# EFFECTIVE SAMPLING AND DETECTING BIOGEOGRAPHIC TRENDS OF THE PAINTED TURTLE, *CHRYSEMYS PICTA*.

by

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## Abstract

Nearly half of the world's turtle species are endangered or threatened with extinction. Conservation efforts need effective sampling programs that provide high quality life history and population parameters on which to base management decisions. These parameters vary from one population to the next, as well as across a species' geographic range, and local variation can be high. In this thesis, I investigate conventional trapping methodologies and examine potential biogeographical trends in body size and degree of sexual dimorphism in the painted turtle, *Chrysemys picta*. Painted turtles in the Okanagan valley of British Columbia, Canada, are nationally listed as Special Concern. Using hoop nets, basking traps, and dip nets, I sampled 13 ponds representing the range of occupied habitats in the valley. My results demonstrate that combining all three trap methods resulted in the highest recapture rates and more precise population estimates than single trap methods alone. Overall, hatchlings and juveniles were best caught by dip netting, and hoop traps performed the worst for adults of both sexes. Capture success of each trap method was not consistent across ponds, and each trap method performed poorly in at least one pond, pointing to the need to combine trap methods to get the most representative sample possible. My thesis research strongly suggests that combining conventional turtle trapping methods in a sampling program can provide stronger inference than a single method alone. I assessed the average body size and the degree of sexual size dimorphism for the turtles at each pond. Painted turtles in the Okanagan are bigger than their southern conspecifics, supporting Bergmann's rule which asserts an inverse relationship between temperature and body size. There was no trend between latitude and degree of dimorphism. My work shows that local variation in biogeographic analyses suggests previously published biogeographic trends for *C. picta* may not be accurate. More research on the causes of local variation in size and growth rate will be valuable in the efforts to protect this and other turtle species in British Columbia.

# Preface

I am responsible for the research contained in this thesis. The studies were designed by me, and field work was done with the assistance of Alexis Friesen, Natasha Lukey, and Andreas Wins-Purdy. I completed the data analyses and writing under the guidance of my supervisor, Dr. Karen Hodges, and my supervisory committee, Dr. Jason Pither, Dr. Michael Russello, and Dr. Christine Bishop.

The data presented in this thesis were collected according to the animal care protocol of the University of British Columbia Research Ethics Board (Animal Care Certificate #A09-0052) and sampling permit PE09-52052 from the British Columbia Ministry of Environment.

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## Dedication

*To Julia Jane,*
*because you can,*
*even when you think you can't.*

## Chapter 1: Introduction

Turtles around the world are in peril. Nearly half (48%) of the 320 recognized turtle species on the globe are threatened with extinction (IUCN 2013). Twelve turtle species occur in Canada, all at the northern edges of their ranges. Of these 12 species, six are listed as Threatened or Endangered by the Committee on the Status of Endangered Wildlife in Canada (Kiester and Olson 2011). Blanding's turtle, *Emydoidea blandingii*, the spotted turtle, *Clemmys guttata*, and the western painted turtle (Pacific coast population), *Chrysemys picta*, are federally listed as Endangered. The eastern musk turtle, *Sternotherus odoratus*, wood turtle, *Glyptemys insculpta*, and the spiny soft-shell turtle, *Apalone spinifera,* are listed as Threatened by COSEWIC (Kiester and Olson 2011).

Overexploitation and habitat loss are the two biggest threats to turtle populations (Gibbons et al. 2000, Kiester and Olson 2011). Commercial turtle harvesting for food, traditional medicines, and exotic pet trade has increased dramatically, both in Asia and North America (Kiester and Olson 2011). Habitat loss has left terrestrial and freshwater turtle ranges fragmented, isolating populations and increasing the risk of local extinctions, even for widespread species (Gardner et al. 2007, Kiester and Olson 2011). Expanding road networks contribute to fragmentation and are a source of direct mortality for dispersing and nesting turtles (Gibbs and Shriver 2002). Road mortality reduces adult survival and can disproportionately affect females, skewing a population's sex ratio toward males (Steen and Gibbs 2004). Population stability in turtles depends on high adult survival, as the long life span, delayed maturity, and naturally low juvenile survival make it difficult for populations to absorb additional adult mortalities (Brooks 1991, Congdon 1993).

Management of turtle populations is becoming increasingly necessary for the conservation of rare species, but also to keep common species common. Population monitoring is an essential component of management, both to determine the status of a species or population and to evaluate whether management has been effective. Parameters of interest include population abundance, density, age and sex ratios, and the dynamic processes that affect them: recruitment, mortality, and movement between populations (Williams et al. 2002). These parameters are required to identify and explain patterns in population dynamics—and importantly, whether the population is declining, stable, or increasing

(Lettink and Armstrong 2003). The quality of estimates relies on capturing a representative sample of individuals in a population (Bluett 2011), which can be extremely difficult when time and funds are limited, as is often the case in wildlife management. High quality data are especially important for threatened and endangered species, where direct management may be required.

Most turtle sampling is done with mark-recapture techniques. For semi-aquatic species, captures usually involve one or a combination of three conventional trapping methods: basking traps, hoop nets, and dip netting. Good data can be hard to obtain using these methods, however, as low and variable rates of capture are common in turtle studies (Bluett 2011). If an insufficient number of turtles are sampled, or the captures are sex or size-biased, population estimates will be incorrect and could lead to inaction or ill-advised interventions. Few studies have quantified capture rates and the biases inherent in the conventional trap methods (Frazer et al. 1990, Gamble 2006), yet this information is important for managers to reduce the biases and to interpret their sampling data accurately.

Another challenge in management of species is that the parameters required to inform population models differ from one population to the next. The basic biology of a species, including life history traits such as body size, age at maturity, growth rate, and clutch size can vary considerably across a geographic range (Moll 1973, Brown et al. 1994). This variation in life history may be genetically determined, or can represent plastic responses to abiotic and biotic conditions. Regardless of the source, variation in life history parameters can be key to the adaptation and survival of species, especially in the face of global biodiversity declines and a changing climate.

Describing the distribution, abundance, and life history of species across their geographic ranges has been a classical pursuit since the beginnings of ecology as a discipline (Kubisch et al. 2014). A first step in understanding range biology is to document the variation and seek patterns of co-variation with environmental factors (St. Clair et al. 1994). Biologists have sought large-scale patterns in variation since the mid-19th century, especially for variation in body size, and a number of biogeographic "rules" have been described (Conover and Present 1990, McLain 1993, Eweleit and Reinhold 2014). Probably the most famous is Bergmann's rule, which describes a negative relationship between temperature and body size, often using latitude as a proxy for temperature. According to Bergmann's rule,

individuals at the northern edge of their range should be bigger than individuals at the southern edge of their range (Blackburn et al. 1999).

Bergmann's rule has been supported for endotherms, and more recently, researchers are finding similar patterns in ectothermic taxa (Blanckenhorn and Demont 2004, Eweleit and Reinhold 2014, Hassall et al. 2014), including reptiles (Ashton and Feldman 2003). Some evidence for Bergmann's rule has been found in turtle species (Ashton and Feldman 2003, Litzgus and Smith 2010). Overall, though, the extension of Bergmann's rule to ectotherms remains controversial (Adams and Church 2008, Meiri 2011) and seems to largely ignore the role of local variation in these broader trends. Local conditions, including the size of drainage basins and food availability, have also been correlated with clines in basic biological traits like size and age at maturity (Iverson 1985, Iverson and Smith 1993, Brown et al. 1994). Any investigation into broad-scale clinal variation in life-history traits should also take into account local variation.

## 1.1  Sampling methods and biogeographic trends in the painted turtle

The painted turtle, *Chrysemys picta*, is an ideal species for addressing sampling techniques and investigating biogeographical patterns and local variation in life-history characteristics. The painted turtle is a semi-aquatic species, using lakes, ponds, or slow-moving water bodies for foraging, mating, and hibernation (Samson 2003). Female painted turtles grow to larger sizes than males and take longer to mature (Iverson and Smith 1993, Samson 2003). Females move up to 300 m into the surrounding upland habitats for nesting (Steen and Gibbs 2004). Painted turtles also require some degree of connectivity between habitats, with connected ponds serving as drought refugia and sources of genetic variation (Samson 2003, Steen and Gibbs 2004).

The painted turtle has been well-studied across its large range, allowing biogeographical comparisons. The painted turtle is widespread across the United States, with the northern edge of its range extending into Canada, and isolated southern populations in Mexico (COSEWIC 2006). Four subspecies of painted turtle have been described (Ernst and Lovich 2009): the western painted turtle, *C. p. bellii*, occurs from north-western Canada through the southwestern United States with isolated populations in Mexico; the midland painted turtle, *C. p. marginata*, occurs in south-central Canada and the central United States;

the eastern painted turtle, *C. p. picta*, lives along the Atlantic coast of the United States, and the southern painted turtle, *C. p. dorsalis*, lives in the south-central United States. The genus, which contains only the four described morphotypes, is currently undergoing taxonomic revisions due to recent genetic work—potentially elevating *Chrysemys dorsalis* to species status (Crother 2012, Jensen et al. in press). All subspecies, including *C. p. dorsalis*, interbreed along their range edges, and variation in life-history traits is more tied to local conditions than to subspecific status (Lindeman 1997). Although common throughout much of its range, some peripheral populations of *C. picta* are now at-risk of extinction (COSEWIC 2006).

British Columbia is home to two of these at-risk peripheral populations. The Committee on the Status of Endangered Wildlife in Canada identified three separate Designatable Units based on their concept of faunal provinces (COSEWIC 2006). The coastal population is listed as Endangered, and turtles in the Okanagan valley of south-central B.C. are a part of the Intermountain-Rocky Mountain Designatable Unit, which is listed as Special Concern. At the time of the COSEWIC assessment, there were no data available on population sizes or trends for the Intermountain-Rocky Mountain populations, and the conservation designation was made on the best anecdotal evidence at the time, which suggested populations in the southern interior of British Columbia were small and likely declining (COSEWIC 2006).

Population declines of the western painted turtle in the Okanagan valley were likely driven by the destruction and degradation of their wetland habitats. Human settlement in the Okanagan continues to expand, putting pressure on the remaining wetland environments, increasing road densities and generalist predators (COSEWIC 2006), and further fragmenting the landscape. Recent initiatives by the provincial and local governments and local conservation collaboratives include regional biodiversity strategies that have identified wetland conservation as a priority and have called for more research on threatened species such as the painted turtles. The lack of baseline data on turtles for the Okanagan, however, makes both research and conservation difficult. At the commencement of this thesis, there had been no studies in the Okanagan of painted turtles that quantified population structures or basic life history traits.

**1.2    Thesis objectives**

My primary goals in this thesis were to investigate conventional trapping methodology and examine potential biogeographic trends in *Chrysemys picta*, by sampling populations near the north-western edge of their range, in the Okanagan valley of south-central British Columbia, Canada.  In Chapter Two, my primary objective was to quantify potential bias in three common trap methods and examine whether estimates are improved by combining multiple trap types in a sampling program.  I used mark-recapture to estimate bias and assess the value of data from each method.  I used a multi-state model to determine the importance of combining more than one trap type during a study, and I make recommendations on the best methods to use in future turtle surveys.  In Chapter 3, my primary objective was to investigate biogeographical trends in body size and sexual dimorphism of *C. picta;* I was particularly interested in comparing local variation to range-wide variation.  In Chapter 4, I summarize my findings and draw conclusions on effective monitoring for *C. picta* and the need to understand local and global variation as the basis for conservation decisions.

# Chapter 2: Can useful demographic data be collected with conventional trap methods for *Chrysemys picta*?

## 2.1 Background and objectives

The distribution of individuals in a population over space and time is of interest to ecologists and wildlife managers alike. Parameters of interest include population abundance, density, age, sex, and the dynamic processes that affect them: recruitment, mortality, and movement between populations (Williams et al. 2002). These parameters are required to identify and explain patterns in population dynamics—and importantly, whether the population is declining, stable, or increasing (Lettink and Armstrong 2003). Mark-recapture models have been used to estimate wildlife population parameters since the 1920's (Lettink and Armstrong 2003) and range from the simple Lincoln-Petersen model designed for short sampling periods with closed populations to much more complex models used in comprehensive long-term studies of open populations. Estimates from all models rely on capturing and recapturing a representative sample of individuals in a population (Bluett 2011), which can be extremely difficult when time and funds are limited, as is often the case in ecology and wildlife management. The need for high quality data is especially important when dealing with species-at-risk, where it is important to identify concerning population trends early.

Turtles are a taxon in decline, with the IUCN classifying 47% of 331 described turtle species as Vulnerable, Endangered, or Critically Endangered (van Dijk et al. 2012). For semi-aquatic turtle species, declines are due largely to land-use changes and habitat destruction (Gibbons et al. 2000), and even turtle species that were once quite common are becoming at-risk and in need of population monitoring. Population density, however, is not likely to be a good indicator of population stability in turtles. Turtles are long-lived, with temperature-dependent sex determination, high mortality rates for eggs and juveniles, and low adult mortality rates (Griffin 2007). Without high quality demographic data, there could be significant time lags between the start of a population decline and our ability to detect it if the increased mortality occurs in hard-to-detect age classes (Samson 2003). Good data can be hard to obtain, however, as low and variable rates of capture are common in turtle studies (Bluett 2011). Population sizes, sex-ratios, age structures, and stage-specific mortality rates

would be of great value to any monitoring program.  If not enough turtles are captured, however, or the traps used capture certain groups preferentially, inferences from these data might be misleading (Lindeman 1990, Koper and Brooks 1998, Gamble 2006).  When more turtles are caught and marked because trap efficiency and capture rates are increased, the precision of the data improves (Seber 1982), and accuracy is improved when capture bias is reduced (Ream and Ream 1966, Bluett 2011).

Common capture methods for freshwater turtles include baited hoop nets, baited and non-baited basking traps, and dip nets.  Capture results for each type of trap are biased by behavioural differences among turtles, and between size classes and sexes (Cagle and Chaney 1950, Frazer et al. 1990, Gamble 2006).  Females may be more attracted to basking traps as they have higher energetic demands due to larger body size and egg production (Lefevre and Brooks 1995, Carrière et al. 2008).  Hatchling and juveniles often elude the hoop nets and basking traps that are successful with adults (Sexton 1959, Ream and Ream 1966, Congdon 1993, Forstner et al. 2013).  The first turtle to enter a hoop net may affect the rest of the trap's catch, as a female caught in the trap might attract significantly more males than other females, particularly in the breeding season (Cagle and Chaney 1950, Frazer et al. 1990), although other researchers have failed to find support for this hypothesis (Vogt 1979, Forstner et al. 2013).  Alternatively, differential rates of escape from hoop nets could skew the sex ratio, so that approximately equal numbers of females and males enter the trap, but if females are more likely to escape they would leave behind a male-biased catch in the trap (Frazer et al. 1990, Brown et al. 2011).  The type and freshness of bait used in traps also affects the resulting catch, with turtles preferring canned bait with jelly-like fluids over fresh bait (Voorhees et al. 1991).

The degree of bias inherent in turtle capture methods and the effect it has on subsequent data inferences have been poorly quantified.  If a trap catches more females than males, for example, is it a result of trap bias, or because there are more females than males in the population?  One of the central assumptions of mark recapture analyses is that every animal has an equal probability of capture, but this assumption is probably violated in most wild populations (Carothers 1971, Seber 1982, Chao 1987, Koper and Brooks 1998).  To truly determine the trap bias and its effect on population estimates, researchers would have to compare the true parameters for a pond to those suggested by the trap results.  Obtaining true

population parameters in a natural, open system, is near impossible (Bluett 2011), although some long-term study designs might come close. Brooks and Koper (1998) compared capture results from several short sampling periods to the population size of adult midland painted turtles, *Chrysemys picta marginata*, in a pond at a long-term study site in Algonquin Park, Ontario, Canada—as all resident adult turtles have been marked since 1990, the authors were confident in their assessment of population size. They found that even when they applied a series of analytical and statistical techniques thought to improve accuracy, only four of the 79 estimates were within 10% of the known population size, with almost all of the estimates underestimating the population size. Although the very short sample periods (two days) and the exclusion of juveniles in the study may have resulted in some of the disparity seen between the sampling data and the presumed population size, it is clear that some bias exists. The question becomes how can researchers and managers minimize bias in turtle studies?

This study focuses on several populations of the western painted turtle, *Chrysemys picta bellii*. The western painted turtle's range extends across the southern border region of Canada from western Ontario to the coast of British Columbia, and extends south through Missouri, northern Oklahoma, eastern Colorado, Wyoming, Idaho, and northern Idaho, with a few isolated populations reported in the southwestern United States and Mexico (Fritz and Havas 2007). The study's focal area, the southwestern region of British Columbia, is nearing the north-western edge of *C. picta bellii*'s range, where the populations are considered at-risk by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2006). There is some debate, however, as to appropriate conservation units for the species (Jensen et al. 2014). Human settlement in the area has resulted in large losses of the natural ecosystems, and most of the wetland habitat favoured by the semi-aquatic western painted turtle is gone (COSEWIC 2006, Lea 2008). *Chrysemys picta* is a semi-aquatic species, dependent on lakes, ponds, or slow-moving water bodies for foraging, mating, and hibernation, as well as upland habitats for nesting (Samson 2003, Steen and Gibbs 2004). In addition to suitable nesting habitats, painted turtles require some connectivity between habitats, with connected ponds serving as drought refugia and sources of genetic variation. At the beginning of this work, no data on fine-scale population structures or sizes existed for the region.

In general, as the sampling effort increases, the quantity and quality of data increases

(Jackson et al. 2008). Conventional turtle trapping wisdom stems from Ream and Ream (1966), who assert bias is inherent in all trap techniques and recommend using multiple trap types and combining the data to minimize bias. Using multiple trap types simultaneously would, in theory, capture a wider sample of the population, assuming that traps were biased in different ways. It might also help negate trap shy responses as animals caught initially in one trap type would not have been exposed to other trap types, thus potentially increasing recapture rates. Few studies have tested either Ream and Ream's assertion of trap bias or the wisdom of combining multiple trap types, and no studies have made comparisons among capture methods across more than two ponds.

The objectives of this study were to a) evaluate performance of three common turtle capture methods, and b) assess whether combining data from multiple trap types benefits a study design by providing the most representative samples. I used mark-recapture methods to assess the efficacy of three common trap methods: hoop nets, basking traps, and dip netting for western painted turtles, *C. p. bellii*, in southern British Columbia, Canada. Since the true population parameters are not known, I cannot assess the degree of bias inherent in a capture method, but by pooling data from 13 different populations, and comparing among trap types, I assess the value of each trap type for capturing different age classes and sexes. Using multi-state modelling to determine transition probabilities, I characterized turtle movement between each trap type to determine whether using multiple trap types increases the likelihood of recapture, which would increase the confidence in mark-recapture estimates. I hypothesize that the age classes and sexes respond differently to each trap type, and that the number of both captures and recaptures are increased by using multiple trap types. I predict that: 1) juveniles and hatchlings will be most often caught in dip nets, since they cannot swim as fast as adults (and are thus easier to dip net) and might be put off by competition from bigger adults in the hoop nets and basking traps; 2) females will be most often caught in basking traps as they typically have higher energetic requirements than males and juveniles; 3) males will be most often caught in hoop nets as they may be attracted to potential mates in the traps; and 4) turtles initially caught in one type of trap will be more likely to be recaught in a different trap type than in the same type of trap again, demonstrating some negative trap response.

## 2.2    Methods

The study was conducted in the Okanagan Valley of south central British Columbia, Canada, between May and September, 2009.  The Okanagan Valley is a semi-arid region, with large lakes on the valley bottom bordered by low-sloped hills of open canopy ponderosa pine (*Pinus ponderosa*) forests, sagebrush (*Artemisia tridentata*) dominated shrub-steppe habitat, and grasslands.   Western painted turtles were trapped at 13 ponds throughout the central and southern valley, ranging in elevation from the valley bottom at 298 m to the highest elevation pond at 925 m.  Ponds ranged from urban to rural and were selected to represent the range of known turtle habitats in the South Okanagan.  Each pond was trapped for a single capture-mark-recapture session of 3-10 days.  The length of each trapping session was determined by the recapture rate—I trapped longer at sites with low recapture rates in an attempt to improve population estimates.  Trapping was done only on sunny days.  Three trapping methods were used at each pond: basking traps, hoop nets, and hand captures with dip nets.  Three hoop nets (76.2 cm diameter, 3.81 cm$^2$ mesh, Memphis Net and Twine, Tennessee, USA) were set at each pond.  Hoop nets were secured with steel posts in the vegetated shallows of the ponds and baited by dangling a pierced can of cat food inside the middle hoop.   Three basking traps were also set at each pond.  These were made of wire ramps attached to a floating PVC frame with a submerged wire basket and also baited with cat food (Sun Deck Turtle Trap, Heinson's Country Store, Texas, USA).  Basking traps were secured at areas of the pond where I observed high numbers of basking turtles.  To keep the trapped area consistent despite the wide range in pond sizes, all trapping activities were conducted within a 50 m diameter of a central point in the pond.

I also used fish landing nets from shore or canoe to scoop turtles from the open water or mud.  To keep trap effort similar across ponds, all hand captures were completed by the same people.   Basking traps and hoop nets were set the afternoon before the first day of the each trapping session.  Turtles were hand captured for the first 1.5 hours of each sampling day, starting midmorning between 09:00 and 10:00, after which the basking traps and hoop nets were emptied.

Turtles were uniquely marked after initial capture using a Dremel™ rotary tool and the shell filing system set out in Cagle (1939).  Small juveniles were marked using nail clippers rather than the rotary tool as their shells were not fully ossified (McAuliffe 1978).

Hatchlings were given unique numbers with a Sharpie marker on their plastrons and carapaces. Plastron length was measured using digital calipers. For the purposes of this analysis, I used the size classifications laid out in Griffin (2007) to assign age classes: hatchlings had plastron lengths $\leq 50$ mm, juveniles had plastrons 50-104 mm, and adults had plastrons $\geq 105$ mm. Adults were further classified as males or females according to the presence or absence of secondary sex characteristics (Frazer et al. 1993). Turtles were classified as adult males if they had a plastron $\geq 105$ mm and had noticeably elongated foreclaws and a lengthened pre-cloacal tail region, with the cloaca located beyond the edge of the carapace. If a turtle lacked the secondary sex characteristics of males, it was classified as a juvenile or as an adult female, depending on plastron size.

### 2.2.1 Analytical methods

Captures were analysed by trap method, with 95% binomial confidence intervals. Analysis of variance (ANOVA) was used to determine differences in mean plastron lengths of turtles in each trap type. The Tukey-Kramer HSD post-hoc test was used to determine significant differences among means.

A multi-state transition model was built for the turtle capture histories as a way of describing how individuals moved between trap types during the capture period. The model was built using the MSM package (V. 0.7.4 2007) for R 2.10.1 (Jackson 2007), and included four states: not caught, caught in basking trap, caught in hoop net, and caught in dip net. The model permitted transitions between any of the four states, as well as allowing turtles to remain in a state by being caught in the same trap type on the next sampling interval, or by remaining uncaught. There are thus 16 possible transitions between capture states. The data were assumed to represent the exact transition movements of the turtles, as it was extremely unlikely that a turtle would have been caught in a trap type, escaped, and then been caught in another trap type. No turtles were observed escaping during the sampling season. Initial values for the transition matrix were set to equal probability of moving between each of the states. The data were fit to the model using maximum likelihood estimates. Transition probabilities and 95% confidence intervals were calculated by bootstrapping the data. The model was run with all age and sex classes combined and then run for each class separately.

Four population estimates were calculated for each pond: one estimate using only

capture data from each single trap method and one estimate using the capture histories from all three trap methods combined. All estimates were calculated using the Lincoln-Petersen model with the Chapman correction for small sample sizes. Recapture rates were calculated for each trap method separately and using all three trap methods combined.

## 2.3    Results

A total of 1111 turtles were caught and marked (Table 2.1). Nearly half of all turtles captured were adult females. Fewer than 4% of the turtles captured were hatchlings. I recaptured 375 of the marked turtles a total of 912 times. Over 60% of all turtles in each class were captured only a single time. Likelihood of recapture was statistically similar (G=2.79, d.f.=3, P=0.425) across age and sex classes, ranging from 29.3% recaptured of adult males to 36.5% of hatchlings. Most recaptured turtles were only recaptured once (Figure 2.1). Only 7% of turtles were caught three times, and fewer still caught four or more times, a trend consistent across all age and sex classes (Figure 2.1). There were not enough turtles caught more than four times to include them in Figure 2.1—only five turtles were caught five times, a single turtle was caught six times, and no turtles were caught more than six times. Females were most likely to be caught in two different trap types and hatchlings were the least likely (Table 2.1). No hatchlings, and fewer than 2% of each of the other classes, were caught in all three trap types.

The mean size of turtles caught in dip nets was significantly smaller than for hoop nets or basking traps (Figure 2.2, $F_{2,1108}$=94.4, p<0.001). When hatchlings and juvenile are removed from the analyses, there is no significant difference between the mean size of turtles caught by each trap method.

Nearly all hatchlings were captured in dip nets (95%) (Table 2.2), with just a single hatchling captured occurring in a basking trap and two captured in hoop nets. Similar to hatchlings, the majority of juvenile captures (67%) (Table 2.2) were made in dip nets. The remaining juvenile captures were evenly split among hoop and basking traps. More females were caught in dip nets than using the other two capture methods, although the distribution among trap types is not statistically significant (G=2.29, d.f.=2, P=0.32). Significantly more males were caught in basking traps than either dip nets or hoop nets (G=11.54, d.f.=2, P=0.003).

Figure 2.3 illustrates the transition probabilities between the four states: not caught, caught in basking trap, caught in hoop net, and caught in dip net. Regardless of the initial state, turtles were most likely to be uncaptured at the next sampling interval, reflecting the low rates of recapture. Within the transitions that reflect recaptured turtles, turtles were most likely to be recaught in the same type of trap, rather than in a different trap type. For example, a turtle caught in a hoop net was six times more likely to be recaught in a hoop net than in a basking trap at the next sampling interval (Figure 2.3A). This pattern is also seen with turtles originally caught in basking traps (Figure 2.3B) and is especially pronounced when the original capture is by dip net, as turtles were ten times more likely to be recaught in a dip net than to be recaptured by either of the other methods (Figure 2.3C). Turtles not caught on one day were most likely to remain uncaught on the next day (Figure 2.3D). Turtles that were captured at time $t+1$ after being not caught at time $t$ were more likely to be caught in dip nets than in hoop or basking traps.

The pattern of being more likely to be recaught in the same trap type as the original capture holds for juveniles, males, and females, for all trap types (Figure 2.4A,E,I). Hatchlings were the exception to the trend as they were more likely to be caught and recaught in dip nets than in the other two trap types, and the small sample size of hatchlings resulted in very large confidence intervals for nearly all possible transitions. Juveniles that did transition between two different trap types were more likely to be recaught in dip nets than in the other trap types.

Figure 2.5 illustrates transition probabilities for sex and age classes of turtles that were not caught in the initial sampling interval, but were caught in the subsequent interval. Both hatchlings and juveniles were much more likely to be caught in a dip net after having not been caught, but had similar probabilities of being caught in basking traps as hoop nets. Both males and females were slightly more likely to be caught in basking traps than hoop or dip nets, after having not been caught.

Population estimates from a single trap method were poor at predicting the population estimate calculated by combining all three trap methods (Figure 2.6). Estimates calculated using only hoop net captures (Figure 2.6A) tended to be underestimates compared to the combined-method estimates, whereas the basking trap estimates and dip net estimates did not consistently overestimate or underestimate the combined estimate (Figure 2.6B,C). Each

method had at least one pond for which the single method estimate had confidence intervals 2-3 times larger than the combined estimate.

Recapture rates were highest when using the combined capture data, for all except two of the smaller ponds (Figure 2.7). Recapture rates were lowest for basking traps in five of six of the smallest ponds, whereas hoop nets had the lowest recapture rates for three of the four biggest ponds.

## 2.4    Discussion

My data demonstrate a definite benefit to combining the use of hoop nets, basking traps, and dip netting when sampling for painted turtles. Both hatchling and juvenile turtles were most often caught in dip nets, and males and females were effectively caught in all three trap types. As individual turtles seemed to repeatedly prefer one trap method over the others, combining trap methods provided a broader sample than using a single capture method alone would have. Using three capture methods together resulted in the highest recapture rates and often gave population estimates with smaller confidence intervals than estimates from captures in a single trap method only.

Hatchling captures were very rare and occurred at only 3 of 13 ponds. While I cannot be certain there are hatchlings present at the ponds where there were no hatchling captures, the cryptic nature of turtle hatchlings is well documented (Ream and Ream 1966, Mazerolle et al. 2007). Dip netting was by far the most effective trap method for hatchlings in this study, but the majority of the hatchling captures came from two ponds: one where recent shore disturbance by cattle had likely dislodged the hatchlings from the mud, and one where hatchlings were hiding at the base of emergent reeds rather than in the mud. I observed several hatchlings floating away from the shallows, and they were too small to swim against any wave action or surface currents. Since they are small enough to pass through the mesh of both hoop nets and basking traps, it is likely that the few hatchling captures in these traps were by chance. With such low capture rates, it is unlikely that good estimates of hatchling abundance could come from these capture methods. Other more specialized trap methods, such as drift fences (Todd et al. 2007) and nesting surveys (Marchand and Litvaitis 2004a, Samson et al. 2007) might provide better hatchling estimates, but these techniques are more intensive and would not provide information on the other age classes.

Juveniles were also most often caught in dip nets. They are bigger and stronger than hatchlings, so they can effectively swim and dive in open water, but they lack the speed of adult turtles and are relatively easy to catch with dip nets. Unlike hatchlings, juveniles are often seen basking and foraging, and hoop nets and basking traps were also effective. Although basking traps and hoop nets accounted for 33% of all juvenile captures, it is unlikely that good estimates of juvenile abundance and size distribution would come from these methods alone.

All three capture techniques were effective at capturing adult females, although dip netting had the highest number of captures. Counter to my predictions, basking traps were not the best trap for females, which is surprising given that females are known to bask longer and more often than males, especially during egg development (Lefevre and Brooks 1995, Krawchuk and Brooks 1998, Carrière et al. 2008). Egg development for turtles in British Columbia occurs in late spring through summer and corresponds to this study's field season (COSEWIC 2006). Also counter to my prediction, hoop nets were not the most effective method for sampling adult males, which were best caught in basking traps. Hoop nets were the least successful of all trap types for both males and females, though they accounted for 25% of captures for both males and females—surprising given the prevalent use of hoop nets in painted turtle studies. Both males and females were observed basking and actively moving within the water column, and both sexes move very quickly underwater, making open water captures difficult.

Counter to my predictions, turtles were more likely to be recaught in the same type of trap as the original capture (Figure 2.2), a trend consistent across all age and sex classes (Figure 2.3)—although overall rates of recapture were low for all groups (Figure 2.1). For the hoop nets and basking traps, which were both baited, the increased likelihood of being recaught in the same trap type could be a result of positive trap response. A positive trap response would not explain the trend for dip netting, however, as all turtles tried to avoid capture by dip net. Hatchling recapture behaviour is unique from all the other classes, as dip netting is the only viable capture technique for sampling hatchlings, and as such the only type of trap likely to recapture hatchlings as well. Only 1% each of juveniles, males, and females were caught in all three trap types, indicating that using multiple trap types should not necessarily increase the number of recaptures and therefore the precision of population

estimates made from the data.  Despite the small number of turtles caught in all three trap types, recapture rates were highest when trap methods were combined for all except two of the very smallest ponds (Figure 2.7).  Taken together, these data indicate that choosing not to use one of the three trap types would have left some turtles completely unaccounted for. This finding supports Ream and Ream (1966) in their original assertion that researchers should use multiple trap types and combine the data as it will sample more turtles and provide a broader representation of the population, potentially increasing the accuracy of estimates.

The only way to truly assess whether combining trap types would reduce bias and improve accuracy would be to compare sampling results to a population with known true values—an almost impossible feat for natural open populations.  Koper and Brooks (1998) assert that combining the three capture methods improved the estimates by increasing the capture intensity and sample size, but that doing so would not reduce the population estimate error such that it would be suitable for either management of populations or ecological research.  Their conclusion seems unnecessarily pessimistic.  All of their population size estimates were negatively biased, underestimating the total size.  From a wildlife management perspective, it would be more precautionary to use an underestimate than an overestimate—though the degree of underestimation could be important when determining conservation status.  Regardless of the population estimate, a sampling design that used all three capture methods would provide minimum numbers alive for age categories and sexes, numbers that would certainly be of value in a population survey or monitoring program. Where population estimates would be useful, my data demonstrate that combining trap types would provide the best estimate.  Each trap method had at least one pond where the single method estimate varied widely from the combined estimate, with much larger confidence intervals, indicating that a specific trap method was particularly poor at capturing and recapturing turtles for that particular pond.  Future work should investigate pond characteristics such as size and productivity that might influence the efficacy of different trap types.

Logistical challenges will also play a role in sampling design.  The prevalence of hoop nets in turtle studies (Koper and Brooks 1998, Samson 2003, Nall and Thomas 2009, Cosentino et al. 2010) is probably because they are affordable, light, and portable.  Many

hoop traps can be moved at the same time (whereas only a single basking trip will fit in the canoe at a time), they are easy to deploy, and they do not require intensive effort once the trap is set. Hoop nets must be set with part of the trap above the water so that captured turtles can breathe, restricting trap use to the shallows of the water body—leaving traps vulnerable to disturbance and vandalism. Basking traps can also be subject to disturbance when placed near shore. Basking traps are best set near existing basking spots, where turtles are used to surfacing. Unlike hoop nets, basking traps are not easily collapsible or portable and are more expensive. Once set, however, they do not require the intensive effort that dip netting requires. Dip netting was the most successful capture method, but requires significantly more person-hours, effort and skill. Unless the pond edges have enough mud and vegetation for the researchers to sneak up on resting turtles, most captures occur in open water, requiring high paddling ability and quick reflexes. Dip netting is an affordable trap method, however, requiring only nets and buckets for the captured turtles.

When designing a sampling program for painted turtles, both the information desired and the logistical challenges should be considered (Table 2.3). While this study demonstrates that using all three trap types is the optimal design because it increases turtle captures and recaptures, it may not always be feasible or necessary to do so. For previously unsampled populations, it would be best to use all three methods to obtain baseline data for the broadest sample of the population possible. In subsequent years, managers or researchers might choose to sample for specific parameters. Concern over the effect of road density and urbanization of ponds, for example, has researchers interested in the survival rates of mature females (Marchand and Litvaitis 2004b, Steen and Gibbs 2004, Aresco 2005). A sampling program to monitor the number of adult females in the population could use just hoop nets and basking traps, significantly reducing the time and effort required, while still obtaining a minimum number alive for mature females. Although adult survival rates are central to the viability of turtle populations (Congdon 1993, Heppell 1998), habitat changes around urban and semi-urban ponds are drawing attention to the importance of recruitment and juvenile survival. Early life-stage survival rates are naturally low, with reported hatchling survival rates varying widely, from 2% (Samson 2003) to 70% (Tinkle et al. 1981), though most reports are under 20% (Wilbur 1975, Mitchell 1988). Hatchling survival rates are likely population-specific and subject to stochastic processes (Samson 2003). Increased pressures

from roads and intense predation in human-dominated landscapes could eliminate recruitment entirely (Marchand and Litvaitis 2004b). Managers concerned primarily with recruitment rates could sample juveniles using only dip netting, using a combination of size and annuli to estimate age classes.

The reality is that all sampling programs are imperfect, but even short-term sampling programs using conventional methods can still provide useful data. The most informative overall picture will be provided by pooling data from all three trap types. While population estimates may be variable, especially for small populations, a minimum number alive of each sex and class can be a useful benchmark for determining population structure, and, if compared across years, population stability. Further studies on the efficacy of capture methods should focus on seasonal timing of trap efforts, compare results for lotic and lentic systems, and assess measures of pond productivity that might influence trap behaviour. By focusing on the information that capture methods can provide and how we can improve that data, researchers and managers can design efficient sampling programs that can detect concerning trends early enough to respond to them.

**Table 2.1.** Western painted turtles captured across all ponds sampled in the Okanagan Valley of southern British Columbia in 2009. Turtles were split into four age and sex categories, according to plastron lengths (PL) and absence/presence of male secondary sex characteristics (SSCs): hatchlings (PL ≤ 50 mm, SSCs absent), juveniles (PL 50-104 mm, SSCs absent), males (PL ≥ 105 mm, SSCs present), and females (PL ≥ 105 mm, SSCs absent).

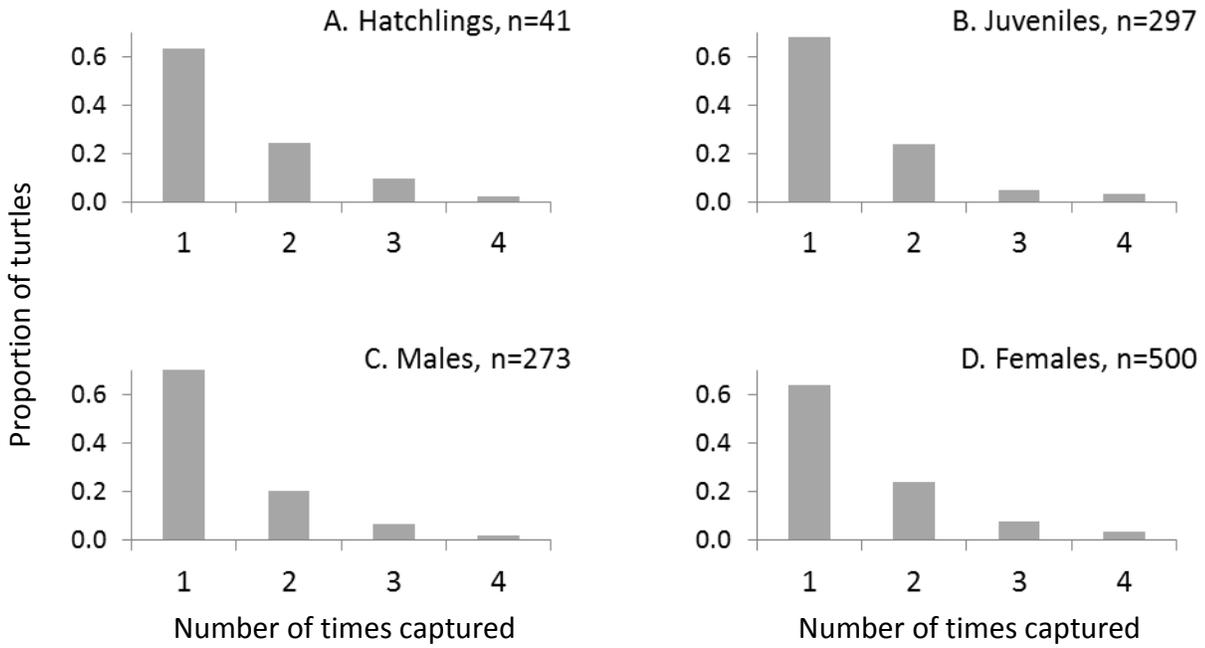| | Number of turtles | Total captures | Percentage of turtles caught more than once | Percentage of turtles caught in two trap types | Percentage of turtles caught in three trap types |
|---|---|---|---|---|---|
| Hatchlings | 41 | 62 | 36.5 | 2.4 | 0 |
| Juveniles | 297 | 429 | 32.3 | 15.4 | 1.7 |
| Males | 273 | 385 | 29.3 | 17.6 | 1.5 |
| Females | 500 | 772 | 36.0 | 22.2 | 1.4 |
| All turtles | 1111 | 1648 | 33.5 | 20.0 | 1.5 |

**Figure 2.1.** Number of recaptures of *Chrysemys picta*, by age and sex class. Results pooled all basking trap, hoop net, and dip net captures across 13 ponds sampled in the Okanagan Valley of southwestern British Columbia in 2009. Not shown are five turtles that were caught five times each, and a single turtle caught six times.
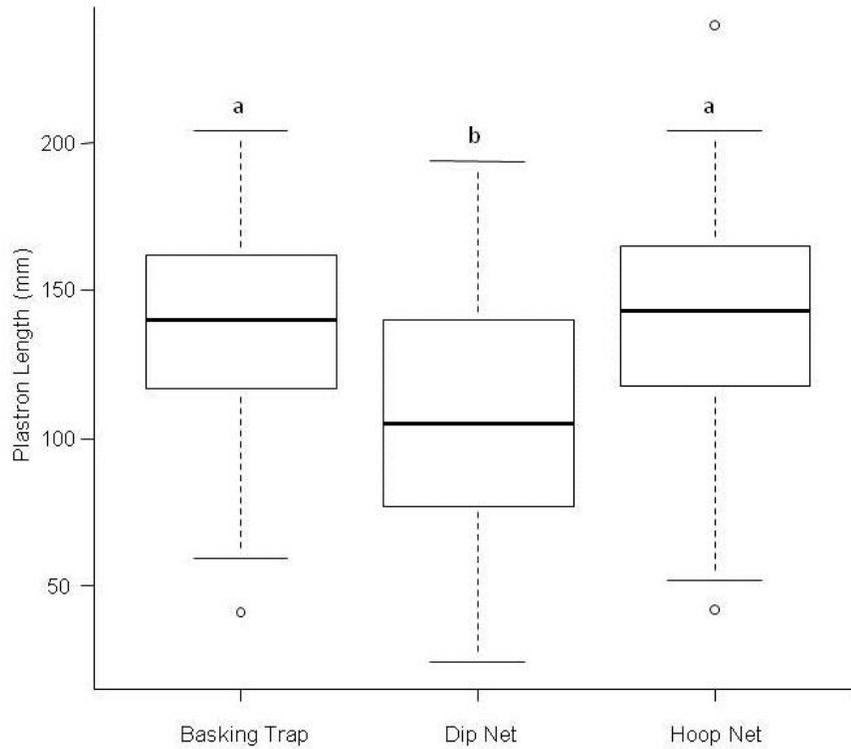
**Figure 2.2.** Plastron lengths of turtles caught initially with one of three trap types. Bolded lines indicate the median plastron length and boxes denote quartiles. Bars and whiskers represent the 10th and 90th percentiles. Hollow points indicate outliers. Trap types with different letters are significantly different (ANOVA, $F_{2,1108}$=94.4, p<0.001).

**Table 2.2.** Proportion of captures of Western painted turtles by each of the three capture methods. Upper and lower 95% binomial confidence intervals are given in parentheses. Data are pooled across 13 ponds sampled in the Okanagan Valley of southern British Columbia in 2009.

|  | **Hoop Net** | **Basking Trap** | **Dip Net** |
|---|---|---|---|
| Hatchlings | 0.03 (0.00,0.11) | 0.02 (0.00,0.09) | 0.95 (0.87,0.99) |
| Juveniles | 0.15 (0.11,0.18) | 0.18 (0.14,0.22) | 0.67 (0.63,0.71) |
| Males | 0.25 (0.21,0.30) | 0.39 (0.35,0.45) | 0.36 (0.31,0.41) |
| Females | 0.26 (0.22,0.28) | 0.32 (0.29,0.35) | 0.42 (0.39,0.46) |
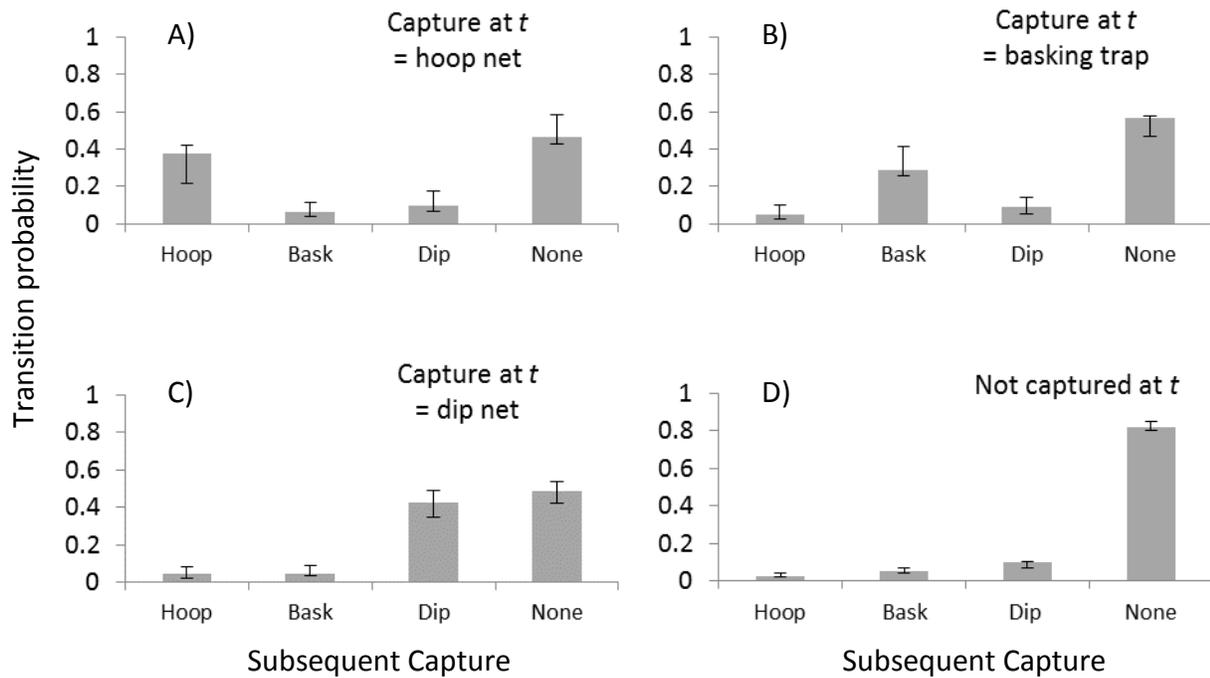
**Figure 2.3.** Transition probabilities for Western painted turtles captured across all ponds sampled in the Okanagan Valley of southwestern British Columbia. Panels represent method of capture at time $t$, and columns represent the likelihood of being caught by each method of capture at time $t+1$. Error bars are bootstrapped 95% confidence intervals. "None" indicates the turtle was not caught at time $t+1$.
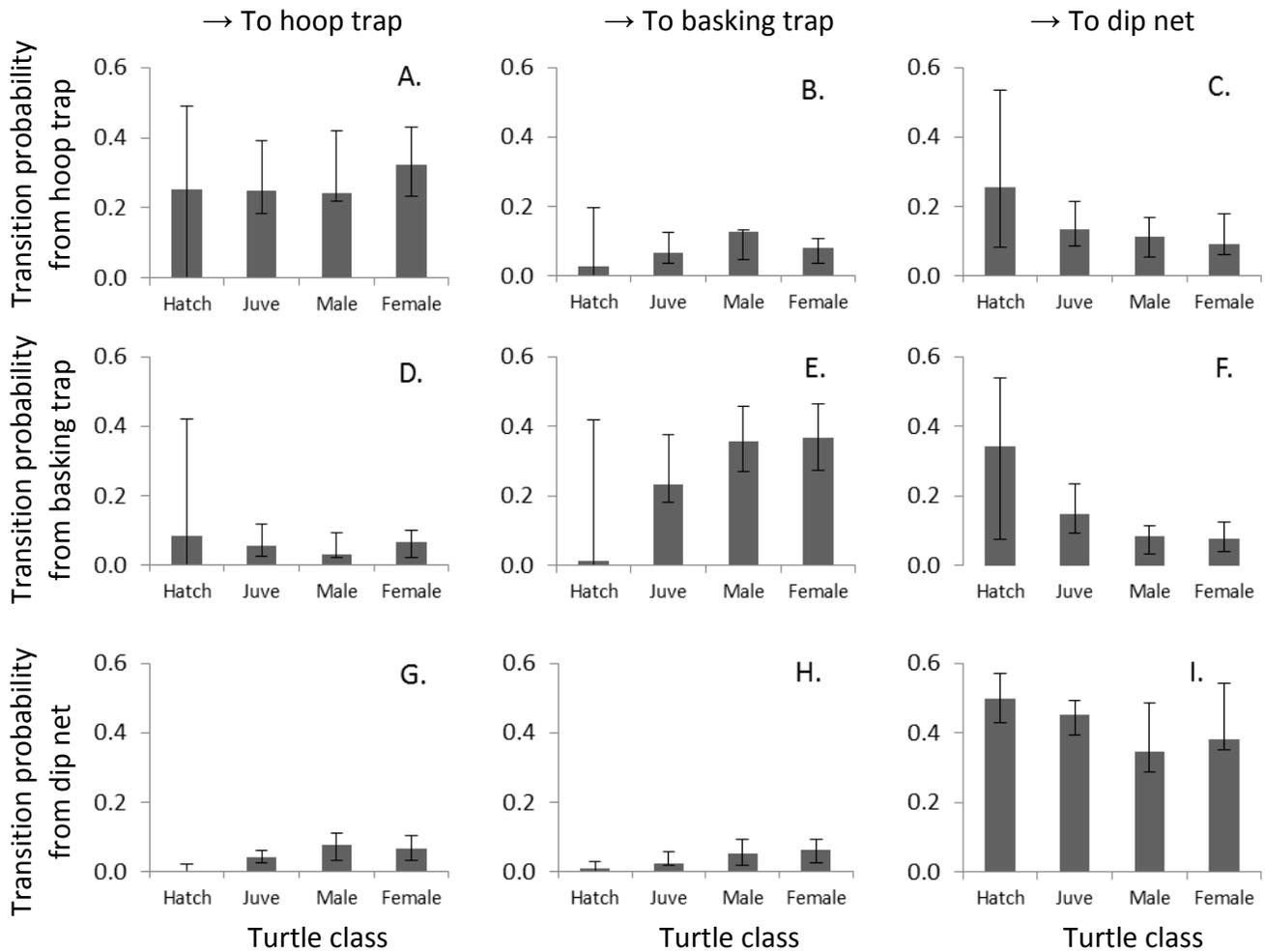
**Figure 2.4.** Transition probabilities for age and sex classes of Western painted turtles. Panels represent transitions between method of capture at time *t* and method of capture at time *t+1*. Error bars are bootstrapped 95% confidence intervals.
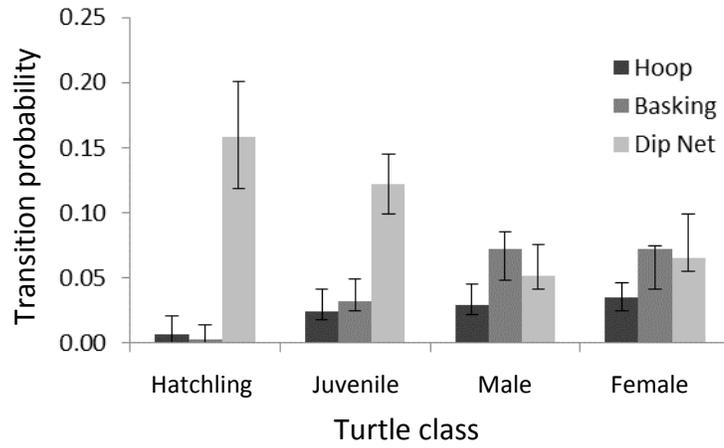
**Figure 2.5** Transition probabilities for age and sex classes of Western painted turtles not caught at time *t* to capture by each method at time *t+1*. Error bars are bootstrapped 95% confidence intervals.

a) Hoop Nets

b) Basking Traps
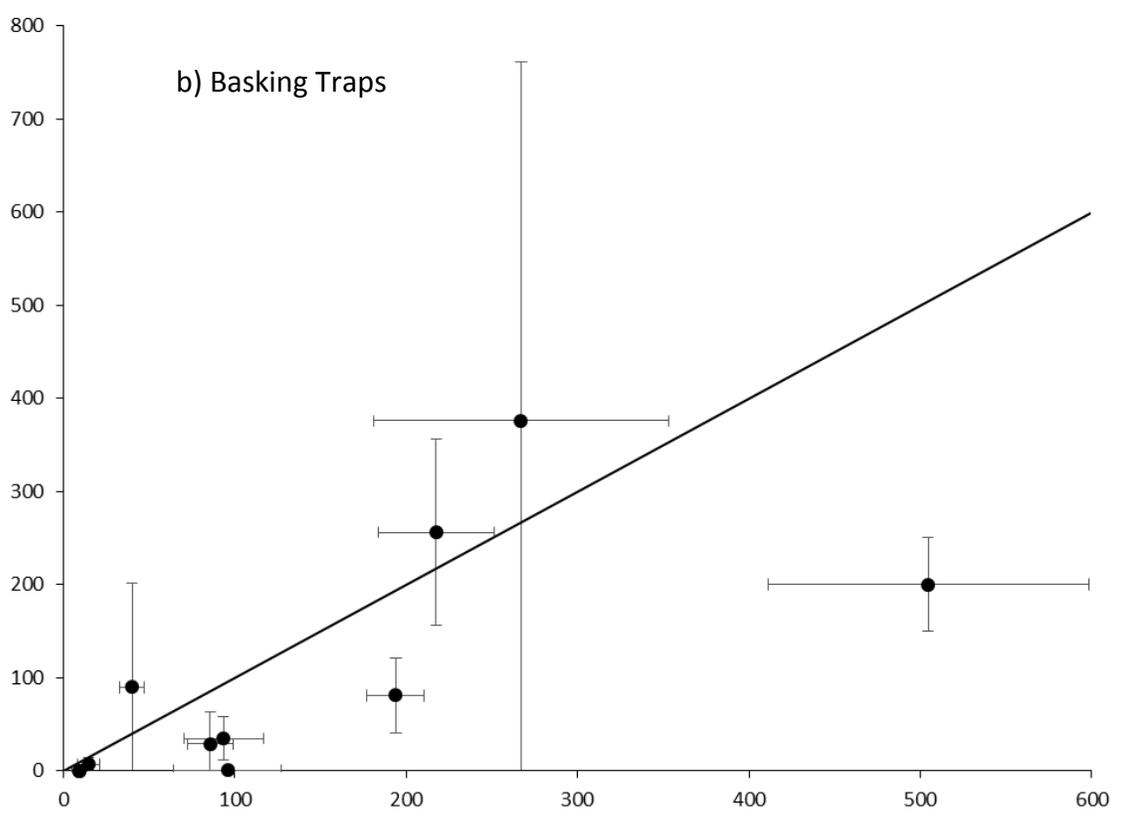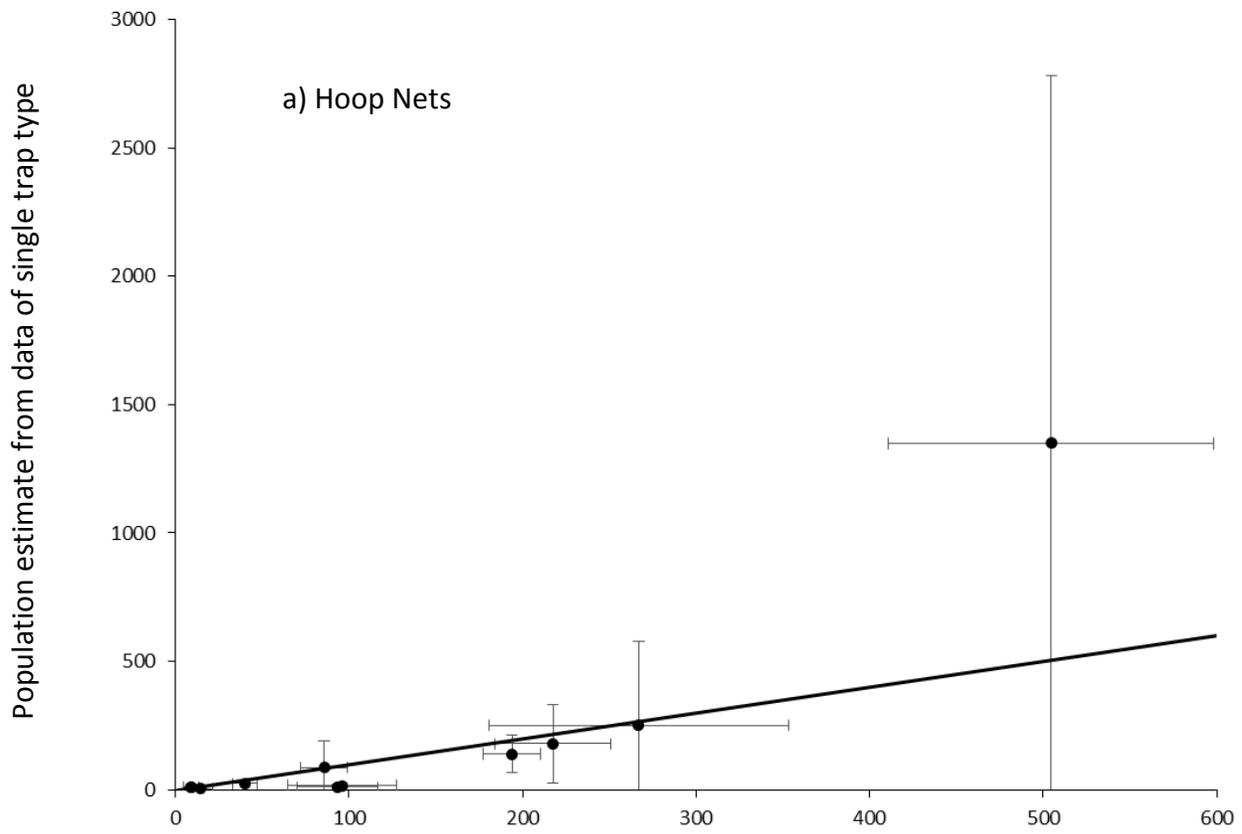
Population estimates from data of all trap types

Population estimate from data of single trap type
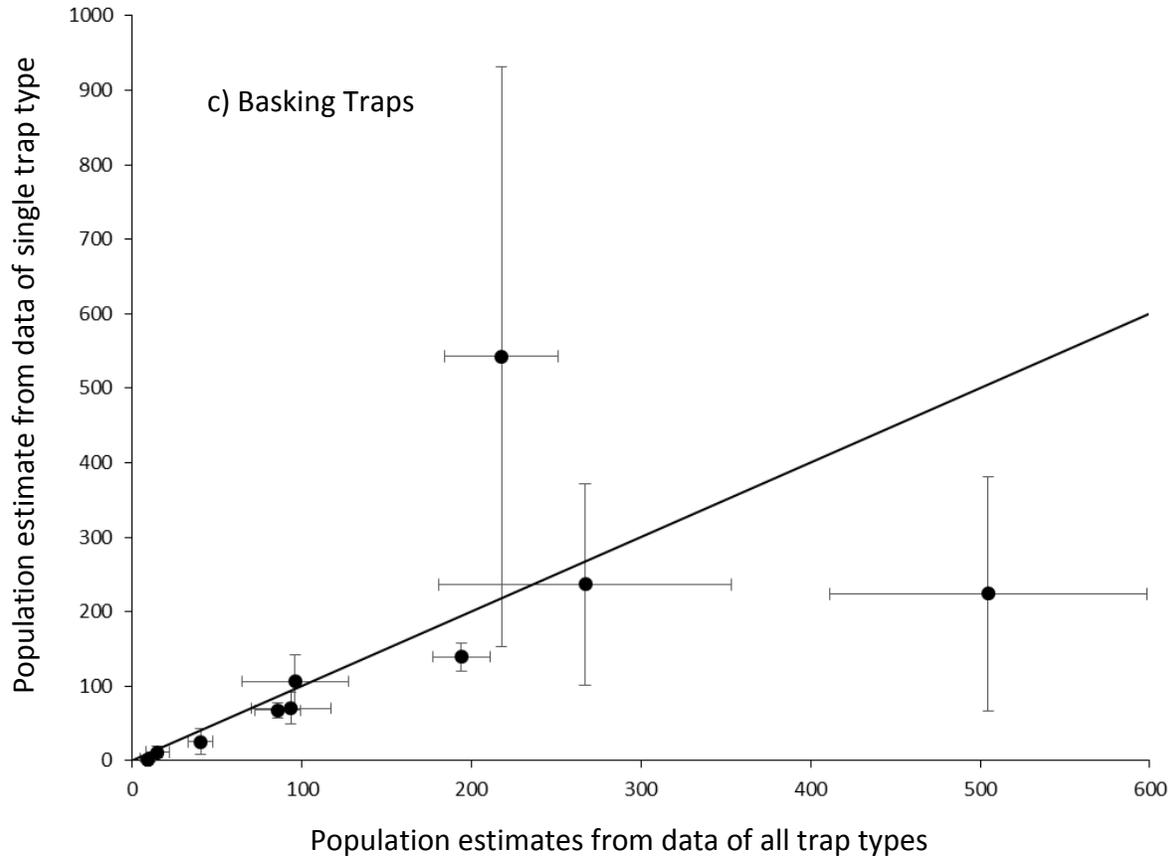
**Figure 2.6.** The pattern of mark-recapture population estimates when calculated from capture histories including only a single trap type and population estimates calculated from capture histories combining data from hoop nets (a), basking traps (b), and dip nets (c) for Western painted turtles captured at ponds sampled in the Okanagan Valley of southwestern British Columbia. All population estimates were calculated using the Lincoln-Petersen method with Chapman's correction for small sample sizes. Error bars are 95% confidence intervals. Vertical axis are scaled to include the full length of the largest error bar. The reference line shows a 1:1 linear relationship.
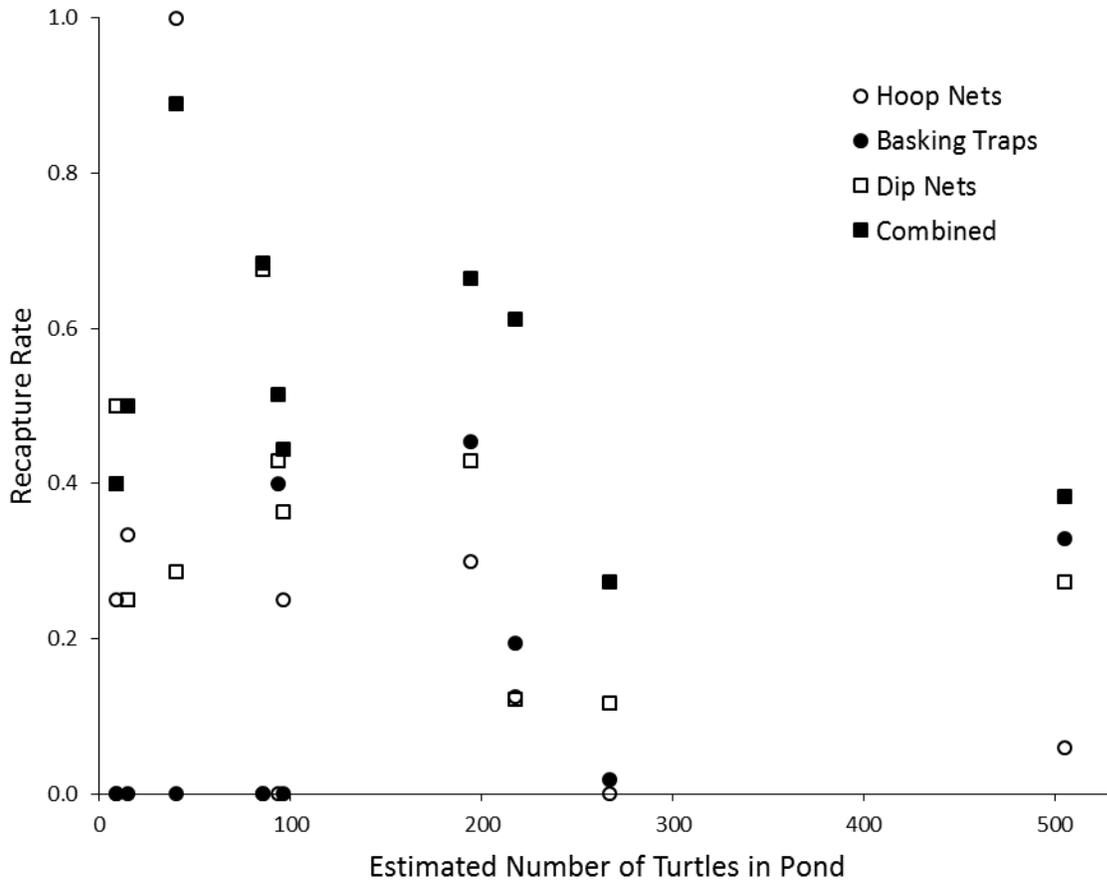
**Figure 2.7.** Recapture rates for Western painted turtles captured at ponds of various population sizes sampled in the Okanagan Valley of southwestern British Columbia. Recapture rates are the number of marked turtles caught in the second sampling period over the total number of turtles caught in the second sampling period. Population estimates were calculated using the Lincoln-Petersen method with Chapman's correction for small sample sizes and were calculated using combined capture data from hoop nets, basking traps, and dip nets.

**Table 2.3.** Summary of capture method benefits and drawbacks for Western painted turtles.

| Capture Type | Sampling Strengths | Sampling Weaknesses | Logistical Considerations |
|---|---|---|---|
| Hoop Nets | Good for adult males and females; easy to standardize catch effort | Will miss hatchlings entirely and poor for catching juveniles; only sampled 25% of adults | Must be set in accessible, shallow water; subject to vandalism; more effective with baits; must be checked daily; can get overcrowded in dense ponds; portable and easy to store; cheaper than basking traps; easy to repair |
| Basking Traps | Better than hoop nets for both males and females; easy to standardize trap effort | Will miss hatchlings entirely and poor for catching juveniles | Must be set in areas suitable for basking; not easily portable; can be secured with anchors or tied to known basking log; requires weather suitable for basking; unlikely to attract shore baskers |
| Dip Nets | Best for hatchlings, juveniles, and females | Difficult to standardize catch effort | Labour intensive; requires skilled field technicians; can be affected by clarity of water; impractical in very large ponds |

# Chapter 3: The importance of local variation and decision rules in describing biogeographic trends: Body size and sexual size dimorphism in the western painted turtle, *Chrysemys picta*.

## 3.1    Background and objectives

The formation and investigation of large scale biogeographic rules remains a popular, but contentious, pursuit (Geist 1987, Blackburn et al. 1999, Ashton 2001).  Bergmann's rule, originally proposed in 1847 to describe a negative relationship between temperature and body size in endotherms (Mayr 1956), is still debated in the literature today.  Often using latitude as a proxy for temperature, current investigations of Bergmann's rule usually centre around possible mechanisms behind the observed patterns, and detecting the trend (or converse trend) in different taxonomic groups.  While Bergmann described the patterns seen in endotherms, researchers have more recently investigated trends in body size in ectothermic taxa, including amphibians (Olalla-Tárraga and Rodríguez 2007, Adams and Church 2008), fish (Rypel 2014), insects and other arthropods (Blanckenhorn and Demont 2004, Eweleit and Reinhold 2014, Hassall et al. 2014), and reptiles (Ashton and Feldman 2003).

In sexually dimorphic taxa, where one sex is consistently larger than the other, clinal variation in body size may differ for males and females.  Sexual size dimorphism is usually explained by biologists as a result of different selective pressures on the sexes (Berry and Shine 1980).  There are three main adaptive explanations proposed for sexual dimorphism (Stephens and Wiens 2009): sexual selection that favours larger males, fecundity selection that favours larger females, and ecological divergence of the sexes because of intraspecific competition, which could explain either sex being larger (Table 3.1).  If male and female body sizes changed similarly with latitude, the degree of dimorphism would remain constant and their slopes would be parallel (Figure 3.1, A1&B1).  If the larger sex has a steeper cline (Figure 3.1, A2&B2), male and female sizes diverge and dimorphism increases with latitude. If the smaller sex has a steeper cline (Figure 3.1, A3&B3), male and female sizes converge and dimorphism decreases with latitude.

Sexual size dimorphism varies geographically in many species of mammals, birds, and reptiles (Lovich and Gibbons 1992).  The sources of this variation may result from geographically disparate selective pressures, but could also result from sampling biases,

inappropriate measures of dimorphism, or improper estimates of size at maturity. The latter is particularly important in species where it is difficult to distinguish between the sexes and identify sexual maturity. The preferred formula for the index of sexual size dimorphism, given by Lovich and Gibbons (1992), considers only mature adults and is calculated as the mean body size of larger sex/mean body size of smaller sex. The threshold size at which an animal is considered a mature adult is thus inherently important, as the inclusion of immature, smaller individuals of either sex will bias the mean body size towards a lower value than if only larger animals were included. Where dimorphism indices are compared, it is especially important that the threshold values used to calculate the average for each sex have either been standardized across studies or represent the true biology of each population.

The painted turtle, *Chrysemys picta*, is an excellent model for investigating geographic clines in life-history variation because it is relatively common and has an extensive range across North America. Four subspecies of painted turtle have been described (Ernst and Lovich 2009): the western painted turtle, *C. p. bellii*, occurs from north-western Canada through the southwestern United States with isolated populations in Mexico; the midland painted turtle, *C. p. marginata*, occurs in south-central Canada and the central United States; the eastern painted turtle, *C. p. picta*, lives along the Atlantic coast of the United States, and the southern painted turtle, *C. p. dorsalis*, lives in the south-central United States. The genus, which contains only the four described morphotypes, is currently undergoing taxonomic revisions due to recent genetic work that potentially elevates *Chrysemys dorsalis* to species status (Crother 2012, Jensen et al. 2014). All subspecies, including *C. p. dorsalis*, interbreed along their range edges, and variation in life-history traits is more tied to local conditions than to subspecific status (Lindeman 1997). All members of the *Chrysemys* genus have female-biased sexual dimorphism, with females reaching much larger sizes than males.

The genus is well-studied throughout the range, and a variety of life-history information is available for populations in at least 21 states or provinces across the United States and Canada. Several researchers have used these data to compare life-history traits across North America. Moll (1973) compared data from 5 states and found evidence for a north-south cline, with age and minimum size at maturity smallest in Louisiana populations (*C. p. dorsalis*) and greatest in Wisconsin populations (*C. p. bellii*). Ashton and Feldman

(2003) assert that *C. picta* follows Bergman's rule and increases in size with latitude, as did Lindeman (1997), although these studies were missing body size data from the north-western and southern extremes of the range.

Along with bigger body sizes, northern *C. picta* mature later at bigger sizes, and have larger clutches and lower clutch frequencies than southern conspecifics (Christiansen and Moll 1973, Iverson and Smith 1993, St. Clair et al. 1994). The patterns suggest that females in cooler, more temperate climates are under more selective pressure to increase body size in order to increase fecundity (Litzgus and Smith 2010). Males would not face this same fecundity-related pressure to increase body size, so the female body size and latitude cline should be steeper than that of the males, and the degree of dimorphism should increase with latitude. Litzgus and Smith (2010) found the opposite trend, however, showing a weak but significant negative relationship between latitude and degree of dimorphism in painted turtles. Field identification of mature females is difficult and usually based on the absence of male secondary sex characteristics in combination with a size threshold. The threshold values used to determine female maturity in the Litzgus and Smith (2010) study ranged widely between studies, from plastron lengths of 97 mm (Mitchell 1988) to 165 mm (Cooley et al. 2003), and few studies provided biological justification for the chosen threshold. Litzgus and Smith (2010) also cited the need for body size data from the north-western and southern extremes of the range.

At the commencement of my study's field component, no population-level field studies had been done in British Columbia, the north-western limit of *C. picta's* range. Additionally, no studies had examined the local variation in body sizes and degree of dimorphism for a variety of populations within a limited geographic area. Most data used in the previous analyses came from studies of a single or two ponds in the area, which were then used as representative data for the area, or sometimes the whole state. Local conditions, however, like ambient air temperatures (Brooks et al. 1992), elevation (Cooley et al. 2003), and habitat productivity (Brown et al. 1994) are important sources of variation in the life-history traits of turtles. In snapping turtles, *Chelydra serpentina serpentina*, for example, a population in Ontario, Canada, had growth rates four time higher and produced clutches nearly 30% larger than a population in a less productive habitat 280 km away (Brown et al. 1994).

In this study, I examine average body size and degree of dimorphism for 10 populations of *Chrysemys picta bellii* in the Okanagan valley of south-central British Columbia, Canada.  My objectives were to a) obtain estimates for *C. picta* body size and dimorphism in the Okanagan valley, b) use these estimates in combination with those available in the literature to see if patterns in body mass of painted turtles are consistent with Bergmann's rule, and c) quantify the local variation in these traits for a small geographic area and compare that variation to the clinal variation observed in the range-wide analysis.  I predict, based on previous analyses of painted turtle variation (Ashton and Feldman 2003, Litzgus and Smith 2010), that: 1) the average body size of male and female turtles in the Okanagan valley will be larger than that of their southern conspecifics, 2) the degree of sexual size dimorphism will be larger in the Okanagan than in southern populations to maximize fecundity via bigger body sizes, and 3) local variation in these measurements will be high.  High local variation may cast doubt on previous biogeographical analyses that used small, single studies to represent entire regions and were based on unjustified mature female size thresholds.

### 3.2    Methods
### 3.2.1    Field sampling in British Columbia

Field work was conducted in the Okanagan Valley of south central British Columbia, Canada, between May and September 2009.  The Okanagan Valley is a part of the northern range edge for *C. picta*.  The region is semi-arid, with large lakes on the valley bottom bordered by low-sloped hills of open canopy ponderosa pine (*Pinus ponderosa*) forests, shrub-steppe habitat dominated by big sagebrush (*Artemisia tridentata*), and grasslands.  I surveyed turtles at 10 ponds throughout the central and southern valley.  The elevations of ponds ranged from 385 m on the valley bottom to 924 m and ponds were selected to represent the range of rural-urban settings in which turtle populations are found in this region (Table 3.2).

Each pond was trapped for a single capture-mark-recapture session of 3-10 days.  The length of each trapping session was determined by the recapture rate—I trapped longer at sites with low recapture rates in an attempt to improve population estimates.  Trapping was done only on sunny days, and three trapping methods were used at each pond: basking traps,

hoop nets, and hand captures with dip nets.  Three hoop nets (76.2 cm diameter, 3.81 cm$^2$ mesh, Memphis Net and Twine, Tennessee, USA) were set at each pond.  Hoop nets were secured with steel posts in the vegetated shallows of the ponds and baited by dangling a pierced can of cat food inside the middle hoop.  Three basking traps (Sun Deck Turtle Trap, Heinson's Country Store, Texas, USA) were also set at each pond.  The traps were made of wire ramps attached to a floating PVC frame with a submerged wire basket that was baited with cat food.  Basking traps were secured at areas of the pond where I observed high numbers of basking turtles.  To keep the trapped area consistent despite the wide range in pond sizes, all trapping activities were conducted within a 50 m diameter of a central point in the pond. I also used fish landing nets from shore or canoe to scoop turtles from the open water or mud.

Turtles were uniquely marked after initial capture using a Dremel™ rotary tool and the shell filing system set out in Cagle (1939).  Plastron length was measured using digital calipers.  For the purposes of this analysis, male turtles were considered mature if they showed well-developed secondary sex characteristics (Frazer et al. 1993), including noticeably elongated foreclaws and a lengthened pre-cloacal tail region, with the cloaca located beyond the edge of the carapace.  I used plastron length as the measure of overall body size for all analyses.

### 3.2.2    Biogeographical analysis

I surveyed published literature for papers containing plastron length data for populations of painted turtles.  I used more conservative decision rules for inclusion in the analysis than did Litzgus and Smith (2010), who used reports of carapace length to predict plastron length and included data points from studies with sample sizes as small as two individuals for the dimorphism calculations (one male and one female).  I included data only if the authors provided the mean plastron length for adult male and adult female turtles, with at least seven turtles total sampled in the population (Table 3.3). I set the inclusion threshold to seven because that was the fewest total turtles caught in the ponds I sampled.  Sample sizes of populations reported in the literature ranged from 19-1959 adult turtles per population.  Mean sample size ± SE (median) was 126 ± 85 (44) for males, and 84 ± 50 (37) for females.  The data represent *C. picta* populations in 12 states and provinces, ranging from 35°-50°N and 76°-107°W.

I calculated the sexual size dimorphism index as described in Lovich and Gibbons (1992) (female body size/male body size). I tested for a relationship between male/female plastron lengths and latitude, and dimorphism index and latitude, using linear regression.

To assess the importance of decision criteria for the biogeographic analyses, I used two different criteria when classifying turtles as adult females. For the first analysis, I followed the criteria in Griffin (2007), and I considered turtles to be adult females if their plastron length exceeded 105 mm and they lacked secondary sex characteristics. This classification is conservative enough to exclude any males but could include both immature and mature females, since females mature at bigger sizes than males; I refer to this calculation as "all females" throughout the text. For the second analysis, I used a threshold plastron size based on work by St. Clair et al. (1994) in British Columbia, who determined the smallest size of gravid turtles in their study population to be 151 mm. This threshold is far less likely to contain immature turtles, and is referred to as the "mature female" calculation.

### 3.3    Results

### 3.3.1    Local variation in turtle size in the Okanagan Valley

In 10 ponds in south-central British Columbia, I captured 7-322 turtles per pond (Appendix A). Of these turtles, I caught 271 male turtles showing well-defined secondary sex characteristics. I caught 496 turtles with plastron lengths >105 mm and lacking secondary sexual characteristics—all of these turtles were classified as female. Of these female turtles, 289 had plastron lengths >151 mm and were considered sexually mature females (St. Clair et al. 1994). The mean plastron length was 121.8±2.4 mm for males (median=119.9, n=271), 151.5±2.7 mm for all females (median=152.8, n=497), and 170.5±2.2 mm for mature females (median=171.1, n=289). The mean male plastron length differed significantly from the mean plastron length of females when all females were included (t=10.92, p<0.001), as well as from the mature females (t=15.79, p<0.001). Sexual dimorphism indices for individual Okanagan populations ranged from 1.15-1.40 when all females were included in the calculations, and from 1.30-1.61 when only mature females were considered. The mean sexual size dimorphism calculated from all females and mature females were significantly different (t=-10.23, p<0.001).

### 3.3.2    Biogeographic patterns in body size

Plastron lengths for males and females had similar positive linear relationships with latitude, although latitude explained only a little over half of the variation (55% for males and 51% for females, Figure 3.2).  The female cline in plastron length was similar to the male cline in plastron length, and the slopes were not significantly different (t=0.013, p=0.99).  The geographic analysis of SDI and latitude showed a very weak negative linear relationship (p=0.32, $r^2$=0.08), with only 8% of the variation in SDI explained by latitude (Figure 3.3).

The local variation in male plastron length for the British Columbia populations spanned about a quarter of the variation across the rest of its geographic range (Figure 3.4). Female plastron lengths in the British Columbia populations were more variable than the male plastron lengths, spanning almost one third of the variation of female plastron lengths as reported across the geographic range (Figure 3.5).  Dimorphism indices for the British Columbia populations had the greatest variation when compared to the variation in indices for the rest of the geographic range (Figure 3.6).  Indeed, local variation in the dimorphism index for the Okanagan valley encompassed most of the geographic variation across the range (Figure 3.6).  When using the plastron length of mature females to calculate the dimorphism index, one of the Okanagan populations had the highest degree of dimorphism recorded in all of North America, and when using the index calculated with all females, one of the Okanagan populations had the lowest degree of dimorphism recorded for North America.  Substantial local variation was also observed in three other jurisdictions that sampled more than one pond: Colorado, Wisconsin, and particularly, Saskatchewan. There was no apparent relationship between latitude and the threshold size at which researchers considered females to be mature (Figure 3.7).

### 3.4    Discussion

Western Painted Turtles in south-central British Columbia were indeed larger than turtles from lower latitudes elsewhere in the range, consistent with the predictions of Bergmann's rule.  Male and female body size increased with latitude with similar slopes, however, rejecting my prediction that the degree of dimorphism would increase with latitude. The amount of geographic variation potentially explained by local variation was smallest for

male plastron lengths and largest for the sexual size dimorphism indices. Some of this variation may come from the use of inconsistent thresholds for the size of female maturity. Importantly, for the dimorphism comparisons, the local variation was so great that it undermines any possible clinal trend. These data thus highlight that when assessing clinal trends in body size or size dimorphism, it is critically important to 1) encompass local variation, and 2) in the absence of true biological size thresholds, standardize the thresholds used for assigning maturity to females.

Turtles from two of the studies in the biogeographical analyses, from Louisiana (Moll 1975) and Tennessee (Moll 1973), are very likely to be southern painted turtles, *C. picta dorsalis*. Recent genetic work gives tentative support for the elevation of *C. p. dorsalis* to its own species, *C. dorsalis* (Crother 2012, Jensen et al. 2014). As *C. p. dorsalis* is able to interbreed with the other *C. picta* subspecies (Lindeman 1997), and the taxonomic change to *C. p. dorsalis* is still unclear, I included the Louisiana and Tennessee populations in the biogeographical analysis. As an exploratory measure, I completed the same biogeographical analyses without these southern populations, and removal did not change the significance of the biogeographical patterns.

These results add support for Bergmann's rule in turtles, which has been found in 19 of 23 species of Chelonians (Ashton and Feldman 2003). The original mechanism proposed for Bergmann's rule was one of heat conservation in endotherms—a reduced surface area to volume ratio in cooler climates minimizes heat loss. Although turtles are ectothermic, a similar hypothesis might explain the trend in turtles. A larger body size, in combination with the thermal properties of the shell, may help turtles maintain elevated body temperatures for longer (Litzgus and Brooks 1998, Ashton and Feldman 2003). This hypothesis would be congruent with the observed reverse-Bergmann trend observed in squamate reptiles, which lack the extra thermodynamic protection of a shell (Ashton and Feldman 2003). A second proposed mechanism behind the observed Bergmann trend in Chelonians relates to the physiological demands of increasingly harsh overwintering periods of northern habitats (Brooks et al. 1992). Larger turtles can accumulate greater energy stores and could be better equipped to deal with the longer periods of food shortage and decreased habitat productivity that come with winter in northern latitudes (Ashton and Feldman 2003).

Along with such selective mechanisms behind the latitudinal size trends, phenotypic plasticity is probably also partially responsible for the observed local variation in body size. In the lab, turtles exposed to different foods and developmental temperatures showed plasticity in body and cell size (Litzgus et al. 2004). Northern populations of turtles tend to be more carnivorous (Cooley et al. 2003), and growth rates of snapping turtles, *Chelydra serpentina*, are higher in habitats with greater primary productivity (Brown et al. 1994). In Colorado, differences in elevation drove differences in growth rates and diet, with higher elevation populations having growth rates and degree of carnivory more similar to northern populations than southern (Cooley et al. 2003). I tested for a relationship between elevation and body sizes and between elevation and degree of dimorphism of turtles in the Okanagan, but found none. The amount of local variation probably changes over time. Growth rates and age at maturity of painted turtles varied from year to year in Michigan (Frazer et al. 1993), strongly suggesting that life-history traits respond to environmental variability.

Phenotypic responses to local environmental conditions likely explain the high variation in plastron lengths for the turtles in the Okanagan valley. A recent genetic analysis of *C. picta* in British Columbia has grouped the Okanagan populations as a discrete genetic unit (Jensen et al. 2014), so it is unlikely that the size variation is a result of genetic differences between the populations. The amount of variation around the mean size was similar for males and females, indicating that whatever environmental condition is driving the variability affects both males and females similarly. As all ponds were sampled by the same team of researchers, in the same year, and classified using the same size thresholds, sampling bias was minimal. Despite this local standardization, if my study only sampled a single pond in the Okanagan, it could have yielded one of the lowest dimorphism indices in North America, or one of the highest, depending on the pond sampled. The wide range of values highlights the danger in using turtles sampled from single ponds to represent a whole region and points to the critical importance of site-specific selective pressures in determining sexual size dimorphisms. Local variation in male and female body size and dimorphism indices is also present in the three other studies that presented data from two ponds each. The variation between sites in these three areas was not as large as the variation shown by the ten Okanagan populations, but it supports the suggestion that local variation might actually comprise most of the range-wide variations. Indeed, local per-pond variation in dimorphism

is of similar magnitude to the reported range-wide variation. This result does not detract from the support for Bergmann's Rule in painted turtles, but rather highlights that because the Bergmann's cline is similar for males and females considered separately, differences in dimorphism among sites instead represent different phenotypically plastic responses to site conditions. In support of this interpretation, in mud turtles, *Kinosternon hirtipes*, dimorphism was positively correlated with the size of the drainage basin and was attributed to difference in food availability (Iverson 1985). Resource availability also affects the degree of dimorphism in bog turtles, *Clemmys muhlenbergii* (Lovich et al. 1998).

Studies of dimorphism are further complicated, however, by the fact that turtles have temperature-dependent sex determination and sexual bimaturation, with males maturing younger and smaller than females. It is much easier to have confidence in the field identification of mature males than it is mature females. Field identification of sex is done on the appearance of male secondary sex characteristics, including noticeably elongated foreclaws and a lengthened pre-cloacal tail region, with the cloaca located beyond the edge of the carapace (Frazer et al. 1993). Turtles with these characteristics are marked as male, and turtles not showing these characteristics that are bigger than a researcher-specified threshold size are marked as females. Although dissections to find ovaries or testes can confirm sex, few field studies use this technique. Researchers can also mark turtles and return in future years to see if turtles previously classified as female develop male characteristics, or could radio-track questionable individuals to see if they mate or nest. The net effect is that size criteria for classifying females are typically arbitrary (i.e. they are seldom confirmed via mating or dissection) and conservative (i.e. at the size by which most males have developed their secondary sex characteristics) (Mitchell 1988, Frazer et al. 1993, Griffin 2007). Failing to use a biologically meaningful threshold would bias the average female size.

Size at maturity, for both male and female turtles, varies geographically, temporally, and with local conditions (Lovich et al. 1990, Frazer et al. 1993). Given the variation in size at maturity, the threshold size used for field classifications should reflect the local biology. Although body sizes showed a positive correlation with latitude, the threshold sizes used by researchers to classify females did not follow the same pattern (Figure 3.7). It is likely, then, that some of the studies included immature turtles, making dimorphism comparisons

difficult, since the indices should consider only sexually mature individuals. Many studies do not distinguish between immature and mature females at all when describing average female body size (Ernst 1971, MacCulloch and Secoy 1983, Mitchell 1988, Griffin 2007) and fail to give a threshold value used in the field classifications—ambiguities that make cross-study comparisons impossible to interpret reliably.

It would be ideal if local knowledge was used to set the female size threshold to reflect the true size at maturity for each population. Then, and only then, is there benefit to making cross-study comparisons with different thresholds—otherwise, including immature turtles because thresholds are set too low will artificially increase variance, as well as, reducing mean estimates. Thresholds that are too conservative and higher than the true size at maturity would leave out some mature females, thus artificially reduce variance and increasing mean estimates. Second to knowing the true biology of each population, the best practice is to set all thresholds to the same value to compare degrees of dimorphism. The resulting indices would better represent differences in the clinal trends for male and female body sizes. Setting a conservative (medium to high) universal threshold for female size at maturity might artificially reduce the variance across the latitudinal range by leaving out some smaller mature females, especially in the south, where some smaller mature females might be excluded from analyses. Despite the lowered variance, such an analysis would give more confidence in the interpretation of the degree of dimorphism between the biggest mature females and average males. Regardless of the threshold used, all comparisons are made stronger when large sample sizes are used to estimate the parameters for an area. The high per-pond variance in my study highlights the need to sample broadly to increase the likelihood that estimates are representative of an area. Range-wide comparisons based on population-level studies are more credible than comparisons that include estimates based on a small number of museum specimens, for example.

My study supports Bergmann's rule in painted turtles, but does not support a clinal difference in sexual size dimorphism. Size dimorphism does vary widely within a small geographic region, but there is no evidence for a systematic change with latitude. Further, disentangling regional patterns in turtle size and dimorphism are plagued by both biological and technical problems. Sexual bimaturation, the difficulty in field identification of females, and the use of inconsistent classification results skew SDI results. Further investigation into

regional and local variation in sexual size dimorphism, using standardized and explicit methods and perhaps focusing on the northern and southern extremes of *C. picta's* range, may allow identification of regional patterns or their lack.  As my work demonstrates, high local variation is possible in body size and degree of sexual size dimorphism.  Additional work on the causes of local variation in growth and maturation is warranted.
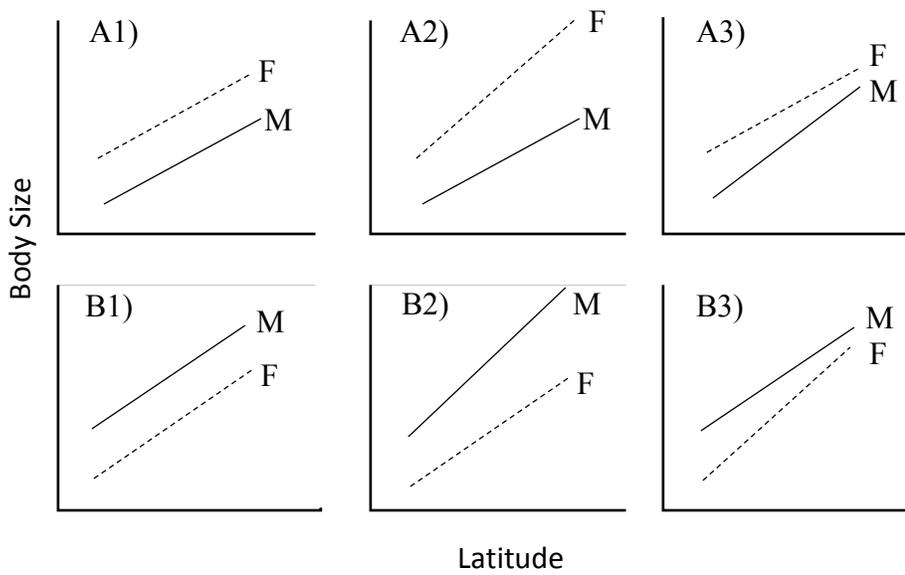
**Figure 3.1.** Possible Bergmann's clines for males and females when females are the larger sex (A1-3) and males are the larger sex (B1-3). If the larger sex has a steeper cline (A2&B2), male and female sizes diverge and dimorphism increases with latitude. If the smaller sex has a steeper cline (A3&B3), male and female sizes converge and dimorphism decreases with latitude. Adapted from Blankenhorn et al. (2006).

**Table 3.1.** Adaptive explanations for the evolution of sexual size dimorphism, as adapted from Stephens & Wiens, 2009.

| Theory behind sexual size dimorphism | Larger sex | Adaptive explanation |
| --- | --- | --- |
| (1) sexual selection | Males | Larger body size confers advantage in species with male-male combat or forced insemination |
| (2) fecundity selection | Females | Larger female body size is selected to produce: larger eggs, more eggs, or more frequent clutches |
| (3) ecological divergence between sexes | Either | Males and females consume different resources to avoid intraspecific competition |

**Table 3.2.** Urban-rural classification of ponds sampled for in the Okanagan Valley of southern British Columbia in 2009.

| Classification | Developed on All Sides | Within City Limits | Paved Road Access | N ponds sampled |
|---|---|---|---|---|
| Urban | Yes | Yes | Yes | 1 |
| Suburban | No | Yes | Yes | 3 |
| Sub-rural | No | No | Yes | 3 |
| Rural | No | No | No | 3 |

**Table 3.4.** Data sources used in meta-analysis of clinal variation in body size and sexual size dimorphism in *Chrysemys picta*.

| State | Study Location | N (males) | N (females) | Citation |
|---|---|---|---|---|
| Louisiana | 31°26'N, 91°38'W | 21 | 37 | Moll, 1975 |
| New Mexico | 35°5'N, 106°37'W | 55 | 54 | Christiansen and Moll, 1973 |
| Tennessee | 36°21'N, 89°9'W | 17 | 19 | Moll, 1973 |
| Colorado | 37°20'N, 107°52'W | 57 | 38 | Cooley et al., 2003 |
| Virginia | 37°32'N, 77°28'W | 1224 | 735 | Mitchell, 1988 |
| Illinois | 39°31'N, 88°31'W | 55 | 45 | Moll, 1973 |
| Pennsylvania | 40°2'N, 76°15'W | 30 | 50 | Ernst, 1971 |
| Minnesota | 44°20'N, 94°15'W | 32 | 23 | Legler, 1954 |
| Wisconsin | 46°42'N, 90°33'W | 32 | 23 | Moll, 1973 |
| Washington | 46°45'N, 116°56'W | 78 | 36 | Lindeman, 1996 |
| Wisconsin | 46°71'N, 90°56'W | 32 | 28 | Christiansen and Moll, 1973 |
| Idaho | 47°27'N, 117°34'W | 57 | 22 | Lindeman, 1996 |
| Saskatchewan | 49°37'N, 103°48'W | 12 | 7 | MacCulloch and Secoy, 1983 |
| Saskatchewan | 50°34'N, 104°52'W | 64 | 61 | MacCulloch and Secoy, 1983 |
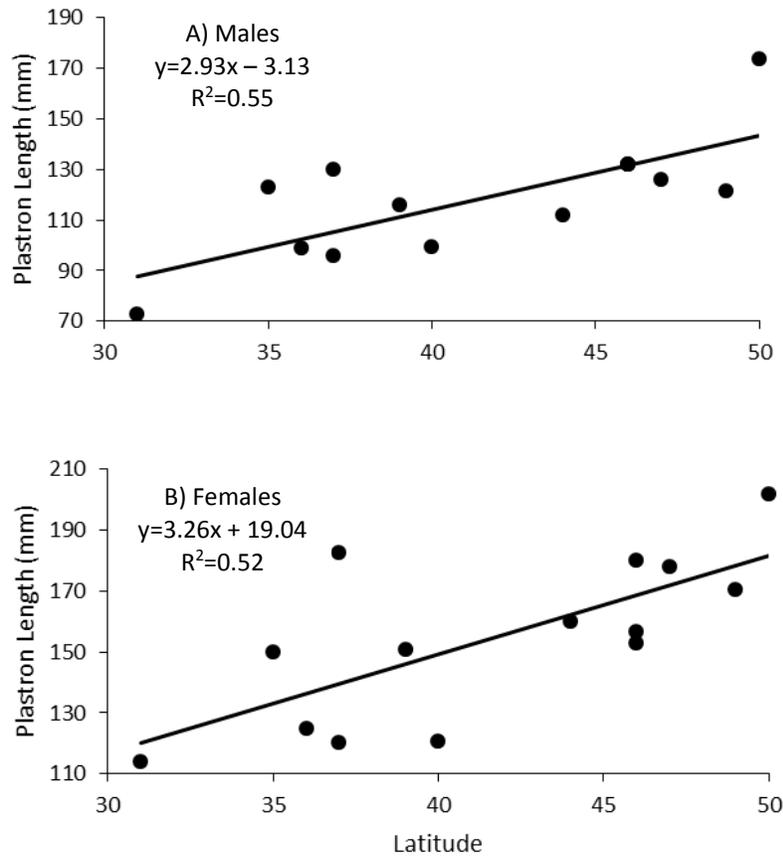
**Figure 3.2.** Geographic variation in male (A) and female (B) plastron length with latitude for 14 locations of *Chrysemys picta* populations in North America. In panel A, the three populations at 46° had similar average male plastron lengths and appear as a single data point. Note the different y-axes. Sample sizes ranged from 19-1959 turtles per population. For populations sampled in the field component of this study, and where an author reported on more than one population within the same parallel, a single weighted average was calculated and used in this analysis. The relationship between plastron length and latitude was significant for both males (F=14.45, P=0.003) and females (F=12.81, P=0.004).
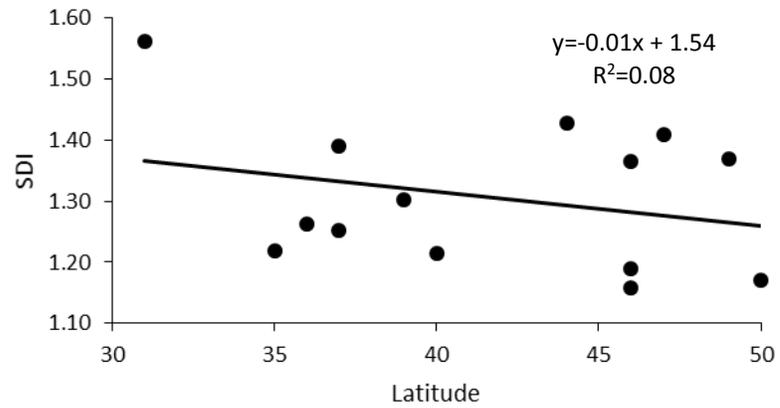
**Figure 3.3.** Geographic variation in sexual size dimorphism index (SDI, average female PL/average male PL) for populations of *Chrysemys picta* sampled in the Okanagan Valley in southern British Columbia. The SDIs from this study were calculated using the mature female cutoff (PL>151 mm). Data from the 10 ponds in this study were combined into a single weighted average. The relationship between SDI and latitude was not statistically significant (n=14, F=1.06, P=0.32).
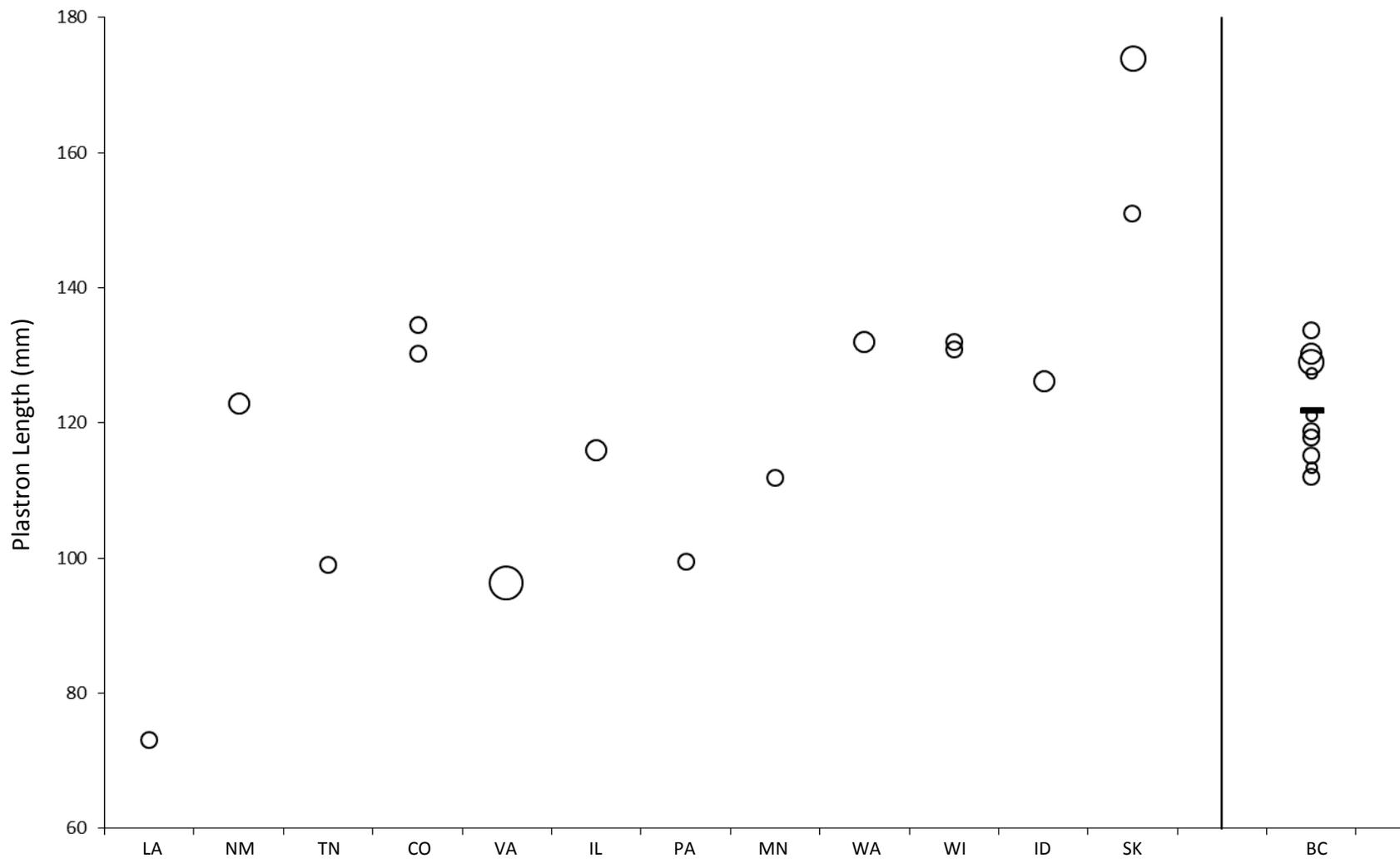
**Figure 3.4.** Local and geographic variation in average male plastron length, in *Chrysemys picta* by state/province (ordered from south (left) to north (right)). Data for BC are from this study. The black bar is the mean plastron length for the populations I sampled in BC. The size of each circle corresponds to the number of males sampled in each study (n=1-1224).

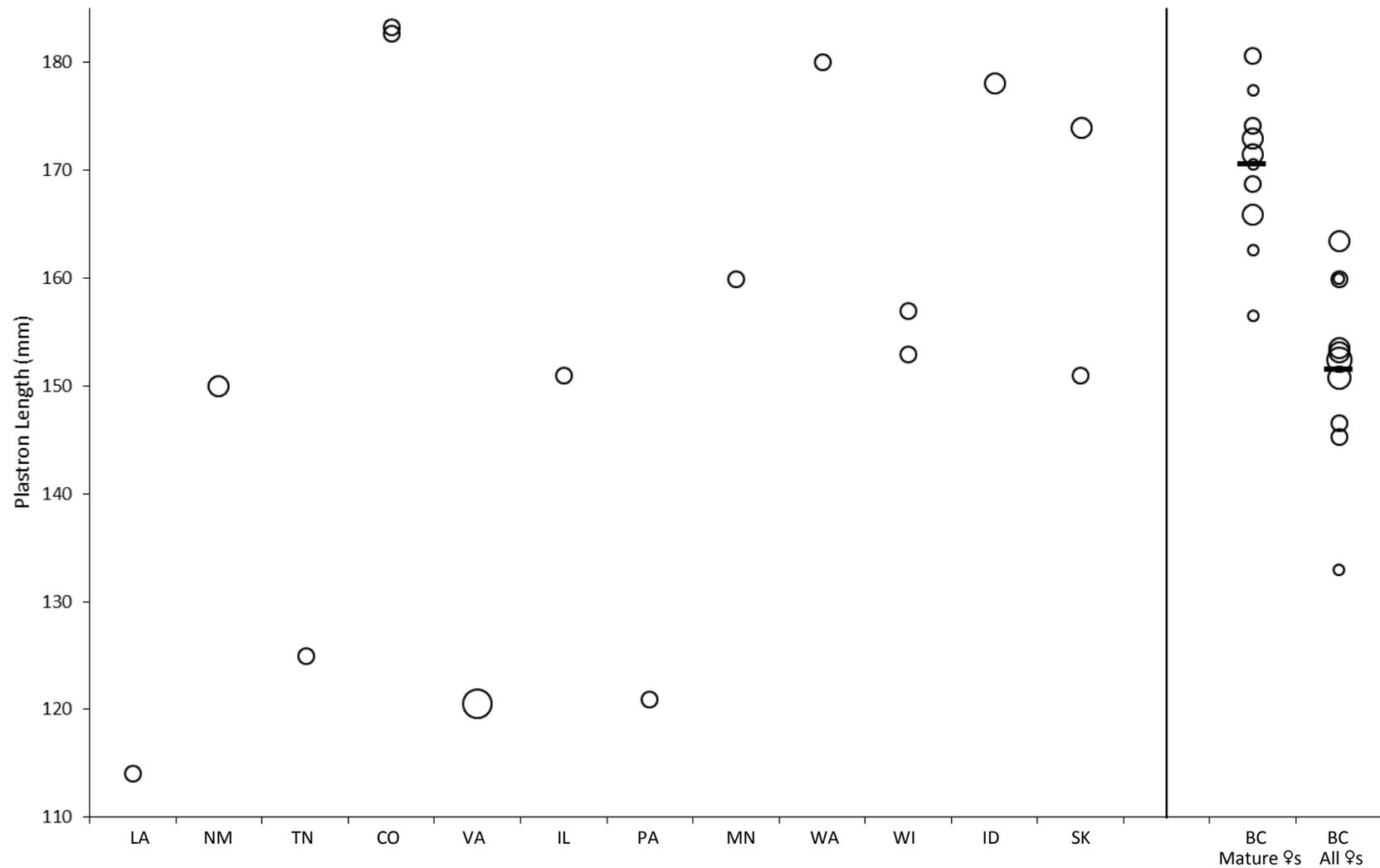**Figure 3.5.** Local and geographic variation in mean female plastron length for *Chrysemys picta* populations by state/province (ordered from south (left) to north (right)). Data for British Columbia are from this study, with mature ♀s (PL>151 mm), all ♀s (PL>105 mm). Black bars are means for the populations I sampled in BC. The size of each circle corresponds to the sample size of each study (n=3-735).
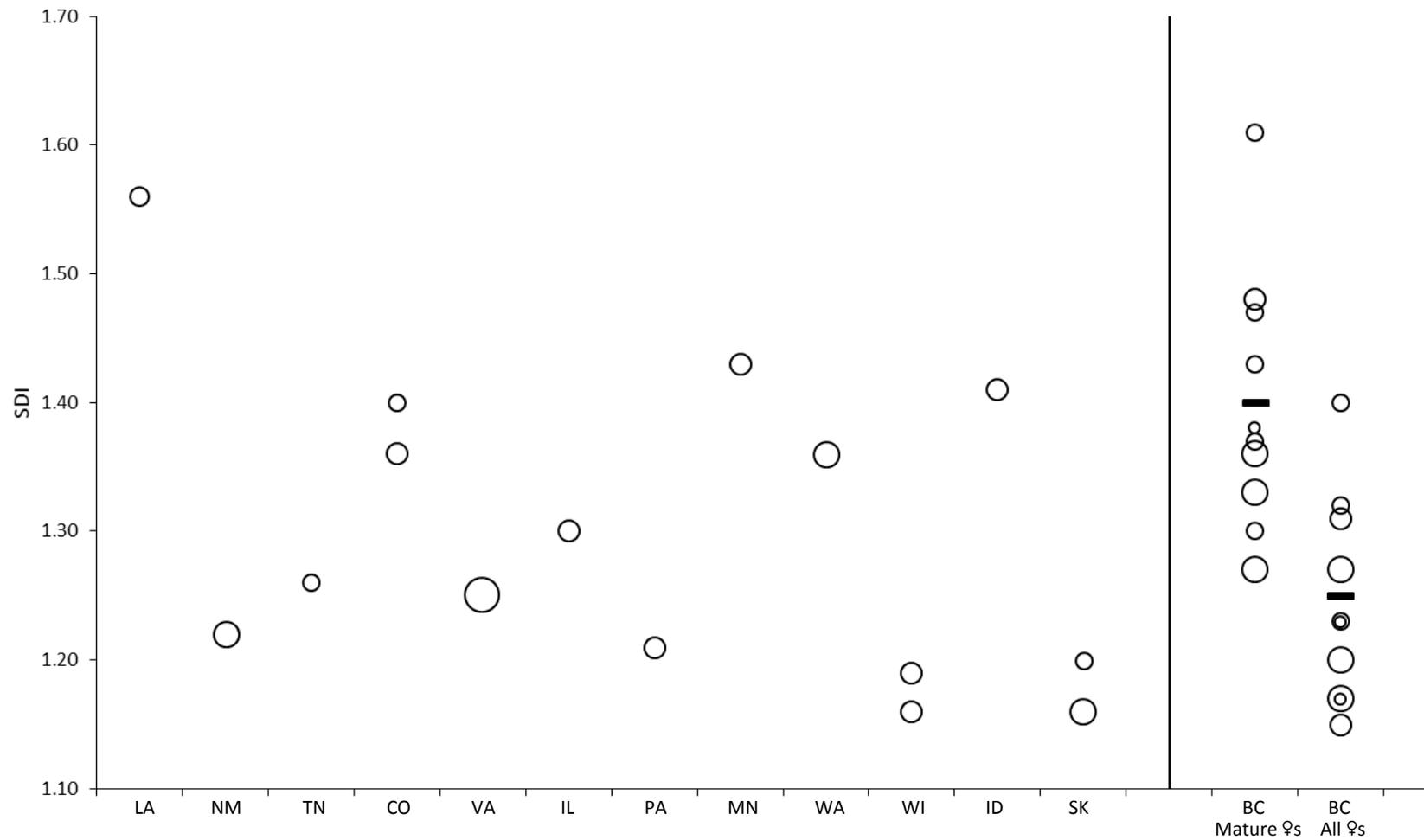
**Figure 3.6.** Local and geographic variation in sexual size dimorphism (SDI, average female PL/average male PL, Lovich and Gibbons 1992) in *Chrysemys picta* by state/province (ordered from south (left) to north (right)). Data for BC are from this study, with mature ♀s (PL>151 mm), all ♀s (PL>105 mm). Black bars are means for the populations I sampled in BC. The size of each circle corresponds to the sample size of each study.

**Figure 3.7.** Geographic variation in the threshold plastron length used to classify *Chrysemys picta* as female. Two of the populations at 37°, used the same threshold plastron length, and so appear as a single data point. The relationship between the threshold value and latitude is not significant (n=14, F=3.39, P=0.09).

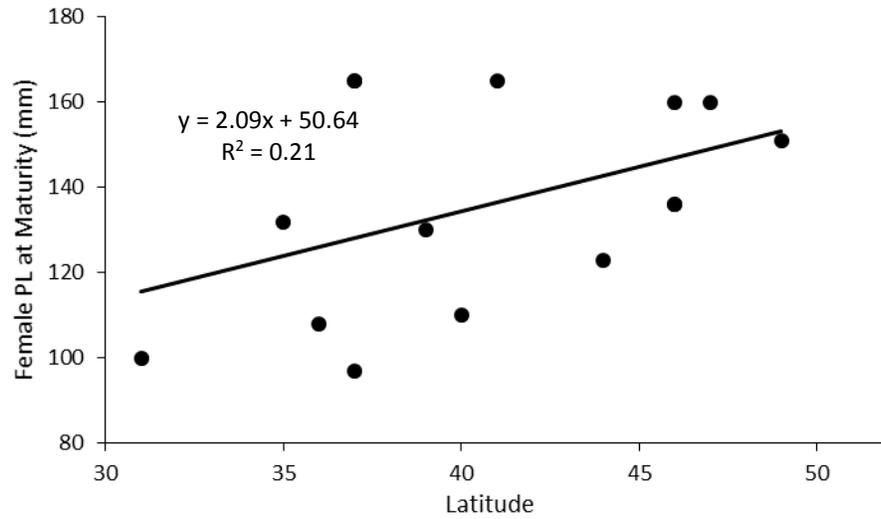## Chapter 4: Conclusion

Many turtle species are heading towards extinction (Kiester and Olson 2011, IUCN 2013). The leading threats to turtles in North America are habitat fragmentation and loss; over-exploitation for consumption, medicine, and the pet trade; and increasing adult mortality on roads (Gibbons et al. 2000, Kiester and Olson 2011). Monitoring of turtle populations is becoming increasingly necessary to provide knowledge of basic life history and population parameters that can be used for population modelling and management. Basic life history traits, however, can vary widely across a species' range and peripheral populations may be distinct from central populations (Iverson and Smith 1993, Litzgus et al. 2004, Litzgus and Smith 2010). For effective turtle conservation, ecologists need good sampling methods and data collected across the geographic range; at present, both methods and range-wide sampling are limited.

My thesis investigated conventional trapping methodology and examined potential biogeographic trends in the painted turtle, *Chrysemys picta*, by sampling populations near the north-western edge of their range, in the Okanagan valley of south-central British Columbia, Canada. The painted turtle is a wide-spread semi-aquatic turtle with a northern range limit that extends into Canada. Two of these peripheral populations are nationally listed as at-risk in British Columbia—the coastal population is Endangered, and turtles in the Okanagan valley of south-central B.C. are of Special Concern (COSEWIC 2006). Central Canadian populations are well-studied and are not listed as at-risk (COSEWIC 2006), but these populations are facing the same threats that have pushed other species towards extinction.

My main objectives were to: 1) quantify potential bias in three common trap methods and examine whether population estimates are improved by combining multiple trap types in a sampling program, and 2) investigate biogeographic trends in body size and sexual dimorphism of *C. picta*. As part of the second objective, I was particularly interested in comparing local variation to range-wide variation because prior efforts seldom focused on local variation.

In Chapter 2, I evaluated the size and sex biases of three common trap methods— hoop nets, basking traps, and dip nets—and I tested the conventional wisdom (Cagle 1953, Ream and Ream 1966, Frazer et al. 1990) of combining data from multiple trap methods to

minimize the biases.  I used the three capture methods at each of 13 ponds across the Okanagan.  My results reinforce and quantify the importance of using multiple trapping methods when surveying populations of *C. picta*.  Using the three capture methods together resulted in the highest recapture rates and often gave population estimates with smaller confidence intervals than estimates from a single capture method only.  Using a sampling design that combines data from all three capture methods would provide better estimates for all age categories and both sexes, numbers that would certainly be of value in a population survey or monitoring program. If cost or logistics prohibit use of multiple trap types, single trap types can be used, but with a loss of data quality.  My data demonstrate that hatchlings and juveniles, for example, are seldom captured in hoop nets or basking traps. Instead, use of dip nets was essential to get information on the recruitment in a pond—nearly all hatchlings and most juveniles were caught in dip nets.  Despite being one of the most common trap types, hoop nets were the least successful capture method for both adult males and adult females.  My data showed that basking traps are good options for adults of both sexes.

I sampled at multiple ponds that represent the range of habitats occupied by *C. picta* in the Okanagan.  Capture and recapture success of each trap method were not consistent across all ponds.  Each trap method performed very poorly in at least one pond—another argument for combining multiple trap types whenever possible.  When designing a sampling program, researchers should therefore consider both the information desired from the surveys and the logistical challenges of each capture method; in Chapter 2, I synthesized the sampling strengths and weaknesses and the logistical considerations for each capture method. Although the capture methods and resulting population estimates will always be imperfect, combining the three trap types will provide the best estimates of population size and population structure, and, if compared across years, population stability.  Data from combining these conventional methods are suitable to inform population monitoring and management programs, whereas data from single trap types need far more careful interpretation because of their biases.

In Chapter 3, I examined support for biogeographical trends in the size and degree of sexual dimorphism of *C. picta*.  According to Bergmann's rule, body size is inversely related to temperature (Blackburn et al. 1999, Ashton and Feldman 2003).  I sampled 10 turtle ponds near the north-western edge of *C. picta's* range and compared these results to those reported

from across the range. I selected the ponds to represent the range of occupied habitat in the Okanagan Valley, B.C., and collected morphological data from 767 turtles, which allowed me to quantify local variation in body size and sexual dimorphism. Turtles near the north-western edge of their range are indeed bigger than their southern conspecifics, and although my research supports Bergmann's rule in *C. picta*, it does not support any sort of biogeographical trend in sexual size dimorphism. The amount of local variation in both male and female body size was high, and the variation in sexual size dimorphism was even higher. Local variation in dimorphism is high enough to cast doubt on previous analyses of the geographic variation in dimorphism. Ponds in the Okanagan had both the highest degree of dimorphism across the entire range of *C. picta*, and the lowest, depending on how adult females were classified—my results highlighted the importance of determining female size at maturity, or at the very least using a consistent size threshold for classification as mature. Thus both local variation and variation in the criteria used in biogeographic analyses suggest previously published biogeographic trends for *C. picta* may not be accurate. Further, my research is complemented by recently completed genetic work on *C. picta* in British Columbia, which shows that Okanagan populations are a similar genetic unit (Jensen 2013)—the local variation observed is most likely a plastic response to local conditions. If local variation in environmental conditions also drives turtle morphology elsewhere in the range, it may be that local variation is far higher than previous analyses have shown.

The ability to respond to local conditions, via plasticity or adaptation, could be key to a species' survival in the face of increasing conservation challenges. The highly variable peripheral populations of *C. picta* in the Okanagan valley are thus worthy of future study. Both local and geographic variation must be considered when looking for range-wide trends. The high variation in body size and sexual size dimorphism I found suggest that the populations show high plasticity in response to local conditions. This plasticity is likely important given the current and coming threats to painted turtles.

These threats point to the need for effective monitoring programs for *C. picta* and for other semi-aquatic turtles. High-quality data are required to inform population modelling and management decisions, and my thesis research strongly suggests that combining conventional turtle trapping methods in a sampling program can provide that data, whereas use of single trap types offers weaker inference. Turtle conservation needs to protect at-risk

species and keep common species common, and a better understanding of how to conserve the painted turtle could benefit many other species.  More research on the causes of local variation in size and growth rate will be valuable in the efforts to protect this and other turtle species in British Columbia.

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**Appendix A: Capture summaries and pond locations.**

**Table A.1.** Capture summaries and pond locations for *Chrysemys picta* captures in the Okanagan Valley of south-central British Columbia in 2009. Population estimates are calculated using Chapman's modification of the Petersen method (Seber 1982) and are shown with 95% confidence intervals.

| Pond | Total Turtles Captured | Males | Females | Juveniles | Hatchlings | Population Estimate N (95%CI) | Minimum number alive after 3 trap days | Trap Days | Pond Location |
|---|---|---|---|---|---|---|---|---|---|
| Skaha Marina | 6 | 2 | 0 | 4 | 0 | 12(10-14) | 5 | 5 | 49°27'N, 119°34'W |
| Redlich Pond | 4 | 0 | 4 | 0 | 0 | NA | 4 | 1 | 49°53'N, 119°27'W |
| Chichester Pond | 38 | 12 | 13 | 12 | 1 | 40(33-47) | 36 | 5 | 49°54'N, 119°23'W |
| Oliver 1 | 3 | 0 | 3 | 0 | 0 | 3(3-3) | 1 | 8 | 49°11'N, 119°33'W |
| Oliver 2 | 8 | 3 | 3 | 2 | 0 | 11(3-19) | 5 | 8 | 49°11'N, 119°33'W |
| Blair Pond | 211 | 52 | 109 | 46 | 4 | 218(1984-251) | 127 | 7 | 49°55'N, 119°27'W |
| Eastside Road | 7 | 1 | 3 | 3 | 0 | 9(5-13) | 3 | 7 | 49°24'N, 119°34'W |
| Green Lake | 65 | 5 | 22 | 9 | 29 | 93(70-117) | 27 | 7 | 49°18'N, 119°34'W |
| Yellow Lake | 70 | 7 | 29 | 31 | 3 | 86(72-99) | 61 | 5 | 49°20'N, 119°45'W |
| Vaseaux Lake | 152 | 60 | 74 | 18 | 0 | 267(181-353) | 48 | 8 | 49°18'N, 119°31'W |
| Ripley Lake | 69 | 14 | 33 | 22 | 0 | 96(52-127) | 44 | 6 | 49°14'N, 119°38'W |
| White Lake | 156 | 33 | 73 | 46 | 4 | 194(177-211) | 143 | 4 | 49°18'N, 119°37'W |
| Burnell Lake | 322 | 84 | 134 | 104 | 0 | 505(411-598) | 322 | 3 | 49°12'N, 119°37'W |
| Total | 1111 | 273 | 500 | 297 | 41 | 1534 | 826 | 74 | |