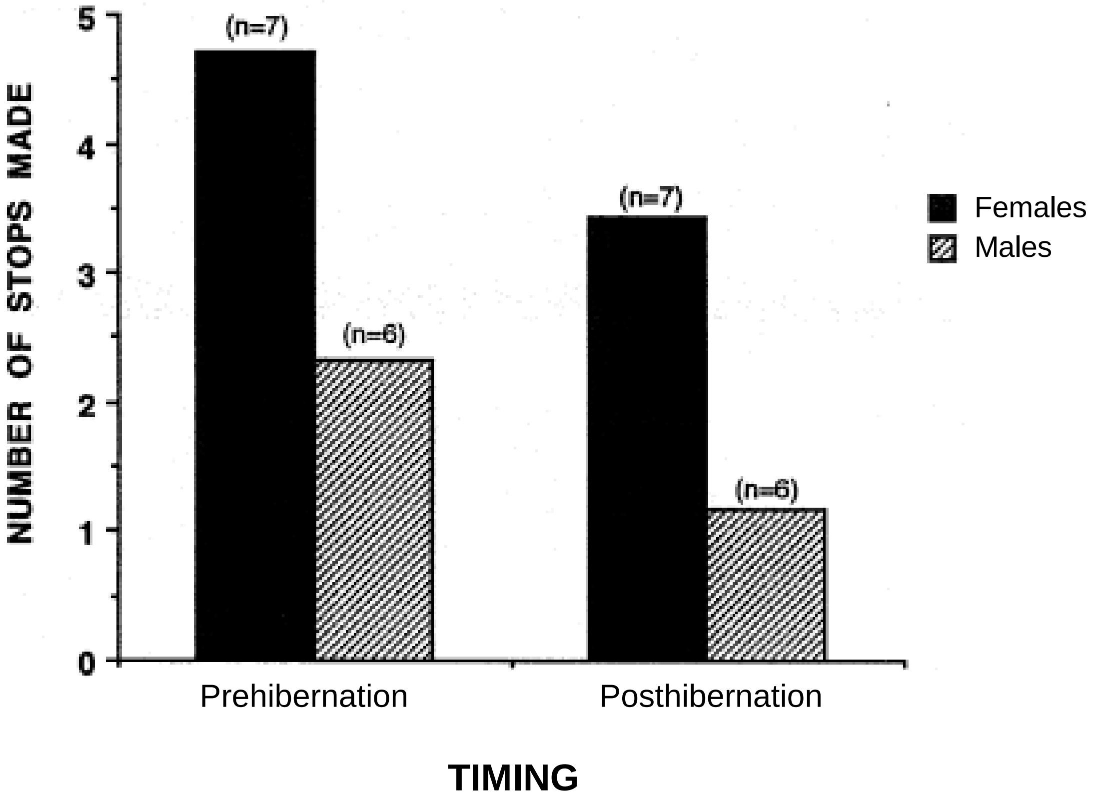


Figure 9-6. Terrestrial stops made prior and subsequent to hibernation by western pond turtles on the mainstem Trinity River (n=sample size).

Table 9-4. Analysis of the effects of year on the timing of overwintering by western pond turtles at the mainstem and south fork Trinity during 1992-1995. P-values were subject to a Bonferroni adjustment for multiple t-tests.

Site	Year 1	Year 2	Timing Variable*	Mean Difference (days)	Paired T	P-value
Main	1992	1993	DEPART	-11.71	-1.49	0.38
Main	1993	1994	DEPART	-7.57	-0.72	2.00
South	1993	1994	DEPART	8.33	0.90	0.82
Main	1992	1993	SETTLE	-13.00	-0.88	0.84
Main	1993	1994	SETTLE	20.20	2.60	0.24
South	1993	1994	SETTLE	31.20	1.71	0.32
Main	1993	1994	LEAVE	-5.28	-0.58	2.32
Main	1993	1994	RETURN	17.17	2.11	0.36

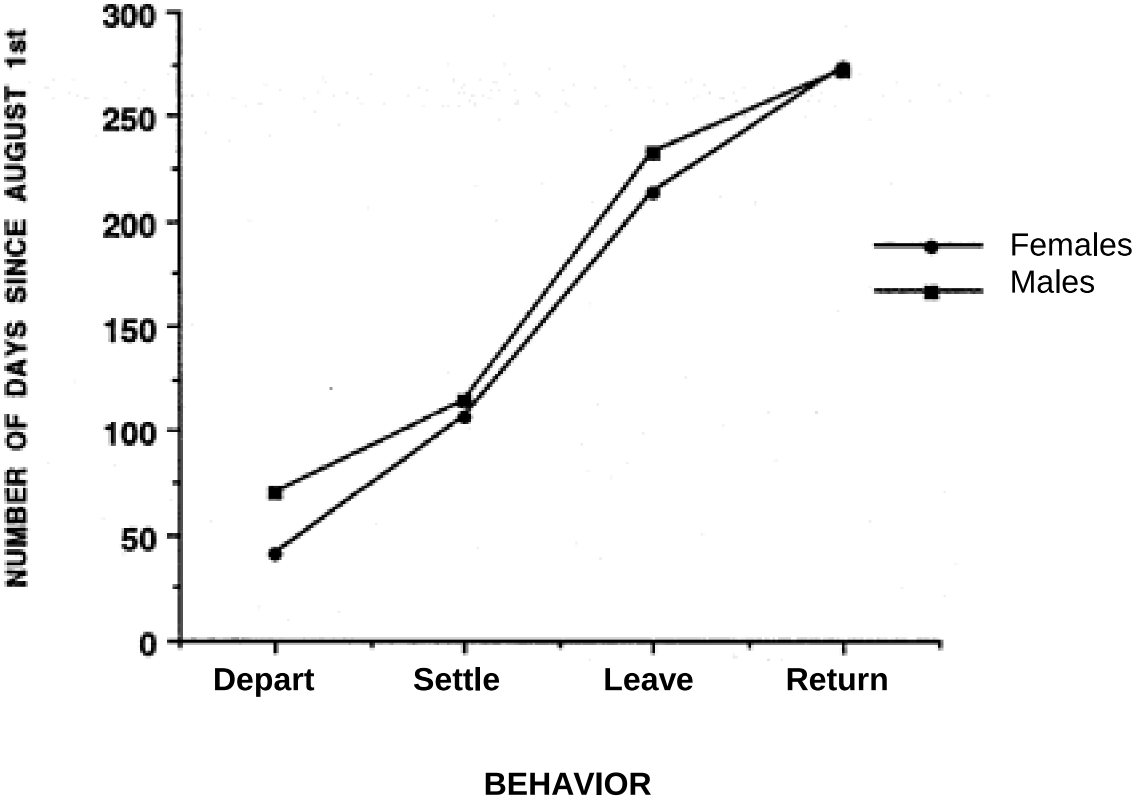
* DEPART = Time of departure from the river, measured as number of days since August 15th
SETTLE = Time of settling at overwinter site, measured as number of days since August 15th
LEAVE = Time of leaving overwinter site, measured as number of days since February 1st
RETURN = Time of returning to the river, measured as number of days since February 1st.

Table 9-5. Analysis of the effects of sex and site on the timing of overwintering by western pond turtles on the mainstem and south fork Trinity during 1993-4.

Timing Variable*	Sex		Site		Interaction	
	F-statistic	P-value	F-statistic	P-value	F-statistic	P-value
DEPART	5.97	.04	0.16	.70	5.65	.04
SETTLE	1.50	.26	3.48	.10	6.10	.04
LEAVE	1.10	.33	0.48	.51	0.16	.70
RETURN	0.23	.64	2.94	.12	0.83	.39

* See Table 9-4 for definitions of timing variables.

Figure 9-7. Depiction of the timing of overwintering behaviors by male and female western pond turtles on the mainstem Trinity River during the 1993-4 winter.



reveal consistent individual behavior across the two sampling winters (Spearman Rho = 0.39, p > .10). Turtles that overwintered for relatively long periods in 1992-3 did not necessarily overwinter for long periods in 1993-4. The analysis (ANOVA) of the effects of sex and site on duration of overwintering yielded a significant interaction term (Table 9-6). Detailed examination using individual t-tests revealed that mainstem females overwintered for longer than mainstem males (T = 5.73, p = .001), while male and female overwintering periods were of similar duration at the south fork site (T = -0.25, p = .818). This result is in accordance with the results of the timing analysis, namely that females initiate overwintering journeys earlier than males at the mainstem but not at the south fork site. When duration was estimated not as the time until returning to the river, but as the time until returning to the river or to an alternative body of water, the results were different. There were significant effects of both sex and site, with females overwintering for longer than males and mainstem turtle overwintering for longer than south fork turtles (Table 9-7).

D. Overwintering: Distance

Mainstem and south fork overwintering points were, on average, at similar distances from the watercourse (Table 9-8). Indeed, the analysis of the effects of sex and site on overwintering distances at the two Trinity River sites indicated no significant relationships (Table 9-9); there was no evidence that distance travelled was different between males and females or between study sites. Considering the equivalent distances travelled and recalling that females departed earlier for overwintering sites but arrived at

Table 9-6. Analysis of the effects of site and sex on the duration of overwintering by western pond turtles on the mainstem and south fork Trinity during 1993-4.

						F-statistic	P-value
Site	Main		South			1.65	0.23
Sex	Female	Male	Female	Male		3.05	0.11
Duration (days)	239	168	221	231	**Interaction**	5.21	0.04

Table 9-7. Analysis of the effects of site and sex on the duration of overwintering by western pond turtles on the mainstem and south fork Trinity during 1993-4, excluding time spent in ponds after hibernation.

						F-statistic	P-value
Site	Main		South			10.07	0.01
Sex	Female	Male	Female	Male		42.90	0.00
Duration (days)	235	168	212	110	**Interaction**	1.87	0.20

Table 9-8. Distances of turtle overwintering points to the watercourse (m) at the mainstem and south fork Trinity River, as well as distances between successive overwintering points for each individual that was monitored for multiple years.

Site	Turtle	1992	1993	1994	1992 & 1993	1993 & 1994
Main	528	111	dead	-	-	-
	678	228	208	lost	38	-
	725	94	117	39	23	556
	335b	44	67	lost	31	-
	560	423	423	423	0	0
	377b	140	125	80	19	76
	868	210	215	lost	5	-
	749	80	81	76	8	8
	215	161	lost	-	-	-
	698	401	54	47	369	10
	773	192	200	199	16	1
	924	-	132	lost	-	-
	797	-	212	213	-	3
	$\bar{X}$	**189**	**167**	**154**	**56**	**93**
South	825	-	152	185	-	33
	848	-	129	77	-	56
	900	-	222	211	-	18
	950	-	228	260	-	88
	972	-	128	126	-	5
	219	-	103	162	-	61
	$\bar{X}$		**160**	**170**		**44**

Table 9-9. Location of overwintering locales relative to the river corridor for western pond turtles on the mainstem and south fork of the Trinity River during 1991-1994.

			Distance from watercourse (m)			Elevation above river (m)		
Turtle #	Sex	Site	'92-'93	'93-94	'94-95	'92-93	'93-'94	'94-'95
528	M	Main	111.0	-	-	6	-	-
678	M	Main	227.8	207.4	-	64	-	-
725	M	Main	94.5	116.9	38.8	8	10	2
335b	M	Main	43.7	66.9	-	0	1	-
560	M	Main	422.8	422.8	422.8	115	115	115
377b	M	Main	140.0	124.9	80.3	2	2	7
		$\bar{X}$	**173.3**	**187.8**	**180.6**	**32**	**32**	**41**
868	F	Main	210.3	215.1	-	17	17	-
749	F	Main	80.4	81.4	75.8	8	8	6
215	F	Main	161.2	-	-	15	-	-
698	F	Main	401.0	53.9	47.2	159	9	9
773	F	Main	192.1	200.0	198.7	61	77	77
797	F	Main	211.8	213.4	-	-	15	15
		$\bar{X}$	**209.5**	**152.8**	**107.2**	**52**	**25**	**27**
950	M	South	-	228.5	259.8	-	82	91
219	M	South	-	102.9	162.3	-	36	67
972	M	South	-	127.8	126.2	-	35	35
		$\bar{X}$		**153.1**	**182.8**		**51**	**64**
825	F	South	-	151.7	184.8	-	57	71
848	F	South	-	128.9	76.8	-	31	21
900	F	South	-	160.0	143.5	-	60	60
		$\bar{X}$		**146.9**	**135.0**		**49**	**51**

approximately the same time (Section C. Overwintering: Timing), I infer that females travelled more slowly. Distance travelled to overwintering points and duration of overwintering journeys were not significantly correlated (Pearson Rho = -0.29, p = 0.26). Comparison of the 1992-3 and 1993-4 winters on the mainstem reveals no evidence that turtles travelled further during either one (paired t = 1.07, p = 0.32). Visual examination of the overwintering locales of individual Trinity River turtles during successive years indicates that individuals returned to nearly the same locations from year to year (Figures 9-8 through 9-10). This was true also for the Santa Rosa turtles that overwintered on land, although exact distances are not available. Distances between successive overwintering points for single individuals averaged 72 meters at the mainstem site and 44 meters at the south fork site and were as small as 1 meter (Table 9-8).

II. Aquatic movements

Schubauer et al. (1990) found that 100% of total estimated home range size for *T. scripta* was achieved after 15-20 weekly telemetry observations. My estimates of aquatic home range size at the mainstem Trinity River site are likely to be quite accurate, considering the large number of riverine locations made for each turtle over the duration of the study (averaging 51; Table 9-10). At the south fork Trinity site, estimates may be less accurate because of the fewer locations per turtle (averaging 13.7; Table 9-10). This is partly attributable to the smaller duration of monitoring at the south fork and partly to the more prolonged use of ponds by the south fork turtles, which decreased the time spent travelling up and down the riverine corridor.

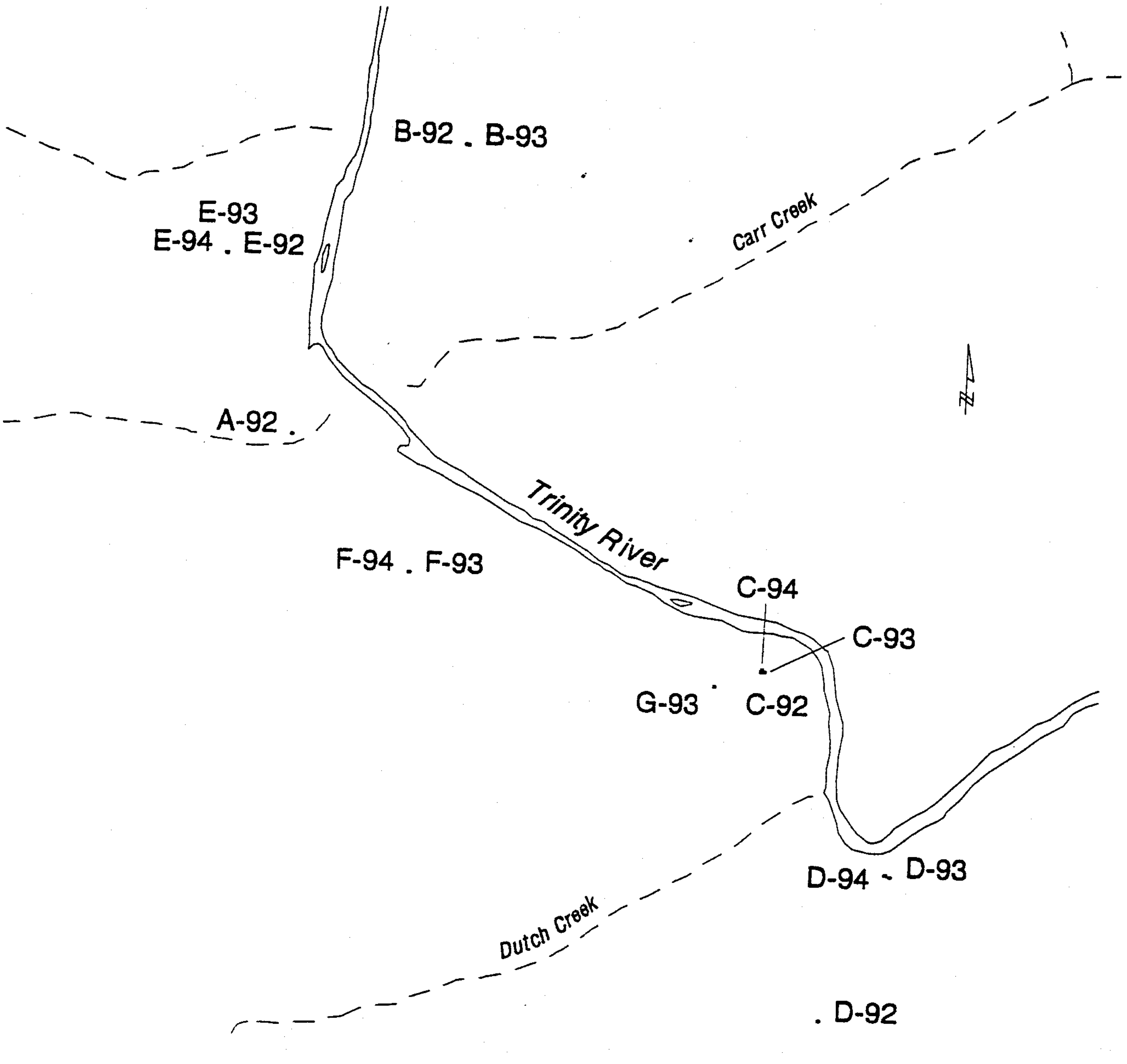


Figure 9-8. Overwintering locations of female western pond turtles on the mainstem Trinity River during 1992-1994 winters.

A. Female 215
B. Female 868
C. Female 749
D. Female 698
E. Female 773
F. Female 797
G. Female 924

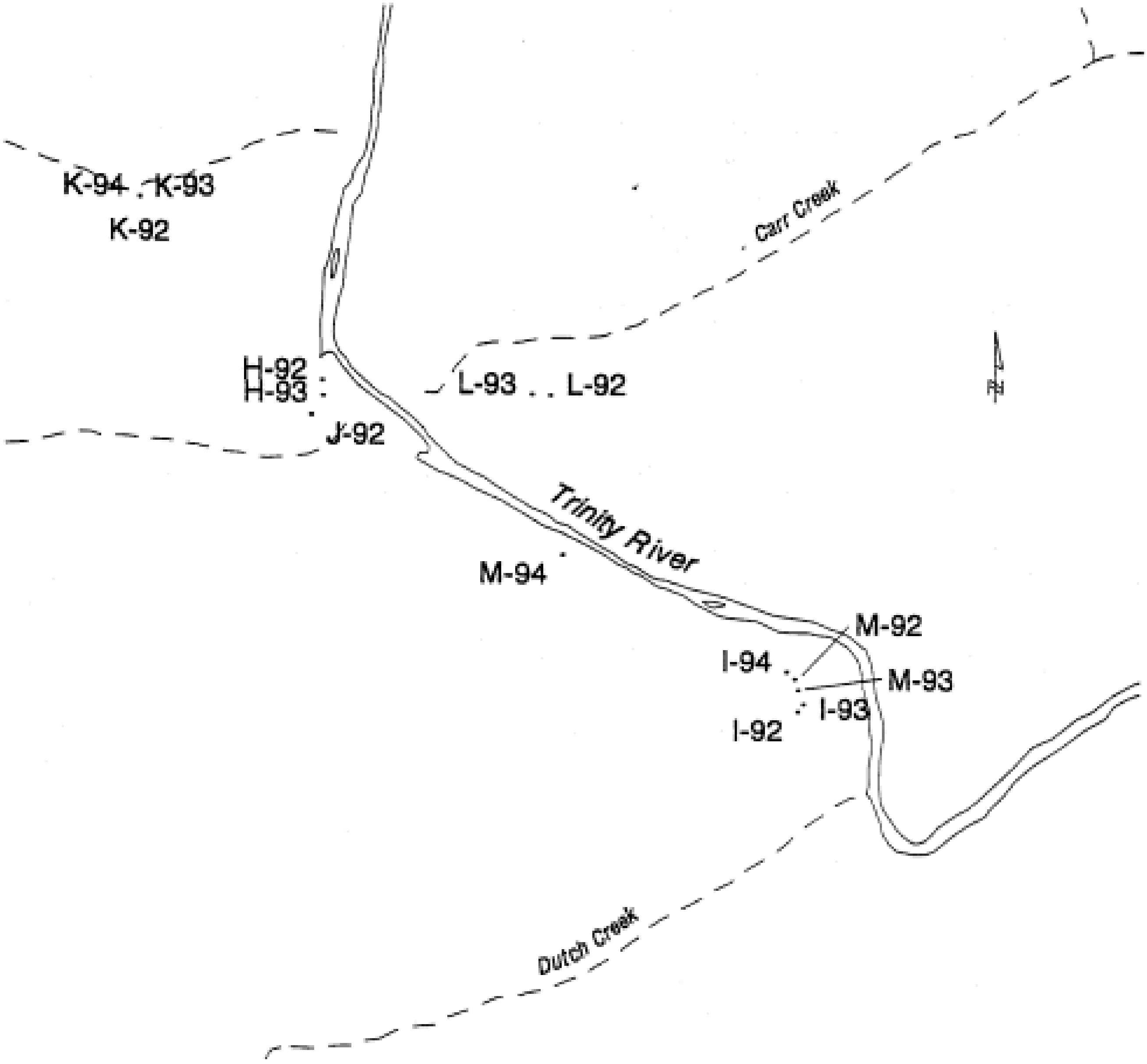
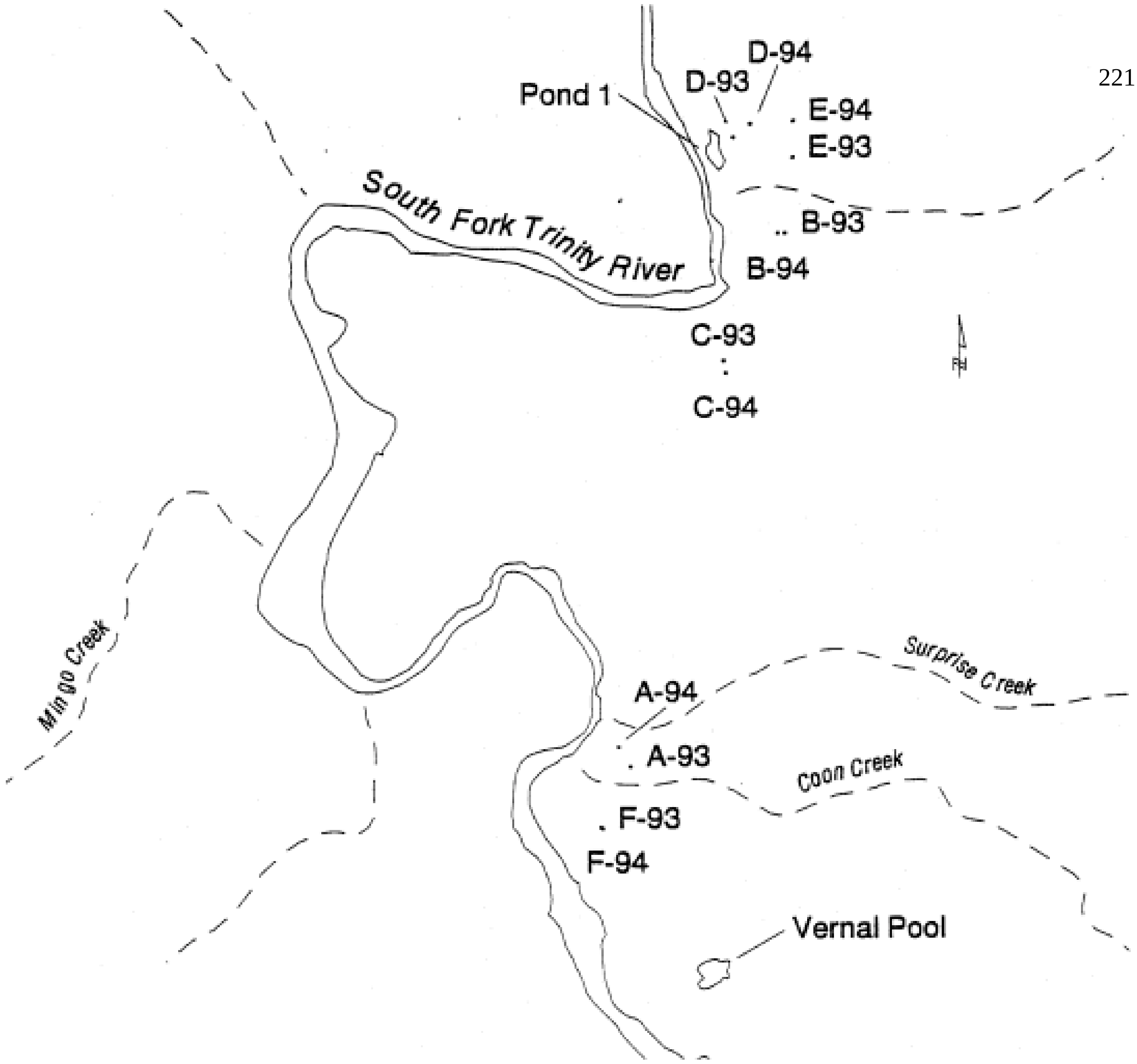


Figure 9-9. Overwintering locations of male western pond turtles on the mainstem Trinity River during 1992-1994 winters.

H. Male 335
I. Male 377
J. Male 528
K. Male 560
L. Male 678
M. Male 725



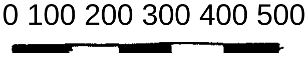


Figure 9-10. Overwintering locations of western pond turtles on the south fork Trinity River during 1993-1994 winters.

A. Female 848
B. Female 900
C. Female 825
D. Male 219
E. Male 950
F. Male 972

Table 9-10. Aquatic home range sizes of western pond turtles on the mainstem and south fork Trinity River generated from radiotelemetry and mark-recapture data.

Turtle #	Sex	Site	Linear home range size (m)	Number of observations
528	M	Mainstem	1667	49
678	M	Mainstem	1655	67
725	M	Mainstem	2326	73
335b	M	Mainstem	1056	27
560	M	Mainstem	688	28
377b	M	Mainstem	1081	40
		$\overline{X}$ males	**1412**	**47**
868	F	Mainstem	500	17
749	F	Mainstem	160	91
215	F	Mainstem	560	48
698	F	Mainstem	1316	85
773	F	Mainstem	641	34
797	F	Mainstem	449	54
		$\overline{X}$ females	**604**	**55**
950	M	South fork	252	15
219	M	South fork	326	13
972	M	South fork	1217	18
		$\overline{X}$ males	**598**	**15**
825	F	South fork	272	5
848	F	South fork	657	8
900	F	South fork	100*	23
		$\overline{X}$ females	**343**	**12**

* Based entirely on movements within a pond adjacent to the south fork, as this female did not visit the river during the course of the study.

The ANOVA revealed effects of both sex (F = 4.94, p = 0.04) and site (F = 5.05, p = 0.04) with a nonsignificant interaction (F = 1.33, p = 0.27). Linear home ranges of mainstem Trinity males were from 688-1667 meters long, averaging 1244 m, while linear home ranges of females were from 160-641 meters long and averaged 449 m. At the south fork, the range for males was 252-1217 m (averaging 598 m) and for females was 100-657 m (averaging 343 m). Thus, male home ranges were 2.8 times the size of female home ranges at the mainstem Trinity site and 1.7 times the size at the south fork Trinity site. Mainstem turtles had larger home ranges than south fork turtles, although this effect may be attributable to the smaller sample sizes of aquatic locations at the south fork site.

DISCUSSION

The results portray a high level of terrestriality with turtles at all three study sites travelling onto land during nearly all months of the year. Research on *C. marmorata* in other parts of its range also reveals frequent terrestrial journeys (Goodman 1994, Holland 1994, Rathbun 1992). The majority of the journeys reported here can be classified into known categories of extrapopulational movements. Gibbons (1986) defined movements of aquatic turtles for nesting, for overwintering, for departure from unsuitable habitats, and for mate searches by males. In addition, Cagle (1944) attributed overland movements to the existence of home ranges that included multiple bodies of water, although Schubauer (1990), in defining home range use, excludes emigration to other water bodies. Seasonal movements by turtles to areas with different resources also occur (Moll and

Legler 1971, Marlow and Tollestrup 1982); they can perhaps be viewed as a form of departure from unsuitable habitats, consisting of a temporary move to obtain resources in short supply.

At all three study sites, journeys that could be categorized as nesting and overwintering occurred. It is not clear whether departure from unsuitable habitats occurred; it is a difficult phenomenon to observe because of its unpredictable timing (Gibbons 1986) and because marked turtles that leave an area permanently are not likely to be recaptured. Even radioed individuals may be difficult to locate, given a weekly monitoring schedule and the potential for long-distance travel. Results from the Santa Rosa site indicated that a western pond turtle can travel nearly a kilometer in a single night (Table 9-1). Mate searching by males is also difficult to identify, but may account for some of the long-distance aquatic journeys by males at the riverine study sites. It also may account for several early spring journeys between ponds by males at the Santa Rosa site. Little is known about the seasonal timing of mating, but observations of turtles mating on the mainstem Trinity and the timing of oviposition suggest that mating activity may be concentrated in early spring.

Journeys between multiple bodies of water occurred at all three sites, and many of them were round-trip, suggesting that Cagle's (1944) definition of home range as inclusive of adjacent bodies of water is warranted. In fact, it is likely that many additional, unidentified ponds and creeks are integral to the life history of the populations examined in this study. Other research (Burke et al. 1995) indicated that the detection of interchange of aquatic turtles between wetlands requires an intensive marking effort over a long period of time; new wetlands used by study populations of *Trachemys scripta* were still being discovered after more than two decades of captures. More prolonged research on *Clemmys marmorata* might expand the estimates of distances travelled overland considerably, particularly in an area like Santa Rosa where the landscape is dotted with myriad small ponds.

Clearly, alternate habitats are important in the life history of *Clemmys marmorata* and other aquatic turtles. Habitats may differ seasonally in their potential to provide resources, whether they be access to mates, food resources, basking sites, cover, or predator-free circumstances. Seasonal shifts in aquatic habitat have been observed in other species, such as *Chrysemys picta*, which moves from shallow marsh areas in the spring to deeper hibernation ponds during the rest of the year (Sexton 1959) and *Malaclemys terrapin terrapin*, which migrates from open, salt marshes into creeks during the winter (Yearicks et al. 1981). Indeed, seasonal patterns of use were often evident in this study, with turtles occupying one waterbody in the summer and another in the winter or visiting a pond before returning to the river after overwintering. The patterns are explainable in light of resource utilization. After overwintering, for example, turtles at both the south fork and the mainstem site visited vernal pools, which support an abundance of aquatic invertebrate prey items (Jain 1976, Zedler 1987). Other species of turtle are known to visit vernal pools in the spring, apparently to take advantage of seasonally abundant foods, for example *Clemmys guttata* in Massachusetts (Graham 1995). Western pond turtles at the south fork and mainstem sites also visited permanent ponds in the spring and fall, times during which the river is fast-flowing and cold. In general, ponded waters may offer milder conditions than lotic habitats at certain times of year and thus generate a pattern of seasonal movements. They may also function as mating areas by virtue of attracting large concentrations of turtles, as occurred in the south fork vernal pool during the spring.

At the Santa Rosa site, movements between ponds that did not appear to be associated with seasonal changes also occurred, for example multiple movements in the course of one summer. Short treks between adjacent ponds during the active season have been made by other species of aquatic turtle, including *Emydoidea blandingii* (Rowe and Moll 1991) *Deirochelys reticularia* (Buhlmann 1995), *Trachemys scripta, Kinosternon subrubrum,* and *Chelydra serpentina* (Gibbons 1970). While the complex home ranges of *Clemmys marmorata* at the Trinity River sites consisted of a portion of river and a single permanent pond or vernal pool, the home ranges of Santa Rosa turtles could include multiple ponds. Riparian habitats at the Santa Rosa site were historically more continuous, consisting of webs of creeks, prior to the advent of small-scale damming for agricultural water diversion. Thus, a system of aquatic corridors for turtle movements has been converted to sets of discrete ponds. The current conditions may require that turtles include multiple ponds in their home ranges and, therefore, travel overland, to obtain sufficient resources.

Journeys that do not fit into the categories of extrapopulational movements defined above also occurred. Thus, an elaborated assessment of the functions of overland travel by aquatic turtles is warranted (Appendix 9-C). In addition to nesting, overwintering, departure from unsuitable habitats, mate searching by males, and complex home ranges, it

APPENDIX 9-C

POTENTIAL FUNCTIONS OF OVERLAND TRAVEL BY AQUATIC TURTLES

1. NESTING
    - A. Exploratory journeys to locate suitable nesting sites
    - B. Oviposition journeys
    - C. Journeys to warm terrestrial microclimates during invitro egg incubation

2. DORMANCY
    - A. Journeys to terrestrial overwintering sites
    - B. Journeys across land to aquatic overwintering sites
    - C. Journeys to estivation sites

3. ESCAPE FROM UNSUITABLE CONDITIONS
    - A. One-way journeys across land to escape unsuitable conditions
    - B. Seasonal journeys to escape unsuitable conditions

4. DISPERSAL/ GENE FLOW
    - A. Movements of hatchlings from the nest to the water
    - B. Mate seeking by adults

5. USE OF A COMPLEX HOME RANGE
    - A. Travel between bodies of water included within the same home range
    - B. Travel to terrestrial locations (e.g. basking sites) within the home range

includes journeys to estivation sites, dispersal by adults, and terrestrial basking. In addition to the estivation reported here (Santa Rosa site), several instances of estivation have been reported previously for this species (Holland 1994). Estivation has also been observed in other species of aquatic turtle, including *Emys orbicularis* (Naulleau 1992), *Clemmys guttata* (Ernst 1982, Ward et al. 1976), and *Deirochelys reticularia* (Bennett et al. 1970, Buhlmann 1995). In all cases, the estivation was associated with the seasonal drying and/or warming of ponds. Further research might reveal this phenomenon to be widespread in western pond turtles that inhabit seasonally dry bodies of water. Dispersal by adults has not been reported *per se*, although mate searching by males could facilitate dispersal from a genetic perspective if it spans long distances. The sporadic, long-distance aquatic and terrestrial movements of males and female turtles reported here and elsewhere (e.g. Morreale et al. 1984, Gibbons 1986) may constitute dispersal.

Finally, preliminary evidence suggests that both males and females engage in behavior that amounts to terrestrial basking, in that radiative warming may be occurring (Rowe and Moll 1991). The prolonged periods of time spent on land by gravid mainstem Trinity females might be motivated by thermoregulatory benefits to themselves and their eggs (Reese and Welsh 1996). Thermoregulation also seems the most likely explanation for the brief, short-distance summer journeys by mainstem Trinity males who burrowed into leaf duff while on land. Excavation of duff burrows, sometimes referred to as "forms", has been observed in other aquatic turtles as well. These situations range from nightly occupation of burrows (e.g. *Clemmys insculpta*, Kaufmann 1992) to prolonged daily occupation (e.g. *Emydoidea blandingii*, Rowe and Moll 1991, *Clemmys guttata*, Graham 1995) to cycles of movement and burrowing for many days (e.g. *Kinosternon subrubrum*, Bennett et al. 1970). *Clemmys marmorata* individuals exhibited the whole range of behaviors, indicating that burrowing provides benefits across a variety of circumstances. It is likely not only to provide buffering from temperature extremes, but also protection from terrestrial predators. It may also prohibit dehydration by reducing water loss from the respiratory track, as in *Kinosternon flavescens* (Seidel 1978).

The most prolonged periods of terrestriality observed were associated with overwintering behavior. It is intriguing that while all Trinity River turtles left the watercourses for the winter, some Santa Rosa turtles remained in ponds and some travelled onto land. Combined with the fact that a variety of overwintering behaviors have been observed by western pond turtles elsewhere in their range, this reveals a plasticity to overwintering behavior of this species. There is evidence that western pond turtles generally use aquatic sites for overwintering in lacustrine habitats, but travel onto land in lotic habitats (Holland 1994). Thus, terrestrial overwintering may be a response to conditions of high flow. This hypothesis is supported by the results presented here and elsewhere (Goodman 1994, Rathbun et al. 1994), in that there was complete departure from the fast-flowing riverine sites. It does not explain the terrestrial overwintering of several pond-dwelling Santa Rosa turtles, especially given that two turtles inhabiting the same small pond displayed different strategies. Thus, additional finer-scale factors may influence overwintering behavior. The majority of individual turtles showed a consistent strategy from year to year, which may reflect the recurrent set of unique conditions each turtle encounters given its geographic location and home range.

It was also striking that individual turtles returned to nearly the same overwintering locations in sequential years. Given the large size of their aquatic home ranges (Table 9-9), it is unlikely that they would end up at these locations by chance; thus, site fidelity seems to be occurring. The apparent fidelity could be driven by significant habitat characteristics for which they are selecting (such as solar exposure) or by the topography of the landscape, for example drainages that funnel their movements along particular trajectories. The habitat diversity of overwintering sites, both in terms of vegetation types and physical features, belies an explanation based on selection for particular characteristics. An explanation based on landscape contours is also not supportable with the current data. Examination of overwintering points against a backdrop of topography (using GIS) revealed no pattern in the locations of points relative to creeks or elevation gradients. Continuing long-term research may reveal that, although annual adjustments are made, general overwintering positions are tied to historical factors (e.g. location of birth sites) or current constraints (e.g. location of aquatic home ranges). Additionally, with further research that increases the sample size of overwintering locales, key habitat features may emerge.

The consistency among individuals in the location of their overwintering points was not coupled with consistency in the duration of overwintering. Duration appeared, in fact, to be unrelated to distance travelled over land. However, given that the timing of all four portions of the overwintering journey was consistent across years on the mainstem Trinity River, I can infer that it was determined by some constant factor, such as day length. Within a given year, considerable variability in timing did exist among individuals.

Part of this was attributable to sex differences, with females initiating overwintering journeys earlier and consequently overwintering for longer than males. This difference may be related to some structural or physiological disparity, in that females travelled more slowly to overwintering sites than males. Another part of the variability was attributable to site differences, with turtles leaving the main channel for longer at the south fork Trinity than the mainstem Trinity. Examination of individual trajectories reveals that overwintering at the south fork was followed by prolonged visits to a pond and vernal pool prior to returning to the watercourse. Where alternative lentic habitats are available on the mainstem Trinity, they also attract turtles (Chapter 8). Thus, the relative duration of overwintering journeys on the south fork may have been exaggerated by the monitoring of a small set of turtles that happened to be in the vicinity of ponds. Ponds play an intriguing role in seasonal activities at both sites, as discussed above.

Overall, the results clarify our understanding of how western pond turtles utilize the landscape. The terrestrial environment contributes substantially to the overall home range size and provides critical habitat year-round. It is clear that protection of upland habitat during all months of the year will be essential for the survival and recovery of this species if one considers the time during which females are on land nesting, eggs and/or hatchlings are in the nest (Reese and Welsh 1996), and both sexes are on land overwintering. Western pond turtle populations face pressures similar to turtle populations in the eastern U.S., for which legal regulations do not mandate adequate buffer zones to encompass upland habitat requirements (Burke and Gibbons 1995). This study and others (Holland 1994) suggest that wetlands would have to be surrounded by protected zones of at least 500 meters to encompass all terrestrial activity of *Clemmys marmorata*. In addition, pond systems such as the one in Santa Rosa would at the least require protected corridors between adjacent ponds, and more likely require restoration of the historical connectedness of the aquatic system. The behavioral plasticity with respect to terrestrial habitat use makes the task of protection particularly challenging, in that variability occurs at all levels (across individuals, sites, seasons, and years). Appropriate management will require a site-specific strategy based on accumulated knowledge of the timing, direction, and extent of movements in the target area.

ACKNOWLEDGEMENTS

I thank the USDI Bureau of Reclamation and Fish and Wildlife Service for funding and facilitating the Trinity River portion. Numerous people deserve credit for the field work. Polly Taylor and Savannah conducted much of the mainstem Trinity River radiotelemetry with incredible dedication. Other Trinity turtle trackers include Don Ashton, Karen Danner, Jenny Glueck, Mark Gutman, Amy Lind, Josh Metz, Sara Mook, Logan Olds, Kari Sadowski, Kary Schlick, Kris Shimizu, Cindy Walker, Doug Welsh, Randy Wilson, and Adrienne Wright. Josh Metz assisted with collecting and processing ground-positioning satellite data. I am very grateful to Kelly Busse for conducting the GIS analyses and showing continual enthusiasm for the iterative process.

Thank you to the Switzer Foundation and to Lawton and Anneke Shurtleff for funding the Santa Rosa portion of the project. I am also very grateful to Greg DeNevers and the California Academy of Sciences for providing housing, materials, ideas, and assistance. Private landowners who offered their ranches for turtle telemetry deserve a special thanks for their generosity; these include Peter Lang, Jim and Karen Slusser, Lawton and Anneke Shurtleff, Douglas and Betty Clegg, California Academy of Sciences Pepperwood Ranch Natural Preserve, and the late Elson Flora. Matthew Kondratieff, Doug Welsh, and Tory Finley were instrumental in collecting data and keeping the Santa Rosa study afloat with minimal supervision. Precocious high school volunteers (including Stephanie Walley, Bart Agapinan, Alison Mackie, Marie Franc, Jason Smith, Wendy Chamberlain, and Margaret Imhof) also deserve credit as turtle trackers for an entire field season. John Rentchler and Cathy Ashley were invaluable volunteers. Jay and Liz Fial were generous to lend their work shed for attachment of turtle radios.

CHAPTER 10

DISCUSSION

The objectives of this research were to further our knowledge of western pond turtle (*Clemmys marmorata*) ecology and demographics in relation to alterations in the landscape, particularly those related to damming. The demographic analysis (Chapter 3) indicated that both mainstem and south fork Trinity River populations are sparse compared to a population in an adjacent stream (Hayfork Creek). Densities of turtles are also substantially higher in streams along the Central Coast of California (Holland, pers. comm.), and pond densities can be as high as 3700 turtles/hectare (Holland 1991). In conjunction with the evidence presented here (Chapters 4, 5, & 8) and elsewhere (Bury 1972) that western pond turtles in flowing waterways are associated with deep, low-velocity waters, it can be surmised that this species is a pool specialist. Pools provide navigable, surface-warmed waters and an accumulation of debris that potentially functions as cover, basking substrate, and material for nutrient cycling and aquatic insect production. To the degree that the Trinity River basin lacks the concentrations of resources that occur in natural ponds or smaller, very productive streams, it may never have harbored high densities of western pond turtles.

Changes in the mainstem brought about by installation of the dams, however, are likely to have further reduced habitat suitability for turtles. Direct habitat manipulation occurred when fluvial river habitat was replaced with the large lake bounded by the dams in the early 1960s (Chapter 6). Although it provides more lentic water, the low temperatures and frequent human disturbance at Lewiston Lake may render it unsuitable for turtles. Downstream of the dams, indirect changes include the replacement of shallow edgewaters with deep, swift waters, the filling of pools with fine sediments, and the elimination of seasonally flooded marshes (Hampton 1995, Petts 1984, Trinity River Restoration Program 1994). The results presented here (Chapter 5) also revealed lower habitat heterogeneity and decreased water temperatures relative to the undammed south fork, both of which can be explained by the unnatural flow regimes. The cumulative outcome of these alterations is a more homogeneous river that lacks the deep, still pools preferred by adult turtles as well as the adjacent sloughs that provide seasonally suitable habitat for both juveniles and adults (Chapters 8 & 9).

The relatively low proportion of juveniles in the lake and the downstream channel of the mainstem Trinity may be testimony to these impacts. Juveniles appear to have more specialized habitat requirements than adults. Their use of basking sites in lower flow areas than adults (Chapter 4) and their disproportionate representation in ponds adjacent to the river (Chapter 6 & 8) suggest a strong association with low-velocity and/or warm waters. This is reasonable, given the higher metabolic rates and poorer swimming abilities conferred by their small body size. Gradual conversion of the mainstem from a wide braided configuration to a trapezoidal channel over the last three decades may have decreased habitat suitability for juveniles enough to induce a biased age-structure. Because salmonid rearing habitat is also characterized by slow-flowing waters, attempts to restore salmon populations along the mainstem Trinity hold promise for western pond turtle populations. However, analysis of current restoration projects indicate that they are too shallow and exposed for juvenile turtles (Chapter 7).

Enhancement of the mainstem Trinity River with respect to pond turtles requires a long-term commitment to the restoration of natural flow regimes. Not only would that immediately improve conditions by providing suitable warm temperatures, but it would also provide the scouring action that transports sediment and maintains deep pools (USDI-BLM 1995). The recovery of natural, fluvial processes would also restore the alternation of gravel bars and riffles that characterizes the south fork Trinity and provides habitat diversity. In the absence of dam removal, which is currently prohibited by financial constraints, practical considerations, and legal mandates, other measures may be taken to enhance western pond turtle habitat. These include continued consideration of how to restore lentic edgewaters. Natural or managed enhancement of structural complexity in the current projects (e.g. through addition of treefalls) may increase their suitability for western pond turtles by generating sheltered microhabitat with more variability in depth.

The radiotelemetry results emphasized that suitable terrestrial habitat is equally essential to the viability of western pond turtle populations as suitable aquatic habitat (Chapters 8 & 9). *C. marmorata* appears to be typical of the genus *Clemmys* in being semi-terrestrial with turtles travelling onto land for a variety of functions, including nesting, overwintering, estivation, basking, and travel between multiple bodies of water within a single home range. Although site-specific variability exists in the relative frequency of different functions, the association of this species with the terrestrial landscape appears to be ubiquitous throughout its range (Chapter 9, Holland 1991, Rathbun et al. 1992, Goodman 1994).

Emys and *Emydoidea*, now postulated to be the closest genetic relatives of *C. marmorata* (Bickham et al. 1996), also exhibit a complex use of the landscape that includes terrestrial components above and beyond nesting. *Emys orbicularis* have been observed travelling from permanent water to vernal pools and back (Lebboroni and Chelazzi 1991), departing from seasonally dry streams, and aestivating on land (Naulleau 1992). *Emydoidea blandingii* make brief, daily terrestrial excursions from ponds as well as treks between ponds (Rowe and Moll 1991). Members of the Deirochelynia clade, including *Deirochelys reticularia* (Buhlmann 1995) and *Trachemys scripta* (Burke et al. 1995, Parker 1984), can also be described as semi-terrestrial. Traditional turtle census techniques (e.g. trapping), by virtue of their focus on the aquatic environment, were unlikely to detect terrestrial movements except those that terminated in another censused waterbody. Thus, *C. marmorata* were believed to be entirely aquatic (Pritchard 1979) with the exception of nesting. The application of radiotelemetry techniques has revealed a much more significant relationship of "aquatic" turtles to the terrestrial landscape.

Because there is potential for some life stage of *Clemmys marmorata* to be on land during every month of the year, all management approaches must regulate human uses of the terrestrial environment, whether they be urbanization, cattle grazing, road construction, logging operations, agriculture, or recreation. However, the difference in the nature and timing of overland movements at the Santa Rosa site, as compared to the riverine sites, illustrates the need for site-specific strategies. Whereas a high management priority at the Santa Rosa site would be the identification and protection of movement corridors between ponds, monitoring of activities that impact overwintering sites might take precedence at the Trinity River. In any case, a buffer zone approach would have to target sizeable areas (on the order of 500 meters wide) to include all western pond turtle activities. It might be equally feasible to manage from an informed perspective that is guided by knowledge of temporal and spatial movement patterns of turtles at each site. The latter approach is facilitated by site philopatry, which has been observed with regard to nesting (Holland 1991) and overwintering (Chapter 9).

Appropriate management for this species and other semi-aquatic turtles is additionally challenging because of the significance of multiple bodies of water in their life histories. Any single pond or creek, even with a terrestrial buffer zone, is not sufficient as the unit of management. Rather, a metapopulation concept (Levies 1970) applies, where groups of populations inhabiting distinct wetlands are linked by dispersal. The long-term viability of populations may require the availability of these linked sets, which together offer a variety of attributes (Burke et al. 1995). Not only does this allow for seasonal shifts to take advantage of ephemeral resources (Chapter 9), but it also promotes persistence over a larger time scale. Over time, a particular population may function as a source or a sink depending on environmental or demographic variables (Ruggiero et al. 1994), and recolonization from adjacent wetland habitats requires that linkages be intact.

Genetic considerations may also warrant maintenance of connectedness. When populations are fragmented and barriers to migration imposed, the fragments in effect become smaller populations. Given that smaller populations are more subject to the deleterious effects of inbreeding and loss of genetic variability, fragmentation can threaten persistence (Gilpin and Soule 1986). For example, DNA fingerprints from *Clemmys guttata* sampled from small bodies of water isolated by human impact were less diverse than those from a large wetland complex including multiple bodies of water (Parker and Whiteman 1993). The reduced genetic diversity of the isolated populations may ultimately limit their response when environmental conditions change. There is evidence that gene flow between populations of semi-aquatic turtles can be accomplished by aquatic or terrestrial dispersal (*Trachemys scripta*, Scribner et al. 1986); however, populations separated by terrestrial habitat showed higher genetic distance than those separated by aquatic habitat. It follows that fragmentation of the landscape can be deleterious to semi-aquatic turtles, particularly when aquatic habitat is partitioned (e.g. creating agricultural ponds from creeks), but also when terrestrial habitat within a movement corridor is altered. Efforts to maintain and/or recover western pond turtle populations must encompass maintenance of systems of waterways and the metapopulations they support.

From this perspective, the relationship of western pond turtles to the landscape is both exciting and disturbing. Having persisted in California for millions of years, this species clearly has characteristics that equip it to deal with radical alterations. These characteristics include generalist habitat requirements, amphibious traits, high adult survivorship, behavioral plasticity, and vagility. While behavioral plasticity and generalist requirements may enable it to remain in changing or unpredictable environments, its capabilities to move across the landscape confer abilities to seek alternative, more suitable environments. Indeed, there is evidence that these capabilities were responsible for it being the only aquatic turtle that colonized California after the droughts of the Oligocene and Miocene (Hutchison 1982). Amphibious traits may also allow individuals to "wait out" periods of aquatic unsuitability by estivating on land or periods of terrestrial unsuitability by remaining in the water. Finally, high adult survivorship maintains a pools of potential breeders in the face of temporary recruitment failures.

Clearly, local extinctions of western pond turtles must have occurred prior to human arrival in response to natural "catastrophes', such as fires, droughts, or geologic events. Given the evidence that survival of metapopulations over time depends upon recolonization of local extinction sites via dispersal (Fahrig and Merriam 1994, Harrison et al. 1988, Ruggiero et al. 1994, Thomas 1994), populations of *Clemmys marmorata* must have persisted in particular regions via recolonization and shifts to adjacent, unimpacted habitats. Historical records indicate that this species was extremely abundant in California prior to European settlement (Smith 1895). The precipitous declines in the last century can be explained not only by impacts of greater magnitude (such as commercial harvest), but also by the loss of connectivity in the aquatic and terrestrial landscape. Recovery plans should focus on removing direct sources of mortality, boosting recruitment, and restoring the interconnected but fluctuating mosaic of suitable habitats.

LITERATURE CITED

Auth, D. L. 1975. Behavioral ecology of basking in the yellow-bellied turtle *Chrysemys scripta scripta* (Schoeff). Bull. Florida State Mus. Biol. Sci. 21:1-45.

Baldwin, J. 1995. U.S. Forest Service, Pacific Southwest Forest and Range Experiment Station, 800 Buchanan Street, Albany, CA 94710.

Barinaga, M. 1990. Where have all the froggies gone? Science 247:1033-1034.

Begon, M., J. L. Harper, and C. R. Townsend. 1986. Ecology: Individuals, Populations, and Communities. Sinauer Associates, Inc., Massachusetts.

Bennett, D. H., J. W. Gibbons, and J. C. Franson. 1970. Terrestrial activity in aquatic turtles. Ecology 51:738-740.

Bickman, J. W., T. Lamb, P. Minx, and J. C. Patton. 1996. Molecular systematics of the genus *Clemmys* and the intergeneric relationships of emydid turtles. Herpetologica 52:89-97.

Blaustein, A. R., D. B. Wake, and W. P. Sousa. 1994. Amphibian declines: Judging stability, persistence, and susceptibility of populations to local and global extinction. Conserv. Biol. 8:60-71.

Boyer, D. R. 1965. Ecology of the basking habit in turtles. Ecology 46:99-118.

Brattstrom, B. H. 1965. Body temperatures of reptiles. Amer. Midl. Nat. 73:376-422.

Brattstrom, B. H. 1988. Habitat destruction in California with special reference to *Clemmys marmorata*: a perspective. *In* H. F. Delisle, P. R. Brown, B. Kaufman, and B. M. McGurty (eds.), Proceedings of a Conference on California Herpetology, pp. 13-24. Southwestern Herpetologists Society, Special Publication (4).

Brewster, K. N. and C. M. Brewster. 1991. Movement and microhabitat use by juvenile wood turtles introduced into a riparian habitat. J. Herpetol. 25:379-382.

Brown, G. P., C. A. Bishop, and R. J. Brooks. 1994. Growth rate, reproductive output, and temperature selection of snapping turtles in habitats of different productivities. J. Herpetol. 28:405-410.

Buhlmann, K. A. 1995. Habitat use, terrestrial movements, and conservation of the turtle, *Deirochelys reticularia* in Virginia. J. Herpetol. 29:173-181.

Buhlmann, K. A. and M. R. Vaughan. 1991. Ecology of the turtle *Pseudemys concinna* in the New River, West Virginia. J. Herpetol. 25:72-78.

Burke, V. J. and J. W. Gibbons. 1995. Terrestrial buffer zones and wetland conservation: A case study of freshwater turtles in a Carolina Bay. Conserv. Biol. 9:1365-1369.

Burke, V. J., J. L. Greene, and J. W. Gibbons. 1995. The effect of sample size and study duration on metapopulation estimates for slider turtles (*Trachemys scripta*). Herpetologica 51:451-456.

Burnham, K. P., D. R. Anderson, G. C. White, C. Brownie, and K. H. Pollock. 1987. Design and analysis methods for fish survival experiments based on release-recapture. American Fisheries Society Monograph 5. Bethesda, Maryland.

Bury, R.B. 1995. USDI National Biological Survey, EPA Environmental Research Lab, Corvallis, Oregon 97333.

Bury, R. B. 1972. Habits and home range of the Pacific pond turtle (*Clemmys marmorata*) in a stream community. Unpubl. Ph.D. Dissertation. Univ. Calif. Berkeley. 205 pp.

Butler, B. O. and T. E. Graham. 1995. Early post-emergent behavior and habitat selection in hatchling Blanding's turtles, *Emydoidea blandingii,* in Massachusetts. Chelonian Conserv. Biol. 1:187-196.

Cagle, F. R. 1939. A system of marking turtles for future identification. Copeia 1939:170-172.

Cagle, F. R. 1944. Home range, homing behavior, and migration in turtles. Misc. Publ. Mus. Zool. Univ. Michigan, No. 61. 37 pp.

California Department of Water Resources. 1982. South Fork Trinity River salmonid habitat enhancement studies. Report to Calif. Department of Fish and Game, Sacramento. 175 pp.

California State Lands Commission. 1993. California's rivers: a public trust report. Prepared for the California State Lands Commission. 334 pp.

Chase, J. D., K. R. Dixon, and J. E. Gates, D. Jacobs, and G. J. Taylor. 1989. Habitat characteristics, population size, and home range of the bog turtle, *Clemmys muhlenbergii,* in Maryland. J. Herpetol. 23:356-362.

Clark, W. B. 1992. Gold Districts of California. California Division of Mines and Geology, Sacramento, California, Bulletin 193. 186 pp.

Congdon, J. D., S. W. Gotte, and R. W. McDiarmid. 1992. Ontogenetic changes in habitat use by juvenile turtles, *Chelydra serpentina* and *Chrysemys picta.* Can. Field Natur. 106:241-248.

Congdon, J. D., A. E Dunham, and R. C. van Loben Sels. 1993. Delayed sexual maturity and demographics of Blanding's turtles (*Emydoidea blandingii*): Implications for conservation and management of long-lived organisms. Conserv. Biol. 7:826-833.

Costanza, M. C. and A. A. Afifi. 1979. Comparison of stopping rules in forward discriminant analysis. Jour. Amer. Stat. Assoc. 74:777-785.

Darroch, J. N. 1959. The multiple recapture census: II. Estimation when there is immigration or death. Biometrika 46:336-351.

Dodd, C. K. J. 1990. Effects of habitat fragmentation on a stream-dwelling species, the flattened musk turtle *Stemotherus depressus.* Biol. Conserv. 54:33-45.

Dunning, J. B., Jr., R. Borgella, Jr., K. Clements, and G. K. Meffe. 1995. Patch isolation, corridor effects, and colonization by a resident sparrow in a managed pine woodland. Conserv. Biol. 9:542-550.

Ernst, C. H. 1971. Growth of the painted turtle, *Chrysemys picta,* in southeastern Pennsylvania. Herpetologica 27:135-141.

Ernst, C. H. 1982. Environmental temperatures and activities in wild spotted turtles, *Clemmys guttata.* J. Herpetol. 16:112-120.

Ernst, C. H. 1986. Environmental temperatures and activities in the wood turtle, *Clemmys insculpta.* J. Herpetol. 20:222-229.

Evans, J. F. 1980. Evaluation of riparian vegetation encroachment - Trinity River, California. Trinity River Basin and Fish and Wildlife Task Force Report, Order No. 0520-R5-78 (USDA Forest Service). 57 pp.

Ewert, M. A. 1976. Nests, nesting and aerial basking of *Macroclemys* under natural conditions, and comparisons with *Chelydra* (Testudines: Chelydridae). Herpetologica 32:150-156.

Fahrig, L. And G. Merriam. 1994. Conservation of fragmented populations. Conserv. Biol. 8:50-59.

Farrell, R. F. and T. E. Graham 1991. Ecological notes on the turtle *Clemmys insculpta* in northwestern New Jersey. J. Herpetol. 25:1-9.

Federal Register. 1993. Volume 58 No 153, page 42717.

Ferner, J. W. 1979. A review of marking techniques for reptiles and amphibians. Society for the study of amphibians and reptiles, Herpetological Circular No.9. 41 pp.

Flint, R. F. 1957. Glacial and Pleistocene Geology. Wiley, New York.

Frazer, N. B., J. W. Gibbons, and J. L. Greene. 1990. Life tables of a slider turtle population. *In* J. W. Gibbons (ed.), Life History and Ecology of the Slider Turtle, pp. 183-200. Smithsonian Institution Press, Washington, D.C.

Frazer, N. B., J. L. Green, and J. W. Gibbons. 1993. Temporal variation in growth rate and age at maturity of male painted turtles, *Chrysemys picta*. Amer. Midl. Nat. 130:314-324.

Gibbons, J. W. 1970. Terrestrial activity and populations dynamics of aquatic turtles. Amer. Mid. Nat. 83:404-414.

Gibbons, J. W. 1986. Movement patterns among turtle populations: Applicability to management of the desert tortoise. Herpetologica 42:104-113.

Gibbons, J. W. 1987. Why do turtles live so long? Bioscience 37:262-269.

Gibbons, J. W., J. L. Greene, and J. D. Congdon. 1990. Temporal and spatial movement patterns of sliders and other turtles. *In* J. W. Gibbons (ed.), Life History and Ecology of the Slider Turtle, pp. 201-215. Smithsonian Institution Press, Washington, D.C.

Gilpin, M. W. and M. E. Soule. 1986. Minimum viable populations: processes of species extinction, p.19-34 *In*: Conservation biology-the science of scarcity and diversity. M. E. Soule (ed.). Sinauer Associates, Sunderland, Massachusetts.

Goodman, R. H. 1994. Report on the biology of the southwestern pond turtle (*Clemmys marmorata pallida*) in the Chino Hills State Park. Report, prepared for the California Department of Parks and Recreation. 81 pp.

Graham, T. E. 1995. Habitat use and population parameters of the spotted turtle, *Clemmys guttata*, a species of special concern in Massachusetts. Chelonian Conservation and Biology 1:207-214.

Hammer, D. A. 1969. Parameters of a marsh snapping turtle population. LaCreek Refuge, South Dakota. J.Wildl. Manage. 33:995-1005.

Hammond, K. A., J. R. Spotila, and E. A. Standora. 1988. Basking behavior of the turtle *Pseudemys scripta:* Effects of digestive state, acclimation, temperature, sex and season. Physiol. Zool. 61:69-77.

Hampton, M. A. 1995. Current status of fish habitat. *In* R. L. Ridenhour (ed.), Proceedings from Trinity River Restoration Program Colloquium, American Fisheries Society. Weaverville, California, 9 March 1995.

Harrison, S., D. D. Murphy, and P. R. Ehrlich. 1988. Distribution of the Bay checkerspot butterfly, *Euphydryas editha bayensis:* Evidence for a metapopulation model. Amer. Nat. 132:360-382.

Hart, D. R. 1983. Dietary and habitat shift with size of red-eared turtles (*Pseudemys scripta*) in a southern Louisiana population. Herpetologica 39:285-290.

Hay, O. P. 1908. The Fossil Turtles of North America. Carnegie Institute of Washington, Washington, D.C.

Heede, B. H. and J. N. Rinne. 1990. Hydrodynamic and fluvial morphologic processes: Implications for fisheries management and research. North American Journal of Fisheries Management 10:249-268.

Hines, J. E. 1990. JOLLY program for running capture-recapture models. USDI National Biological Service, Patuxent Environmental Science Center, Laurel, Maryland.

Holland, D. C. Camp Pendleton Amphibian and Reptile Survey, 334A East Fallbrook, Fallbrook, CA 92028.

Holland, D. C. 1985. An ecological and quantitative study of the western pond turtle (*Clemmys marmorata*) in San Luis Obispo County, California. Unpubl. M.A. Thesis, California State Univ., Fresno.

Holland, D. C. 1991. A synopsis of the ecology and current status of the western pond turtle (*Clemmys marmorata*) in 1991. Report to USDI Fish and Wildlife Service, National Ecology Research Center, San Simeon, California. 141 pp.

Holland, D. C. 1992. Level and pattern in morphological variation: A phylogeographic study of the western pond turtle (*Clemmys marmorata*). Unpubl. PhD Dissertation, Univ. of Southwestern Louisiana, Lafayette.

Holland, D. C. 1994. Final report on the western pond turtle project. Report, prepared for Wildlife Diversity Division, Oregon Department of Fish and Wildlife, Portland.

Holland, D. C., Hayes, M. P. and Jennings, M. R. 1992. Petition to list the California red-legged frog (*Rana aurora draytonii*) and western pond turtle (*Clemmys marmorata*). Federal Register Vol.57 (193), October 5, 1992.

Hutchison, J. H. 1982. Turtle, crocodilian, and champsosaur diversity changes in the Cenozoic of the north-central region of western United States. Palaeogeography, Palaeoclimtology, Palaeoecology 37:149-164.

Jain, S. K. (ed.) 1976. Vernal pools: their conservation and ecology. Univ. California Davis, Inst. Ecol. Publ. 9:1-93.

Janzen, F. J., G. L. Paukstis, and E. D. Brodie III. 1992. Observations on basking behavior of hatchling turtles in the wild. J. Herpetol. 26:217-219.

Jennings, M. R. and M. P. Hayes. 1994. Amphibian and reptile species of special concern in California. Report to California Department of Fish and Game, Rancho Cordova.

Johnston, R. F., P. W. Frank, and C. D. Michener. 1990. Multivariate analysis in ecology and systematics: panacea or pandora's box. Ann. Rev. Ecol. Syst. 21:129-66.

Jones, R. L. 1995. Population size and growth in the turtle *Graptemys oculifera*. Journal of Herpetology 29:426-436.

Jolly, G. M. 1965. Explicit estimates for capture-recapture data with both death and immigration-stochastic model. Biometrika 52:225-247.

Kaufmann, J. H. 1992. Habitat use by wood turtles in central Pennsylvania. J. Herpetol. 26:315-321.

Kepenis, V. and J. J. McManus. 1974. Bioenergetics of young painted turtles, *Chrysemys picta*. Comp. Biochem Physiol. 48A:309-317.

Kofron, C. P. And A. A. Schreiber. 1985. Ecology of two endangered aquatic turtles in Missouri: *Kinosternon flavescens* and *Emydoidea blandingii*. J. Herpetol. 19:27-40.

Lebberoni, M. and G. Chelazzi. 1991. Activity patterns of *Emys orbicularis* L. (Chelonia Emydidae) in central Italy. Ethology, Ecology & Evolution 3:257-268.

Lebreton, J. D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: A unified approach within case studies. Ecological Monographs 62:67-118.

Leslie, P. H., D. Chitty, and H. Chitty. 1953. The estimation of population parameters from data obtained by means of the capture-recapture method: III. An example of the practical applications of the method. Biometrika 40:147-169.

Lefevre, K. and R. J. Brooks. 1995. Effects of sex and body size on basking behavior in a northern population of the painted turtle, *Chrysemys picta.* Herpetologica 51:217-224.

Levins, R. 1968. Evolution in changing environments.Princeton University Press, Princeton, New Jersey.

Levins, R. 1970. Extinction. *In* Some Mathematical Questions in Biology, pp. 76-107. American Mathematical Society, Providence, Rhode Island.

Lind, A. J., R. A. Wilson, and H. H. Welsh, Jr. 1992. Distribution and habitat associations of the willow flycatcher, western pond turtle, and foothill yellow-legged frog on the main fork Trinity River. Interim report to Trinity River Restoration Project, USDI Bureau of Reclamation and Fish and Wildlife Service, Weaverville, California. 45 pp.

Lind, A. J., D. A. Reese, and H. H. Welsh, Jr. 1995. An assessment of habitat quality of man-made side channels and bank feathering projects for the western pond turtle and foothill yellow-legged frog. Final Report to Trinity River Restoration Project, USDI Bureau of Reclamation and Fish and Wildlife Service, Weaverville, California. 21 pp.

Lord, J. M. and D. A. Norton. 1990. Scale and the spatial concept of fragmentation. Conserv. Biol. 4:197-202.

Lovich, J. E. 1988. Geographic variation in the seasonal activity cycle of spotted turtles, *Clemmys guttata.* J. Herpetol. 22:482-4.85.

Marlow, R. W. and K. Tollestrup. 1982. Mining and exploitation of natural mineral deposits by the desert tortoise, *Gopherus agassizii.* Anim. Behav. 30:475-478

Mayer, K. E. and W. F. Laudenslayer, Jr. (eds.). 1988. A guide to wildlife habitats of California. Calif. Department of Forestry and Fire Protection. Sacramento. 166 pp.

McCain, M., D. Fuller, L. Decker, C. Overton. 1990. Stream habitat classification and inventory procedures for northern California. Fish Habitat Relationships Tech. Bulletin 1. U.S. Forest Service Six Rivers National Forest, Eureka. 15 pp.

Metz, J. 1995. Course project for Introduction to Geographic Information Systems, Level 1, Humboldt State University, Arcata, California.

Moll, E. O. and J. M. Legler. 1971. The life history of a neotropical slider turtle, *Pseudemys scripta* (Schoepff) in Panama. Natural History Museum, Los Angeles County Science Bulletin 11:1-102.

Morreale, S. J., J. W. Gibbons, and J. D. Congdon. 1984. Significance of activity and movement in the yellow-bellied slider turtle (*Pseudemys scripta*). Can. J. Zool. 62:1038-1042.

Moyle, P. B. 1973. Effects of introduced bullfrogs, *Rana catesbiana,* on the native frogs of the San Joaquin Valley, California. Copeia 1:18-22.

Muegel, L. A. and D. L. Claussen. 1994. Effects of slope on voluntary locomotor performance in the turtle, *Terrapene carolina carolina*. J. Herpetol. 28:6-11.

Naulleau, G. 1992. Study of terrestrial activity and aestivation in Emys *orbicularis* (Reptilia: Chelonia) using telemetry. *In* Z. Korsos and I. Kiss (eds.), Proc. Sixth Ord. Gen. Meet. S. E. H., Budapest 1991, pp. 343-346.

Nichols, J. 1995. USDI National Biological Service, Patuxent Environmental Science Center, Laurel, MD. Personal communication in September, 1995.

Obbard, M. E. and R. J. Brooks. 1979. Factors affecting basking in a northern population of the common snapping turtle, *Chelydra serpentina.* Can. J. Zool. 57:435-440.

Pacific Watershed Associates. 1994. Action Plan for Restoration of the South Fork Trinity River Watershed and its Fisheries. U.S. Bureau of Reclamation and Trinity River Task Force, Weaverville, California. 277 pp.

Pappas, M. J. and B. J. Brecke. 1992. Habitat selection of juvenile Blanding's turles, *Emydoidea blandingii.* J. Herpetol. 26:233-234.

Parker, W. S. 1984. Immigration and dispersal of slider turtles (*Pseudemys scripta*) in Mississippi farm ponds: Amer. Midl. Nat. 112:280-293.

Parker, P. G. and H. H. Whiteman. 1993. Genetic diversity in fragmented populations of *Clemmys guttata* and *Chrysemys picta marginata* as shown by DNA fingerprinting. Copeia 3:841-846.

Pechmann, J. H. K., D. E. Scott, R. D. Semlitsch, J. P. Caldwell, L. J. Vitt, and W. Gibbons. 1991. Declining amphibian populations: the problem of separating human impacts from natural populations. Science 253:892-895.

Petts, G. E. 1984. Impounded Rivers: Perspectives for Ecological Management. John Wiley & Sons, New York.

Phillips, K. 1990. Where have all the frogs and toads gone? Bioscience 40:422-424.

Pimm, S. L., H. L. Jones, and J. Diamond. 1988. On the risk of extinction. Amer. Nat. 132:757-785.

Pluto, T. G. and E. D. Bellis. 1986. Habitat utilization by a turtle, *Graptemys geographica,* along a river. J. Herpetol. 20:22-31.

Pollock, K. H. 1981. Capture-recapture models allowing for age-dependent survival and capture rates. Biometrics 37:521-529.

Pollock, K. H., J. D. Nichols, C. Brownie, and J. E. Hines. 1990. Statistical inference for capture-recapture experiments. Wildlife Monographs 107, supplement to J. Wildl. Manage. 54(1).

Pollock, K. H. 1974. The assumption of equal catchability of animals in tag-recapture experiments. PhD Thesis, Cornell Univ., Ithaca, New York. 82pp.

Preston, R. 1981. Vanishing Landscapes: Land and Life in the Tulare Lake Basin. Univ. Calif. Press, Berkeley, California.

Rathbun, G. B., N. Seipel and D. Holland. 1992. Nesting behavior and movements of western pond turtles, *Clemmys marmorata*. S.W. Natural. 37:319-324.

Rathbun, G. B., M. R. Jennings, T. G. Murphey, and N. R. Siepel. 1993. Status and ecology of sensitive aquatic vertebrates in lower San Simeon and Pico Creeks, San Luis Obispo County, California. Report to California Department of Parks and Recreation, San Simeon Region. 103 pp.

Reese, D. A. and H. H. Welsh. 1996. Use of terrestrial habitat by western pond turtles, *Clemmys marmorata*: implications for management. *In* J. Van Abbema (ed.), Proceedings: Conservation, Restoration and Management of Tortoises and Turtles-An International Conference. July 1993, Purchase, New York, WCS Turtle Recovery Program and the New York Turtle and Tortoise Society. In press.

Reese, D. A., H. H. Welsh, and C. Roberts. 1994. Examination of turtle populations in Lewiston Lake. Interim Report. Prepared for Wildlife Task Group, Trinity River Restoration Project, Weaverville, California.

Rencher, A. C. 1992. Interpretation of canonical discriminant functions, canonical variates, and principal components. Amer. Stat. 46:217-225.

Rowe, J. W. and E. O. Moll. 1991. A radiotelemetric study of activity and movements of the Blanding's turtle (*Emydoidea blandingi*) in northeastern Illinois. J. Herpetol. 25:178-185.

Ruggiero, L. F., G. D. Hayward, and J. R. Squires. 1994. Viability analysis in biological evaluations: Concepts of population viability analysis, biological population, and ecological scale. Conserv. Biol. 8:364-372.

SAS. 1990. SAS Institute, Inc., SAS/STAT User's Guide, Version 6, Fourth Edition, Volume 1, Cary, NC: SAS Institute Inc., 1989. 943 pp.

Savitz, J., P. Fish, and R. Wassail. 1983. Effects of forage on home-range size of largemouth bass. Trans. Amer. Fish. Soc. 112:772-776.

Schneider, B. 1977. Where the Grizzly Walks. Mountain Press, Missoula, MT.

Schubauer, J. P., J. W. Gibbons, and J. R. Spotila. 1990. Home range and movement patterns of slider turtles inhabiting Par Pond. *In* J. W. Gibbons (ed.), Life History and Ecology of the Slider Turtle, pp. 201-215. Smithsonian Institution Press, Washington, D.C.

Schwarzkopf, L. and R. J. Brooks. 1985. Application of operative environmental temperatures to analysis of basking behavior in *Chrysemys picta.* Herpetologica 41:206-212.

Scribner, K. T., J. E. Evans, S. J. Morreale, M. H. Smith, and J. W. Gibbons. 1986. Genetic divergence among populations of the yellow-bellied slider turtle (*Pseudemys scripta*) separated by aquatic and terrestrial habitats. Copeia 3:691-700:

Seber, G. A. F. 1965. A note on the multiple-recapture census. Biometrika 52: 49-259.

Seidel, M. E. 1978. Terrestrial dormancy in the turtle *Kinosternon flavescens:* respiratory metabolism and dehydration. Comp. Biochem. Physiol. A. 61:1-4.

Sexton, O. J. 1959. Spatial and temporal movements of a population of the painted turtle, *Chrysemys picta marginata* (Agassiz). Ecol. Monogr. 29:113-140.

Silverman, B. W. 1986. Density Estimation for Statistics and Data Analysis. Chapman and Hall, New York. 175 pp.

Smith, H. M. 1895. Notes on a reconnoissance of the fisheries of the Pacific coast of the United States in 1884. Bull. U.S. Fish Comet. 14:223-288.

Sokal, R. R. and F. J. Rolph. 1981. Biometry. W.H. Freeman and Co., San Francisco, California. 895 pp.

Spotila, J. R. and D. M. Gates. 1975. Body size, insulation and optimum body temperatures of homeotherms. *In* D. M. Gates and R. B. Schmerl (eds.), Perspectives on Biophysical Ecology, pp. 291-301. Springer-Verlag, New York.

Stebbins, R. C. 1985. Field Guide to Western Reptiles and Amphibians. Houghton Mifflin Co., Boston, Massachusetts. 279 pp.

Stevens, J. 1986. Applied Multivariate Statistics for the Social Sciences. Lawrence Erlbaum Associates, New Jersey. 515 pp.

Storer, T. M. 1930. Notes on the range and life-history of the Pacific fresh-water turtle, *Clemmys marmorata*. Univ. Calif. Publ. Zool. 32:429-441.

Strang, C. A. 1983. Spatial and temporal activity patterns in two terrestrial turtles. J. Herpetol. 17:43-47.

Thomas, C. D. 1994. Extinction, colonization, and matapopulations: Environmental tracking by rare species. Conserv. Biol. 8:373-378.

Titus, K., J. A. Moser, and B. K. Williams. 1984. Chance-corrected classification for use in discriminant analysis: Ecological applications. Amer. Midl. Nat. 111:1-7.

Toft, C. A. 1991. Reply to Seaman and Jaeger: an appeal to common sense, In: points of view: a controversy in statistical ecology. Herpetologica 46:357-361.

Trinity River Restoration Program 1994. Restoration of the Mainstem Trinity River, Background Report. USDI Fish and Wildlife Service, Trinity River Fishery Field Office, Weaverville, California. 14pp.

USDA Forest Service. 1992. Final environmental impact statement on management of the South Fork of the Trinity Wild and Scenic River. Hayfork, California. 101 pp.

USDI Bureau of Land Management. 1995. Watershed Analysis of the Mainstem Trinity River. Report compiled by USDI Bureau of Land Management, Redding Resource Area, California.

USDI Bureau of Reclamation, Mid-Pacific Region. 1992. Long-term Central Valley Project operations criteria and plan CVP-OCAP, October 1992.

USDI Fish and Wildlife Service and Trinity County Department of Transportation. 1992. Draft Environmental Assessment and Environmental Impact Report for Anadromous Fish Habitat Improvement Plan for the Trinity River. Trinity River Restoration Program, California. November.

USDI Fish and Wildlife Service. 1995. Data from Trinity River Flow Evaluation, California, water years 1942-1946, 1959-1961, 1964-1983, 1987-1992. Lewiston guaging station, mainstem Trinity River, Trinity County.

Wake, D. B. 1991. Declining amphibian populations. Science 253:860.

Ward, F. P., C. J. Hohmann, J. F. Ulrich, and S. E. Hill. 1976. Seasonal microhabitat selections of spotted turtles (*Clemmys guttata*) in Maryland elucidated by radioisotope tracking. Herpetologica 32:60-64.

Washington Department of Wildlife. 1993. Status of the western pond turtle in Washington. Report to Wash. Dept. Wildlife, Olympia.

Western, D. 1991. Biology and conservation: Making the relevant connection. Conserv. Biol. 5:431-433.

White, G. C., D. R. Anderson, K. P. Burnham, and D. L. Otis. 1982. Capture-recapture and removal methods for sampling closed populations. United States Department of Energy, Los Alamos National Laboratory Publication LA-8787-NERP.

Williams, G. P. and M. G. Wolman. 1984. Downstream effects of dams on alluvial rivers. U.S.D.I. Geological Survey Professional Paper 1286.

Wilson, R. A., A. J. Lind, and H. H. Welsh. 1991. Trinity River Riparian Wildlife Survey -1990. Final Report to Trinity River Restoration Project, USDI Bureau of Reclamation and Fish and Wildlife Service, Weaverville, California. 98 pp.

Wilson, R. A. 1993. Trinity River riparian vegetation mapping - G.I.S. Final Report to USDI Bureau of Reclamation and Fish and Wildlife Service, Weaverville, California. 62 pp.

Wyman, R. L. 1990. What's happening to the amphibians? Conserv. Biol. 4:350-352.

Zar, J. H. 1984. Biostatistical Analysis. Prentice-Hall Inc., Englewood Cliffs, New Jersey.

Zedler, P. H. 1987. The ecology of southern California vernal pools: a community profile. U.S. Fish and Wildlife Service Biological Report 85:1-136.

Zug, G. R. 1991. Age Determination in Reptiles. Society for the Study of Amphibians and Reptiles, Herpetological Circular No. 20.