# SPATIAL ECOLOGY AND CONSERVATION OF THE NORTH AMERICAN WOOD TURTLE (*Glyptemys insculpta*) IN A FRAGMENTED AGRI-FOREST LANDSCAPE

by

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# ABSTRACT

The impact of agricultural practices on wood turtle (*Glyptemys insculpta*) movements and survivorship was investigated in a fragmented agri-forest landscape over two years. Agricultural activities and machinery contributed to the death of 20% of radio-tracked turtles. Annual survivorship of adults was 0.904 and 0.868 and for juveniles it was 0.815 and 0.831 for 1998 and 1999, respectively. Mutilation rates in adults were 90% ± 3% in both years; in contrast, the maximum rate in juveniles was 57%. Setting the cutting height of disc mowers to 100 mm would increase harvest yields, reduce wear on machinery, decrease soil erosion, and reduce turtle mortality and mutilation rates. The concepts of integral, statistical, and linear range are introduced as distinct estimators of turtle movements. Since integral ranges include all habitats critical to survival, they provide an important contribution to our knowledge of imperilled species. Statistical ranges are stable and easily promote within and between study comparisons. Linear ranges quantify migratory and ranging movements. Thread-trailing techniques were used to record the fine-scale movements of six adult male *G. insculpta* translocated to an experimental hayfield patch-matrix. Although patch size had no effect on move length or path sinuosity, habitat structure did. Paths were generally straighter and move length longer in the harvested portion of a hayfield. Apparent habitat boundaries were shown to be permeable. Subjects exhibit three movement phases: agitation dispersal, local search, and ranging. Thus, *G. insculpta* exhibit predetermined movement patterns and move to maximize the likelihood of locating resources, while minimizing the probability of revisiting previously searched areas. Recent changes in agricultural practices and machinery are having a decidedly negative impact on *G. insculpta*. This study provides new insights into the movements of *G. insculpta*. Such knowledge will be an essential component of future conservation efforts. Without changes in agricultural practices however, this population will be extirpated.

# RÉSUMÉ

L'impact des pratiques agricoles sur les déplacements et le taux de survie des Tortue des bois (*Glyptemys insculpta*) habitant un paysage agro-forestier fragmenté fut examiné pendant deux ans. Des tortues suivies à l'aide de la radio-télémétrie, 20% périrent des suites des pratiques agricoles en place. Les taux annuels de survie pour les années 1998 et 1999 furent respectivement de 0,904 et 0,868 pour les adultes et de 0,815 et 0,831 pour les juvéniles. Le taux de mutilation des adultes fut de 90% ± 3% les deux années alors que la fréquence maximale rapportée pour les juvéniles fut de 57%. Ajuster la hauteur de coupe des disques de faucheuses à 100 mm augmenterait le rendement des récoltes, réduirait l'usure de la machinerie, réduirait l'érosion du sol et abaisserait les taux de mortalité et de mutilation. Les notions de domaines intégraux, statistiques et linéaires sont introduites en tant qu'estimateurs distincts des mouvements de la faune. Les domaines intégraux englobent tous les habitats critiques pour la survie et conviennent donc particulièrement bien aux études d'espèces en danger. Les domaines statistiques sont stables et conséquemment plus appropriés pour les comparaisons intra et inter étude. Les domaines linéaires sont mieux adaptés à la quantification des mouvements migratoires et d'acquisition d'habitat. Des techniques d'observation à l'aide de fil déroulant furent utilisées pour caractériser les mouvements de faible amplitude de six mâles adultes *G. insculpta* déplacées au sein d'une matrice de parcelles dans un champ expérimental. La taille des parcelles n'eut aucun effet sur la distance parcourue ou sur la sinuosité du parcours, alors que la structure de l'habitat en eut un. Les parcours furent généralement plus directs et la distance parcourue plus grande dans la portion fauchée d'un champ. Les parcours à la limite des parcelles révélèrent également que la perméabilité est absolue. Trois phases de mouvement sont observées chez les sujets : agitation de dispersion, investigation locale et acquisition d'habitat. *Glyptemys insculpta* démontre donc des phases de mouvement prédéterminé et se déplace de façon à maximiser la probabilité de repérer des ressources tout en minimisant la probabilité de retourner au sein de secteurs déjà visités. Des changements récents aux pratiques et machineries agricoles ont un impact décidément néfaste sur *G. insculpta*. Cette étude nous permet de mieux comprendre les déplacements de *G. insculpta*. L'acquisition de ces connaissances sera essentielle aux travaux de conservation futurs. Sans modifications au niveau des pratiques agricoles, cette population sera extirpée.

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# PREFACE

This dissertation consists of an introductory literature review, three manuscripts, and a concluding section. The manuscripts have been prepared for submission to scholarly journals and each chapter is comprised of an Introduction, Materials and Methods, Results, Discussion, and Literature Cited section with a series of Tables and Figures.

This dissertation format is in accordance with the "Guidelines for Thesis Preparation" prepared by the Faculty of Graduate Studies and Research of McGill University which states:

> "Candidates have the option of including, as part of the thesis, the text of one or more papers submitted or to be submitted for publication, or the clearly-duplicated text of one or more published papers. These texts must be bound as an integral part of the thesis.
>
> If this option is chosen, connecting texts that provide logical bridges between the different papers are mandatory. The thesis must be written in such a way that it is more than a mere collection of manuscripts; in other words, results of a series of papers must be integrated.
>
> The thesis must still conform to all other requirements of the "Guidelines for Thesis Preparation". The thesis must include: A Table of Contents, an Abstract in English and French, an Introduction which clearly states the rationale and objectives of the study, a comprehensive review of the literature, a final conclusion and summary, and a thorough bibliography or reference list.

> Additional material must be provided where appropriate (*e.g.* in appendices) and in sufficient detail to allow a clear and precise judgment to be made of the importance and originality of the research reported in the thesis.
>
> In the case of manuscripts co-authored by the candidate and others, the candidate is required to make an explicit statement in the thesis as to who contributed to such work and to what extent. Supervisors must attest to the accuracy of such statements at the doctoral oral defense. Since the task of the examiners is made more difficult in these cases, it is in the candidate's interest to make perfectly clear the responsibilities of all authors of the co-authored papers."

Three manuscripts will be submitted to peer-reviewed journals for publication, co-authored by the candidate and his supervisors, Drs. Rodger Titman and Tom Herman. I was responsible for initial study design, writing grant proposals, acquiring research permits, hiring field assistants, purchasing research equipment, collecting and supervising the collection of field data, conducting analyses, and writing the three manuscripts. Drs. Titman and Herman offered advice concerning the design of the studies, as well as editorial comments on each of the three manuscripts.

The handling of wood turtles was approved under McGill Animal Use Protocol # 4097 (Appendix I), in compliance with guidelines outlined by the Canadian Council on Animal Care.

# CHAPTER 1

# INTRODUCTION

North American wood turtle (*Glyptemys insculpta*) populations are declining as a direct result of collecting, habitat destruction, and vehicular traffic (Garber and Burger, 1995; Ernst, 2001). Wood turtles, however, are often encountered in large numbers in agricultural landscapes (Farrell and Graham, 1991; Niederberger and Seidel, 1999). Moreover, studies have suggested that *G. insculpta* actively select ecotone habitats (Kaufmann, 1992). Consequently, several authors have speculated that the species might benefit from increased habitat heterogeneity created by moderate agricultural development (Harding, 1991; Kaufmann, 1992; Foscarini and Brooks, 1997). Frazer (1992) stated, "how we define a problem often will determine what we are willing to consider as solutions". Thus, detailed studies of the effect(s) of agriculture on *G. insculpta* are required before any potential benefits can be assessed.

Saumure and Bider (1998) attempted to evaluate the impact of agricultural development on *G. insculpta* by comparing the age structures, growth, and mutilation rates of an agricultural and forested population. Their results suggested that agricultural development increased adult mortality and reduced predation, growth, and recruitment rates. Due to the limited scope of their investigation, several important questions remained unanswered. The current study expands upon the research of Saumure and Bider (1998) and seeks to increase our knowledge of the spatial ecology of *G. insculpta* inhabiting the same fragmented agri-forest landscape. The specific objectives of Chapter 2 are: (*i*) to document the rates and causes of both mutilation and mortality, (*ii*) to develop a standardized method to quantify the severity of injuries in turtles, and (*iii*) to propose management recommendations designed to increase turtle survivorship. The second part of the investigation concerns the *in situ* movements of *G. insculpta*. Thus, the objectives of Chapter 3 are: (*i*) to standardize methodologies for estimating ranges, (*ii*) to ascertain if correlations exist between range size and turtle mass, length and injury intensity, and (*iii*) to investigate the relationship between level of exogenous landscape alteration and range size. The last part of this study investigates the fine-scale movements of translocated *G. insculpta*. In Chapter 4, the objectives are: (*i*) to ascertain whether adult male *G. insculpta* translocated to a hayfield patch-matrix exhibit discernable movement patterns, and (*ii*) to determine the effects of habitat structure and patch size on path sinuosity, turning angle, and move length.

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> "*Where grows? Where grows it not? If vain our toil,*
> *We ought to blame the culture, not the soil.*"
>
> Alexander Pope

# LITERATURE REVIEW

The following review is presented in three sections. Firstly, the general progression of agriculture in North America is reviewed. Secondly, known impacts of agriculture on wildlife are summarized. Lastly, an overview of the impact of agriculture on turtles and tortoises is presented, with an emphasis on papers not discussed in other parts of the dissertation.

## A BRIEF HISTORY OF AGRICULTURE

North America's eastern woodlands have been exposed to small-scale gardening by Native American peoples for approximately 4,000 years (Yarnell, 1993). When the first European colonists arrived in the early 1600s, large-scale farming and crop storage had been established for 1,000 years in North America (Scarry, 1993). At that time, an estimated 170 million ha of temperate forest were present, of which only 10 million ha remained by the 1980s (Goudie, 1990). The impact of agriculture was never confined to land, as wetlands were some of the first habitats to be exploited for their rich organic soils. In the United States, agricultural development was responsible for the loss of 54% of wetlands (Goudie, 1990).

The mechanization of agriculture began in the 1800s. It was not until the 1840s that horse-drawn machinery came into popular use (Danhof, 1972). The 1930s saw the advent of rubber-tired tractors and complementary machinery. Crop diversity decreased between 1934 and 1982 as soybean and corn came to dominate the landscape (Medley et al., 1995). Moreover, there was an observed trend towards farm expansion through coalescence and/or leases. These trends were driven by family traditions and availability of better equipment.

Today, farm traditions can be rooted quite deeply. For instance, new guidelines for radial tractor tire pressures that reduce soil compaction and tire wear, while increasing traction and controlling power hop, are virtually ignored by skeptical farmers (Wiley, 1995). Matson et al. (1998) found that the timing of nitrogen fertilization could reduce nitrogen losses without affecting grain yield or quality. Since less fertilizer is required, farmers adopting the alternative fertilizer regime would increase net profits by 12 - 17%. However, after the aforementioned benefits were promoted for five years, few farmers had adopted the new methodology (Manning, 2002). Farmers, it seems, are a conservative lot. From their perspective, why fix what is not broken?

## AGRICULTURE AND WILDLIFE

For some species of wildlife, agricultural development is clearly beneficial. Well-known examples are the white-tailed deer, *Odocoileus virginianus*, and the raccoon, *Procyon lotor* (Baker, 1983; Zeveloff, 2002). For others, the impact of agricultural development and machinery is most likely negative. Whiffen (1913) reported early anecdotal evidence of declines in the massasauga rattlesnake (*Sistrurus catenatus*) in New York State. Interestingly, the author remarked that massasaugas were "frequently cut in two by the knives of the mowing-machines." Declines, however, were attributed primarily to senseless slaughter and draining of wetlands for agriculture.

Most early studies focused on the effects of agricultural practices on commercially important game birds. The ring-necked pheasant (*Phasianus colchicus*) benefited from agricultural practices in North America prior to the 1930s (Warner and Etter, 1989). Thereafter, tractor-powered cutter bars were recognized as a serious threat to reproductive females nesting in hayfields. The authors documented that an average of 65% of pheasants were struck by haying machinery while incubating nests. Labisky (1957) reported that in 1954 hay mowers destroyed 78% of active blue-winged teal (*Anas discors*) and mallard (*Aythya americana*) nests. Haying delays due to inclement weather in 1955 increased the number of successfully hatched nests, thereby reducing mower mortality to 30%. Similarly, Gates (1965) noted that 83% of mallard and 56% of blue-winged teal nests in hayfields were unsuccessful, with mowing responsible for the majority of nest failures. Despite such failures, the data suggested that the absence of suitable brood habitat was the main factor limiting duck recruitment. In Manitoba, Cowan (1982) observed that total duck production was 3.8 times higher on zero tillage farms than conventional farms. The author also proposed that seeding zero tillage crops in the fall may enhance nest success rate.

Recently, ornithologists have realized that non-gamebird species are declining in agricultural landscapes. For instance, research in northern Illinois suggested that bobolink (*Dolichonyx oryzivorus*) populations declined by > 90% from 1966 - 1992 (Herkert, 1997). Decreased areas of alfalfa hay, oats, and pasture accounted for 85% of the annual variability in bobolink numbers. Changes in hay harvesting methods were also implicated. Specifically, the median harvest date was approximately two weeks sooner and between-harvest times 5 - 15 days shorter over 40 years. Research was also undertaken on the effects of haying on grassland birds in Saskatchewan (Dale et al., 1997). The authors recommended that most fields be mowed biennially, but that some be left idle for at least three years. Blackwell and Dolbeer (2001) examined population trends for red-winged blackbird (*Agelaius phoeniceus*) in Ohio from 1965 - 1996. They concluded that this abundant species was affected negatively by earlier hay harvests, reduced non-alfalfa hay production, and row crop increases. Agricultural intensification was cited as the most likely cause for the observed declines. Hunter et al. (2001) noted that there were 17 disturbance-dependent avian species in eastern North America, of which four are extinct, twelve endangered, and two threatened. Such declines are not confined to North America. A British study documented that 85% of farmland bird species experienced range contractions between 1970 and 1990 (Fuller et al., 1995). Moreover, 15 species were less abundant at the end of the study, and seven had declined by at least 50%. The authors attributed declines since 1970 to several factors including: (*i*) reduction in spring sowing of cereals, (*ii*) reduction in crop rotations, (*iii*) increase in the use of insecticides, herbicides, and fungicides, and (*iv*) intensification of grassland management.

Fleischner (1994) noted, "the destruction caused by livestock grazing is so pervasive and has existed for so long that it frequently goes unnoticed." When studies are undertaken, however, the results can be alarming. Strassmann (1987) reported that 981,954 ha of the US National Wildlife Refuge System were grazed by cattle owned by private ranchers and farmers "to benefit refuge wildlife". Administering grazing and haying can consume up to 55% of staff time and 50% of a given refuge's funds. Refuge managers believed that 86 species of wildlife were positively affected, whereas 82 were negatively impacted. Prescribed burning was proposed as a better management option than grazing and haying programs. One study documented that the bunchgrass lizard

(*Sceloporus scalaris slevini*) was ten times more abundant on ungrazed land than on grazed parcels (Bock et al., 1990). Similarly, Bélanger and Picard (1999) documented that ungrazed and moderately grazed island prairies in Québec had ten times more ducks and six times more birds than intensively grazed areas. Conversely, in the Saskatchewan prairie pothole region, duck nest success for nine species was much greater on pasture than in cropland (Ignatiuk and Duncan, 2001). However, the authors noted that large pastures typically have uneven grazing pressure and cattle distribution. Moreover, they advocated rotational grazing systems because it provided improved vegetative cover around wetlands. This cover may, in turn, attract ducks away from less productive habitats and increase brood survival. Although some bird species are sensitive to grazing, temporal variability should be considered. Stanley and Knopf (2002) noted that riparian habitats for such sensitive bird species in a Colorado wildlife refuge could be restored even if late-season grazing took place, albeit at a slower rate than if cattle were excluded altogether. Holechek et al. (1982) provide an extensive review of how controlled grazing can maintain or enhance wildlife habitat. They concluded that most rangelands could not tolerate the removal of more than 50% of palatable vegetation per year and still be beneficial to wildlife.

Other than direct trauma or nest destruction, agricultural development may also have indirect impacts upon wildlife. For instance, agricultural development may result in habitat islands, where patches of natural habitat are isolated by agricultural lands (Mader, 1984). Wegner and Merriam (1979) noted that white-footed mice (*Peromyscus leucopus*) and chipmunks (*Tamias striatus*) seldom ventured into or crossed grass fields. Similarly, few birds would fly over a 300 m field to reach another wood patch. Those that did venture across occasionally were American robins (*Turdus migratorius*), blue jays (*Cyanocitta cristata*), and starlings (*Sturnus vulgaris*). Kolozsvary and Swihart (1999) noted that the ability of amphibian species to move between isolated woodlands/wetlands was critical to persistence in agricultural landscapes.

Sietman et al. (1994) observed that the relative abundance of several species of small mammals was lowest in a hayfield and highest in an old field. This difference was attributed to the physical characteristics (i.e. canopy cover and vertical structure) of the habitats themselves. The removal of riparian forest cover may also result in shifts in fish assemblages, with an increase of species that live in deeper, slower water and species that guard their young in nests (Jones et al., 1999). Fritz et al. (2003) documented a threshold size for riparian agricultural fields in Zimbabwe. At field sizes of 3.2 ha or greater, the density and diversity of small and medium-sized carnivores and herbivores decreased.

Different forms of agricultural practices can also determine the abundance of invertebrates, a key component of the diet of many wildlife species. For instance, Basore et al. (1987) noted significant differences in arthropod abundance between soybean and corn crops. Chiverton and Sotherton (1991) noted an increased abundance of arthropods in a 12 m wheat headland that was not sprayed with herbicides. Increased arthropod abundance is correlated to increased survival of gamebird chicks. Another study noted that invertebrate abundance increased from woodland to grazed woodland to pasture, but only for the most abundant orders (Bromham et al., 1999). For the majority of the least abundant orders, the pattern was reversed. These abundance patterns were attributed to differences in litter layers and vegetation.

## AGRICULTURE AND CHELONIA

At times, turtles can be incredibly resilient to disturbances; at others, the slightest alteration can be devastating. Despite the extensive degradation of the Illinois River, five turtle species have seemingly thrived on the bloated bodies of fish, pollution tolerant insects, and an introduced clam (Moll, 1980). Benign modifications for one species can be lethal to another. For instance, Burger and Branch (1994) noted that electrified fences were useful in restricting the movements of porcupines (*Hystrix africaeaustralis*) and bushpig (*Potamochoerus porcus*) in a South African nature reserve. Fifty leopard tortoises (*Geochelone pardalis*), a marsh terrapin (*Pelomedusa subrufa*) and one angulated tortoise (*Chersina angulata*), however, were found dead along the 8.4 km of electric fence. As only tortoises of a sufficient height were electrocuted, the solution was obvious and easily implemented. Other cases are not so easily solved, particularly when related to substantial habitat degradation. Bayley and Highfield (1996) found that deforestation and agriculture had a negative effect on the spur-thighed tortoise (*Testudo graeca*) in southern Morocco. Deforestation resulted in an influx of tortoises from degraded argan forests into agricultural fields. Not surprisingly, this resulted in some hostilities by farm laborers, as well as a few road mortalities. Interestingly, the tortoises have adopted hedges of introduced prickly pear cacti (*Opuntia ficus indica*) as their preferred habitat when not foraging on crops.

The effects of livestock grazing have been studied for several species of turtles and tortoises. The impact of grazing on the desert tortoise (*Gopherus agassizii*) is difficult to ascertain because the Mojave Desert rangelands have been grazed extensively in the past. Some 7.6 million cattle grazed the western United States as early as 1886 (Oldemeyer, 1994). Many studies have offered the unsupported opinion that insufficient forage remained for *G. agassizii* after grazing. Based on a thorough review of the literature, however, experimental data on the impact of livestock grazing was found to be deficient. Subsequently, Avery and Neibergs (1997) documented a dietary overlap between cattle and *G. agassizii*. In early spring, both consumed fresh annuals, whereas by late spring their diets had diverged completely. Tortoise burrows however, were trampled by cattle during the winter grazing period. As tortoises could not enter completely destroyed burrows, the authors suggested that digging new burrows could increase energetic costs and risk of mortality. Interestingly, a study of Texas tortoise (*Gopherus berlandieri*) on grazed and ungrazed pastures concluded that the species was tolerant of intermediate levels of cattle grazing (Kazmaier et al., 2001). The authors noted, however, that this tolerance might be because the region was historically grazed by *Bison* sp. The tortoises at this site had larger home ranges in ungrazed pasture than grazed pastures (Kazmaier et al., 2002). Livestock overgrazing in Argentina, however, resulted in the displacement of *Geochelone chilensis* to marginal habitats such as road edges, edges of salt lakes, sand hills, and rugged landscapes (Waller and Micucci, 1997). For one species, however, moderate cattle grazing can retard succession and thus be beneficial. Bog turtles (*Glyptemys muhlenbergii*) inhabit fens, spring fed bogs, or wet meadows and cattle grazing is advocated as a means of maintaining critical habitats for this threatened species (Morrow et al., 2001).

Chemical alterations of aquatic habitats can also affect turtle populations. A comparative study of two adjacent farm ponds in Alabama revealed that a fertilized fishing / irrigation pond had a greater abundance of eastern mud turtles (*Kinosternon* *subrubrum*) than an unfertilized pond used for livestock watering, irrigation, and fishing (Stone et al., 1993). Recently, Lindsay and Dorcas (2001) documented that *K. subrubrum* size and egg size were inversely correlated with overall cattle impact, as well as aquatic concentrations of ammonia and nitrite/nitrate. No such correlations were detected for painted turtles (*Chrysemys picta*). Other chemicals, such as algicides and herbicides, have been observed to increase the rate of emigration of red-eared sliders (*Trachemys scripta*) from a Mississippi farm pond (Parker, 1996).

Lastly, agricultural fields are used by several freshwater turtle species for nesting, including Blanding's turtles (*Emydoidea blandingii*), red-eared sliders (*Trachemys scripta*), and wood turtles (*Glyptemys insculpta*) (Linck et al., 1989; Kaufmann, 1992; Tucker and Warner, 2000). Such migrations are not always without consequence. Mud accumulation has been observed on several *T. scripta* and one *C. picta* crossing newly cultivated fields during nesting migrations (Tucker and Warner, 2000). In extreme cases, such accumulations on the plastrons immobilized turtles.

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# CHAPTER 2

## Effects of Haying and Agricultural Practices on an Imperiled Species: the North American Wood Turtle, *Glyptemys insculpta*

> "*As for diversity, what remains of our native fauna and flora*
> *remains only because agriculture has not got around to destroying it.*"
> Aldo Leopold

# INTRODUCTION

Wood turtle (*Glyptemys insculpta*) populations are declining throughout their range as a direct result of such anthropogenic activities as habitat destruction, vehicular traffic, and collecting (Ernst and McBreen, 1991; Harding, 1991; Garber and Burger, 1995; Ernst, 2001). Fortunately, the species is now protected from commercial exploitation in most states and provinces within its range (Levell, 2000). *Glyptemys insculpta* occurs from Virginia north to Nova Scotia, and west through the Great Lakes region to Minnesota (Ernst et al., 1994). The species is semi-aquatic, with populations centered upon small rivers and streams characterized by sand or gravel substrates, relatively clear waters, and slow to moderate currents. Riparian habitats frequented include various types of forests, meadows, bogs, swamps, fields, and pastures (Harding and Bloomer, 1979).

The potential impact of current agricultural practices and machinery on *G. insculpta* has not been adequately addressed. Native American peoples have been engaged in small-scale gardening in eastern woodlands for ~ 4,000 years (Yarnell, 1993). Large-scale farming and crop storage, however, have been well established for only 1,000 years in North America (Scarry, 1993). Although *G. insculpta* populations have co-existed with agrarian native peoples for millennia, agricultural practices have changed considerably since the arrival of the first colonists in the early 1600s. In fact, of the 170 million ha of forest present in 1620, only 10 million ha remained by the 1980s as a result of deforestation (Goudie, 1990). Several authors have speculated that *G. insculpta* might benefit from the increased habitat heterogeneity created by agricultural development (Harding, 1991; Kaufmann, 1992*a*; Foscarini and Brooks, 1997). Conversely, Brewster (1985) reported that *G. insculpta* were affected adversely by agricultural development in southern Wisconsin, but provided no supportive data. Furthermore, Kaufmann (1992*a*) suggested that farm machinery and crop rotations might be hazardous and agricultural machinery has since been implicated in injuries observed in *G. insculpta*. Of 82 *G. insculpta* examined by Tuttle (1996) in New Hampshire, 4.9% had injuries that were attributed to hay mowers. Ernst (2001) examined 88 turtles in Pennsylvania from 1965 to 1988 and noted that 2.3% had carapace injuries inflicted by mowers. Saumure and Bider (1998) conducted the first comparative study on the impact of agricultural development on *G. insculpta*. By examining the age structures, growth, and mutilation rates of agricultural and forest populations, they concluded that agricultural development might have resulted in increased adult mortality, as well as reduced predation, growth, and recruitment rates. Determination of the causative agent(s), however, was beyond the scope of their study.

The present study investigated the impact of anthropogenic activities on a population of *G. insculpta* inhabiting an agri-forest landscape. The specific objectives were to determine rates and causes of mortality, as well as the frequency, pattern, and sources of injuries. In addition, we wished to develop a standardized method to quantify the severity of injuries in turtles. The final objective was to produce a series of management recommendations based on the results of the study.

## MATERIALS AND METHODS

*Study Site.*—The study site is located along 6.3 km of meandering river flowing north-south in Brome County, Québec, Canada. The exact location of the population is not disclosed, per the conservation recommendations of Litzgus and Brooks (1996). The site encompasses 330 ha of privately owned land, which includes seven farms, 103 ha of which is deciduous forest. Cattle pastures, cash crops (i.e., hay, corn and oats), and oldfields account for 177 ha of the remaining habitat. Hayfields border 3.1 km of the river. Most of this hayfield-river ecotone (2.7 km) is located along the western side of the river. Due to historical removal of riparian vegetation, erosion along fields and pastures is extensive (Fig. 1). To alleviate the erosion problem temporarily, approximately 1.5 linear km of the river was dredged in 1999 and the gravel used to shore up the banks (Fig. 2). The main river is bordered by a railroad track to the east and a paved road to the west, both of which run parallel to the river at distances ranging from 20 - 640 m. Specific habitat characteristics have been described elsewhere (Daigle, 1997; Saumure and Bider, 1998).

*Subjects.*—We captured *G. insculpta* by hand during the 1995 and 1998 – 1999 field seasons. In addition, 12 of the 13 males tracked in 1999 were monitored sporadically during May – August 2000 as part of an additional study. Turtles were captured, marked, aged, sexed, measured, and photographed as described in Saumure and Bider (1998). In addition, we determined the maximum carapace height (CH) of every turtle recaptured in 1999 using Haglof tree calipers (± 1mm). CH was defined as the maximum height of the entire shell as measured perpendicular to the plastron (Mosimann and Bider, 1960). Injuries were recorded as previously described in Saumure and Bider (1998). Injuries that resulted in death of a given turtle were excluded from mutilation analyses. We conducted post-harvest field surveys to locate any dead turtles that were not part of our telemetry sample.

*Radio-telemetry.*—We equipped turtles with radio-transmitters (Holohil Systems Ltd, Ont., Canada) during the 1998 – 1999 field seasons. Twenty adult turtles were equipped with transmitters (Model AI-2) that were encased in brass cylinders and bolted to the posterior right marginal scutes. Neither movement nor copulation is compromised by this low-profile transmitter placement (Kaufmann, 1992*b*; pers. obs.). The complete transmitter assembly weighed 32.5 g. Five adults and five juveniles were equipped with glue-on transmitters (Model RI-2Csp). The transmitters were immobilized on the posterior carapace with 5-minute epoxy and then sealed with PC-7®, a waterproof epoxy resin (Protective Coating Co., Pa., USA). This dual epoxy technique proved ideal. These transmitters, including epoxy, weighed $\leq 13$ g and remained firmly attached for $> 2$ years. Post-attachment transmitter mass ranged from 1 to 4.5% of turtle body mass. Minimum battery life for both transmitter models was two years. We located each turtle once or twice per week with an LA-12Q receiver (AVM Instrument Company Ltd, Calif., USA) and a collapsible three-element Yagi antenna (AF Antronics, Ill., USA). Transmitters removed from dead turtles were re-used. We preserved the remains of several turtles and deposited them in the Canadian Museum of Nature herpetology collection (CMNAR).

*Survivorship.*—We used the computer program MARK to calculate survivorship (*S*) from radio-telemetry data (White and Burnham, 1999). Mark-recapture data were not used to estimate *S* because of low recapture probabilities, opportunistic sampling, and small sample sizes. Analyses of the radio-telemetry sample were conducted using information-theoretic methods (Anderson et al., 2000; 2001*a*). The 'known fate' radio-telemetry data gathered were compiled into two groups (i.e., g = adults and juveniles) of monthly encounter histories. Known fate data assume that the probabilities of live recapture ($p$), dead reporting ($r$), and site fidelity ($F$) all equal 1.0. Second order Akaike's Information Criterion (AIC$_c$) and Akaike weights ($w_i$) were used to isolate the most parsimonious models based on minimization of the AIC$_c$ (White and Burnham, 1999). The sin link function was used for all analyses. The $w_i$ values were interpreted to be the relative degree of certainty that a given model is the best (Anderson et al., 2001*b*). As no one model had strong support ($w_i > 0.9$), model averaging was used to calculate weighted averages of the best models (White et al., 2002). Monthly survivorship ($\hat{S}$) was converted to an annual survival probability with the formula $\hat{S}^x$, where $\hat{S}$ is monthly survivorship and $x$ is number of monthly sampling occasions. Mortality is defined as $1 - S$. Model notations follow those of Anderson et al. (2000).

*Injuries.*—To date, most studies have reported only the prevalence of injuries within a given *G. insculpta* population (e.g. Brooks et al., 1992). Others have endeavored to compile the prevalence of injuries at specific morphological locations (Saumure and Bider, 1998; Walde et al., 2003). In order to standardize and quantify analyses of the severity of injuries, we derived a Carapace Mutilation Index (CMI). The carapace was chosen because of: (*i*) the defensive function it serves, (*ii*) the large prominent surface area, (*iii*) the persistence of old injuries, and (*iv*) the high number of carapace injuries previously reported (Saumure and Bider, 1998). To calculate the CMI, the carapace was subdivided into four distinct numbered quadrants (Fig. 3). The levels of injury sustained in each quadrant were then assigned the following qualitative values: intact = 0; minor = 1; moderate = 2; and severe = 3. Minor injuries were defined as small scrapes, scratches, and gouges confined to the scute layer of the shell. Such injuries are most often found on the marginal scutes. Moderate injuries were defined as large areas of damage confined to the scute layer; as well as small cracks, dents, and gouges that damaged both the bone and scute layers. In addition, moderate injuries included sections of marginal scutes that were missing. Severe injuries were defined as large gouges, clefts, and shell fractures not confined solely to the marginal scute area. Injuries that damaged the neural bones of the vertebral column and/or exposed the turtles' internal organs also were categorized as severe. In each turtle, the highest level of injury was recorded for each of the four quadrants; these values were then summed. The summed values, which can theoretically range between 0 and 12, were divided by 12 in order to create an index value (CMI) between 0 and 1.

Due to the non-normality of CMI values, Kruskal-Wallis one-way analysis of variance was used to detect differences in CMI values between males, females, and juveniles; whereas, the Mann-Whitney *U*-test was used for pair-wise comparisons. The Wilcoxon signed ranks test was used to test for the non-random distribution of the more serious level 2 and 3 carapace injuries of adults. Specifically, we tested for lateral (left-right) and anterior-posterior differences in CMI values.

## RESULTS

Sixty-six *G. insculpta* (22 males, 28 females, 16 juveniles) were captured 978 times during the combined 1995 and 1998 – 1999 field seasons; 42 individuals (15 males, 18 females, 9 juveniles) during the 1998 – 1999 field seasons. Of 52 individual turtles captured in 1995 (Daigle, 1997; Saumure and Bider, 1998), only 59.6% (n = 31) were recaptured during 1998 – 1999 despite a 12-fold increase in sampling effort. Overall, the number of individuals captured between 1995 and 1998 – 1999 declined by 19.2%.

Thirty turtles (13 males, 12 females, 5 juveniles) were equipped with transmitters during 1998 – 1999. Two of these turtles (1 male, 1 female) had limb amputations, as defined by Harding (1985). The number of turtles tracked at any one time varied from 20 to 26, depending upon capture effort and mortality. Turtles were monitored for periods ranging from 51 to 507 days. Shorter tracking periods were due to mortality.

The male: female sex ratio (0.83:1) for the 33 adult turtles captured in 1998 – 99 did not differ significantly from 1:1 ($\chi^2 = 0.27$, $P > 0.05$). The ratio of adults to juveniles was 3.67:1 for 1998 – 99. Mean CH ± standard deviation (range) for 31 adults (15 males, 16 females) was 74.17 mm ± 5.35 (65 – 82 mm) and 73.06 mm ± 4.13 (63 – 79 mm) for males and females, respectively. There were no intersexual differences in adult CH at this site ($t$ = - 0.646, d.f. = 29, $P = 0.524$). As one would expect, CH for seven juveniles was significantly less than for adults: 52.36 mm ± 8.20 (41 – 61 mm).

*Agricultural activities.*—Two new landowners converted hayfields and leased pastures to corn production during 1998 – 99. Haying occurred twice each summer. Harvest was dependent upon weather, but generally took place over several days. In 1998 – 99, the first harvest period occurred during the last few days of June and the first week of July. The second harvest occurred during the last few days of August and the first week of September. Hayfields were cut with either sicklebar or rotary disc mowers, after which tedders (a series of rotating steel tines that stir, fluff, and spread the swath of hay) were used to accelerate drying time (Fig. 4). Finally, rakes and hay balers completed the removal operation.

*Survivorship.*—Of the 30 turtles tracked in 1998 – 2000, six died as a result of agricultural activities; none died of natural causes. Turtles were killed during June –

August. Mortality was 20% (n = 6) of the 1998 – 2000 telemetry sample (3 males, 1 female, 2 juveniles). Of these, four turtles (13.3%) are known to have died because of impacts with rotary disc mowers. Mower deaths occurred on only two of the seven farms, both of which used disc mowers. Severely mutilated males were recovered from hayfields in July 1998 and 1999. One male (CMNAR # 35433) was severed completely in half, with an irregular fracture running transversely from the posterior right marginals to the marginals over the left bridge. A second male (CMNAR # 35442) clearly shows the dorso-lateral path of the disc mower blade on the right side of the carapace (Fig. 5). One female sustained injuries to the posterior left and anterior right limbs in June 1999. In addition, this turtle likely sustained internal injuries; when initially discovered it was bleeding from the mouth and the following day it was found dead in the field. A seventh mortality was reported to us by a farmer who had hit the specimen with a disc mower during haying in July 1999. Moreover, the farmer observed a coyote remove the carcass later the same evening. This was the third report of *G. insculpta* mortality on this particular farm in 1998 – 99. All surviving turtles tracked during 1998 – 99 had returned to the river by the time the second harvests had begun.

The remaining mortalities (1 male, 2 juveniles) resulted from *G. insculpta* being buried alive. One juvenile (CMNAR # 35432) was trapped by the collapse of a riverbank in June 1998. Its carcass was unearthed approximately 21 days later in an advanced state of decay. Another juvenile was buried in August 1999 when gravel from the riverbed was bulldozed up onto the banks in an effort to stabilize them. It was unearthed, still alive, approximately 25 days later from beneath 46 cm of gravel and tangled limb branches. Since this turtle would not have escaped without human intervention, it is considered dead for the purpose of this study. Finally, a male (CMNAR # 35431) was buried in June 2000 beneath 40 cm of hard packed sandy loam when a new landowner ploughed a 30 ha cattle pasture in order to seed corn; its carcass was unearthed approximately 36 days later.

No mortalities were observed along roads or the railroad track. In addition, no turtles were known to have been killed by cattle; in fact, one adult male *G. insculpta* survived a stampede of approximately 2 dozen cows and calves completely unscathed. There was no evidence of commercial poaching at this site.

The recorded mortalities enabled us to compute estimates of survivorship and mortality from the sample population. The most parsimonious survivorship model for our radio-telemetry data in both 1998 and 1999 was the constant survival model $\hat{S}(.)$ (Table 1). This model, however, did not have unequivocally strong support in either year, based on the $w_i$ values. The group effect model $\hat{S}(g)$ was the second most supported model in both years. Consequently, weighted averages of $\hat{S}$ for both models were calculated. The weighted average $\hat{S}$ for adults and juveniles in 1998 were 0.98 and 0.96 / month, respectively (Table 2). In 1999, the weighted average $\hat{S}$ for adults and juveniles were 0.98 / month and 0.974 / month, respectively (Table 3). As no mortalities occurred from October through May in either year, $S$ for that period was 1.00. Consequently, annual $S$ for adults in 1998 was 0.904; whereas, it was 0.815 for juveniles. For 1999, annual $S$ was 0.868 for adults and 0.831 for juveniles. Finally, annual mortality rates $(1 - S)$ were derived from the weighted average annual survivorship values. Adult and juvenile mortality estimates for 1998 were 0.096 and 0.185, respectively. Similarly, for 1999 these values were 0.132 and 0.169, respectively.

*Injuries.*—Mutilation rates were higher in 1998 and 1999 than they were in 1995 for both sexes (Table 4). Adult mutilation rates were 90% ± 3% in 1998 and 1999. The mutilation rate of juveniles did not differ significantly between years. Ten of the 33 turtles (30.3%) captured in 1995 had sustained additional injuries to the carapace by the end of 1999. Of the 20 turtles captured in both 1998 and 1999, 40% ($n = 8$) sustained carapace injuries during that period. The frequencies of carapace, plastron, and limb injuries were all higher in 1998 and 1999 than for 1995 (Table 5). Twelve percent (4 males, 3 females, 1 juvenile) of the 66 *G. insculpta* marked at this site since 1995 had limb amputations. Six additional turtles had minor injuries consisting of missing claws or phalanges, for an overall limb mutilation rate of 21.2%. Only two turtles with limb amputations were captured in 1998 – 99. Both were recaptures from 1995 and neither appeared to have impaired mobility, although the male, missing a right foreleg, was killed by a disc mower in 1999. Interestingly, seven of the eight turtles (87.5%) had right limbs amputated and no turtle had more than one limb amputated.

Mean CMI values for mutilated males ($n = 22$), females ($n = 29$) and juveniles ($n = 15$) were 0.20, 0.14, and 0.07, respectively. Based on the CMI values, severity of carapace injuries differed between male, female, and juvenile wood turtles ($H = 7.453$, df = 2, $P = 0.024$) (Table 6). Analysis of CMI data for adults with level 2 and level 3 trauma revealed that significantly more adults were injured on the right side of the carapace ($Z = -2.561$, $P = 0.010$). A definite trend was detected in the distribution of injuries between the anterior and posterior of the carapace ($Z = -1.874$, $P = 0.061$).

Based on our examination of agricultural machinery, we were able to attribute certain carapace injuries to specific devices. Level 1 injuries to marginal scutes were consistent with impacts from the tines of tedders (Fig. 4). Similarly, narrow level 2 gouges were also most likely the result of encounters with tedders. Level 2 fractures to the marginal scutes could be produced by either disc mowers or tedders. Severe level 3 fractures and clefts were most likely the result of sub-lethal impacts from the blades of disc mowers.

## DISCUSSION

*Survivorship.*—Long-term studies show that turtle populations are most sensitive to decreases in adult *S* (Brooks et al., 1991; Congdon et al., 1993; 1994; Heppell, 1998). Moreover, chronic reductions in adult *S* require increases in the already high juvenile *S* in order to maintain population stability (Congdon et al., 1993; 1994). However, turtles appear to lack such a density-dependent response (Brooks et al., 1991). Regardless, compensatory changes in juvenile survivorship at our site seem unlikely, given the anthropogenic nature of the mortalities. Harding and Bloomer (1979) first speculated that increases in anthropogenic mortality of adult *G. insculpta* would result in population declines. At the time, however, it was believed that *G. insculpta* populations could maintain themselves in agricultural areas and public lands. Evidence now suggests that the continual removal of *G. insculpta* by outdoor enthusiasts (e.g. fishermen and hikers) can result in local extinction within 10 years (Garber and Burger, 1995). Furthermore, Compton's (1999) sensitivity analyses showed that the harvest of two or three specimens annually from a population of 100 *G. insculpta* lead to population extinction in 76 and 50 years, respectively. Mortalities at this site clearly are occurring at a rate that makes the population unsustainable, as one in five turtles were killed within a two-year period. Both Brooks et al. (1991) and Heppell (1998) stressed that new sources of anthropogenic mortality in vulnerable life stages result in a much greater likelihood of extirpation. We conclude that agricultural activities at our site reduced *S* of adults by 9.6 – 13.2% and of juveniles by as much as 16.9 – 18.5%. Such survivorship values support the contention that 23% fewer juveniles and 40% fewer adults in the 20+ age class compared to a forest population is indicative of a population decline (Saumure and Bider, 1998). Without some form of intervention, this population will continue to decline, collapse (i.e. "ghost population" *sensu* Compton, 1999) and eventually be extirpated.

None of the mortalities we recorded were the result of natural causes (i.e., predation, disease, senescence). Consequently, *S* in an agricultural landscape over a two-year period was 1.00 during periods of agricultural inactivity. This finding is consistent with the results of previous studies on *G. insculpta* that have reported very low natural (e.g., predation) mortality of 0.95 – 5.2% over three to nine years (Farrell and Graham, 1991; Brooks et al., 1992; Foscarini, 1994; Garber and Burger, 1995; Walde et al., 2003; Compton, 1999).

An analysis of our sex ratio data sheds further light on *G. insculpta* survivorship. Daigle (1997) documented a male: female sex ratio of 0.83:1 for the 52 wood turtles captured at this site in 1995. The 1998 – 99 sex ratio for the 42 adults captured remains identical.

*Agricultural machinery.*—Horse-powered mowing machines did not come into popular use until after 1840 (Danhof, 1972). Although sickle cutterbar mowers have been in use for approximately 200 years, rubber-tired tractors and complementary machinery only came into wide use during the 1930s. If this machinery had a negative effect on turtles, then populations would have been extirpated long ago. Disc mowers, however, were first introduced to the US from Europe in the mid-1970's (Rider and Barr, 1987). Fundamental differences exist between the cutting mechanisms of sickle cutterbar and disc mowers (Rider and Barr, 1987; Miller and Rotz, 1995). Specifically, sickle cutterbars are characterized by a series of reciprocating blades that are protected from solid objects, such as stumps and rocks, by guards located along the cutterbar. In addition, the blades cut parallel to the ground at a relatively slow speed. Conversely, rotary disc mowers have two blades bolted to each of a series of discs that rotate at speeds of up to 283 km/hour. Cutting height is adjusted by tilting the angle of the cutterbar downwards, which angles the rotating blades towards the soil. Field speed is only limited by the operator's ability to maneuver the machinery. The combination of angled blades, absence of blade guards, and high field and blade speeds in disc mowers, however, results in extensive trauma and death of adult *G. insculpta.*

Kaufmann (1992*a*) warned that crop rotations might have a negative impact on *G. insculpta.* Similarly, Dodd (2001) reported anecdotal evidence suggesting that many box turtles (*Terrapene* sp.) are killed each year by mowers. Bayley and Highfield (1996) warned that a change from traditional to mechanized ploughing techniques in Morocco would likely threaten aestivating Mediterranean spur-thighed tortoises (*Testudo graeca*). Hailey (2000) calculated that tortoise (*Testudo hermanni*) mortality resulting from ploughing and bulldozing was approximately 50% in affected areas of his site in northern Greece. The entombment and death of a *G. insculpta* in a pasture ploughed to cultivate corn provides the first concrete evidence that turtle populations also can incur losses from crop rotations and ploughs. In small populations, even the loss of a single adult turtle can seriously compromise the stability of the population as a whole (Congdon et al., 1993; 1994).

*Injuries.*—Saumure and Bider (1998) observed numerous scrapes, gouges, and dents on carapaces of turtles at this agricultural site. They suspected that these shell injuries were the result of passenger vehicles, agricultural machinery, or cattle. We found that agricultural machinery (i.e., disc mowers, tedders, rakes) was the source of injury. In addition, injuries were consistent with the mechanical action of tedders and rakes. Overall, agricultural machinery led to an increase of at least 11.5% in the frequency of mutilated turtles since 1995 (Table 4). This higher frequency was due to an increase in mutilation to both carapace and plastron (Table 5). Such data confirm that turtles continue to frequent fields during agricultural operations and that at least some survive encounters with machinery. Those adults that do survive encounters however, do not do so unscathed. Future research should investigate the impact of mutilation on turtle growth, fecundity, and behavior (e.g., habitat selection).

The Carapace Mutilation Index (CMI) did not detect any intersexual differences in the severity of carapace mutilations. As previously stated, no gender bias was expected based on turtle CH. We did detect, however, a significant difference between males and juveniles. Juveniles were not only less mutilated, but the severity of mutilations was significantly less as well. Harding (1985) reported that most *G. insculpta* are injured after attaining sexual maturity. Our data suggest that mutilation rates are a function of habitat use, exposure time, and turtle size. We suspect that the significantly lower shell profiles of juveniles contributed, at least in part, to the absence of trauma inflicted by disc mowers. Differences in habitat use between adults and juveniles also contributed (unpubl. data). Alternatively, the incompletely ossified carapaces of juveniles may increase the probability of death (Moll and Legler, 1971; Wilbur, 1975; Magwene, 1999) and hence decrease the probability of encountering injured juveniles.

Level 2 and 3 carapace injuries were not randomly distributed on *G. insculpta*. Adult turtles had significantly more injuries on the right side of the carapace (i.e., quadrants 2 and 4), with a definite trend towards the anterior (i.e., quadrants 1 and 2) (Fig. 3). Ernst (2001) reported that two *G. insculpta* had clefts in their carapaces, which he believed were inflicted by mowers. Both of his turtles were injured in quadrant 2 (Ernst, pers. comm.). As successive discs on a modular cutterbar rotate in opposite directions, then based on the mechanical action of the machinery alone, one would expect a random distribution of carapace fractures. Babcock (1993) documented that fossilized trilobites also bear significantly more scars on the right side of the carapace. In the present case, the non-random distribution of carapace injuries may be influenced by specific turtle behaviors, traditional harvesting practices, and the type of mower used. Firstly, *G. insculpta* actively select 'edge' habitats, including hayfield margins (Kaufmann, 1992*a*; Tuttle and Carroll, 1997; Arvisais et al., 2002; Compton et al., 2002). Secondly, they have excellent hearing, comparable to that of a domestic cat, as measured by electrical potentials in response to sounds (Wever and Vernon, 1956). In addition, turtles have the ability to detect vibrations through their shells (Rosenberg, 1986). Thus, the approach of agricultural mowers should be detected easily. *Glyptemys insculpta* also are known to seek the safety of a river when danger is perceived (McCurdy, 1995; Saumure and Bider, 1998). Moreover, *G. insculpta* have well-developed spatial orientation and homing abilities (Tinklepaugh, 1932; Carroll and Ehrenfeld, 1978; Barzilay, 1980).

Consequently, *G. insculpta* likely move directly towards the home river. Field margins are typically harvested first and, by tradition, at least one swath is cut around the perimeter of a hayfield in a counterclockwise direction (Rider and Barr, 1987; pers. obs.). Consequently, turtles fleeing field margins expose their right sides to mowers that are cutting counterclockwise along the rivers edge. Only a disc mower set to a low cutting height can cause many of the mutilation patterns observed. Since the right side of the turtle faces the on-coming disc mower blades (Fig. 5), the direction in which the mower blades are rotating does not determine the side that is hit, as it would if a turtle was hit head-on. The preceding scenario is consistent with movement observations gathered from a distance via radio-telemetry during harvesting. Several turtles with large clefts previously inflicted by disc mowers, present in hayfields when harvesting commenced, successfully escaped to the river without further injury (pers. obs.). This suggests a learned response, particularly since those that were killed lacked severe carapace injuries prior to their deaths.

The limb injuries of *G. insculpta* have been attributed to predation from raccoons, *Procyon lotor* (Harding and Bloomer, 1979; Harding, 1985; Farrell and Graham, 1991; Foscarini, 1994). The present study supports the recent discovery that limb injuries also can occur due to encounters with agricultural mowers (Tuttle, 1996). Harding (1985) found that the recapture rate of turtles with amputated limbs was significantly lower than for intact turtles. This suggests that the long-term survival of *G. insculpta* with mutilated limbs is compromised. Only two of eight *G. insculpta* with mutilated limbs captured in 1995 were recaptured in 1998 – 99. Whether the missing turtles emigrated, were subsequently killed, or died as a result of reduced mobility remains unknown. The two recaptured turtles, however, were followed via radio-telemetry during our 2-year study and had *S* = 0.50. We suggest that researchers with access to larger *G. insculpta* populations compare *S* in turtles with different severity and number of limb amputations.

By excluding minor limb injuries (i.e., missing claws and phalanges), our amputation rate of 12% is consistent with the 9 – 13% recorded for other *G. insculpta* populations (Harding, 1985; Farrell and Graham, 1991; Foscarini, 1994; Tuttle, 1996; Walde et al., 2003). As with the distribution of carapace mutilation, limb amputations revealed a strong right-sided bias. These data provide additional support for the aforementioned theory on the non-random distribution of carapace injuries.

*Erosion.*—Although erosion is a natural process, the historical removal of most riparian woody vegetation along field edges clearly exacerbated the situation at our site. Grasses can only withstand about ⅓ the sheer stress that well-developed root systems of woody vegetation can (Schmetterling et al., 2001). Bank erosion, and subsequent attempts at stabilization, accounted for the entombment of two of the five juvenile *G. insculpta* we tracked. Tuttle and Carroll (1997) tracked the movements of neonatal *G. insculpta* and found that they frequently moved to the herbaceous cover along hayfield banks. Since approximately 1.5 km of river was dredged and the banks 'stabilized', it is likely that other turtles were trapped also. As mentioned previously, Hailey (2000) reported that mechanical habitat destruction accounted for approximately 50% mortality of *T. hermanni* in affected habitats. Consequently, we believe that the paucity of juveniles documented at this site by Saumure and Bider (1998) can, at least in part, be attributed to juvenile mortality related to dredging operations and the frequent collapse of severely eroded banks.

*Management recommendations.*—Garber and Burger (1995) attributed part of their population decline to the loss of reproductive female *G. insculpta*. Iverson (1991) believed that conservation efforts should be aimed at adult females. Indeed, sensitivity analyses for the desert tortoise (*Gopherus agassizii*) suggest that increasing the survivorship of large adult females can reverse population declines (Doak et al., 1994). Similarly, we believe that management strategies for the conservation of *G. insculpta* in agricultural landscapes should focus on increasing adult survivorship, as there does not appear to be any intersexual difference in mortality at our site. Frazer (1992) clearly outlined the futility of protecting nests, head-starting, and captive breeding if the sources of adult mortality are not addressed. To that end, mortalities and injuries can be reduced greatly if hayfields are not cropped to within 25 – 51 mm of the soil. Wildlife biologists are criticized often for failing to address the socio-economic needs of private landowners (Warner and Brady, 1996). An immediate benefit to farmers is that raising cutting heights will reduce wear to the discs and knives (Rider and Barr, 1987). If blades are set to cut higher, mower blades and discs should last longer and easily pass over the carapaces of adult *G. insculpta*. Miller and Rotz (1995) recommended that forages be severed 50 – 100 mm above the soil. With limbs retracted, the maximum height of *G. insculpta* at our site was 82 mm; however, the species has been reported to attain a CH of 87 mm (Smith, 2002). Consequently, we recommend a cutting height of 100 mm (4 inches) for fields within the range of *G. insculpta*. Realistically, however, landowners may not willingly adopt such a conservation measure due to the perceived loss of forage yield. We do not advocate that farmers schedule harvest times based on turtle movements nor do we advocate that agricultural areas be searched prior to mowing as suggested by some (Kaufmann, 1992*a*; Foscarini and Brooks, 1997; Dodd, 2001). *Glyptemys insculpta* are difficult enough for researchers to locate in fields with the help of radio-telemetry equipment (pers. obs.). Fortunately, there exists a mutually beneficial solution. Agricultural research has shown that: (*i*) the lower portion of the forage stem has relatively little nutritive value, (*ii*) higher stubble promotes the retention of soil humidity, which results in increased yield in the subsequent harvest, and (*iii*) higher cropping reduces erosion due to runoff (Smith, 1978; Sharp et al., 1995). At our site, the turtles retreat to the river by the time of the second harvest. Therefore, farmers could crop down to 25 mm during the second harvest without jeopardizing turtles. Without even discussing the precarious status of a turtle, landowners can be shown that a small change in cutting height can increase annual yield and thus be profitable. Some landowners, however, are sympathetic to wildlife conservation. For these individuals, we would recommend that an unmowed buffer strip of at least 10 m be left on the perimeter of hayfields at the time of the first harvest. Originally, this technique was suggested to create a nesting refuge and/or escape cover for birds, e.g. ducks (Labisky, 1957; Clubine, 1995). It should reduce turtle-mower encounters as well. Although ~ 300 m buffer zones have been recommended by several authors (Burke and Gibbons, 1995; Compton, 1999; Arvisais et al., 2002; Semlitsch and Bodie, 2003), we do not foresee their implementation on private agricultural lands without financial compensation. Although seemingly ideal, such a buffer zone would encompass every field at our site. Another technique that might prove beneficial would be to mow the part of the hayfield farthest from the river first. As the turtles naturally flee towards the river, this would provide a temporal buffer as well.

Although the risk of mortality due to machinery can be reduced, it cannot be eliminated altogether.

It should be noted that the indiscriminate destruction of fish habitat is a criminal offense in Québec (Société de la Faune et des Parcs du Québec, 2003). Consequently, the disturbance of riverbed aggregates could be stopped through legal action. Such action, however, does not solve the current erosion problem. We propose that a riparian zone restoration project based on multi-level community partnerships is the best solution. The use of soil bioengineering techniques can allow quick stabilization and the establishment of a long-lasting, native, riparian ecosystem (Isenhart et al., 1997; Lewis, 2002). The benefits of riparian vegetation and natural riverbanks over riprap type banks for fish are numerous (Schmetterling et al., 2001). In addition, fencing has been shown to ensure the quickest recovery of riparian zones (Holechek et al., 1982). Managers should, however, heed the recommendations of Buech et al. (1997) and keep some natural erosion zones intact, since these areas are used by wood turtles for nesting. Although Québec law stipulates that it is legal for herds to ford and/or drink from water bodies, we recommend that streambank fencing be added, or reinforced, to prevent cattle from destroying the new riparian vegetation and further eroding riverbanks (Hafner and Brittingham, 1993).

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Table 1. Most parsimonious survivorship models based on monthly known fate data for *Glyptemys insculpta* in 1998 ($n = 22$) and 1999 ($n = 28$) at an agri-forest site in southern Québec, Canada.

| Year | Model | AIC$_c$ | $\Delta_i$ | $w_i$ | $K_i$ | Deviance |
|---|---|---|---|---|---|---|
| 1998 | {$S$(.)} | 21.09 | 0.00 | 0.615 | 1 | 7.88 |
|  | {$S$(g)} | 22.03 | 0.94 | 0.385 | 2 | 6.72 |
| 1999 | {$S$(.)} | 31.19 | 0.00 | 0.695 | 1 | 7.58 |
|  | {$S$(g)} | 32.84 | 1.65 | 0.305 | 2 | 7.17 |

Notation follows that of Anderson et al. (2000): (.) = constant across months; (g) = group-dependant; AIC$_c$ = Akaike Information Criterion, second order; $\Delta_i$ = AIC$_c$ differences; $w_i$ = Akaike weight; $K_i$ = parameter number.

Table 2. Monthly survivorship ($\hat{S}$) estimates for 22 *Glyptemys insculpta* (18 adults, 4 juveniles) tracked via radio-telemetry from May - September 1998 at an agri-forest site in Québec, Canada.

| | | | | 95 % CI | |
|---|---|---|---|---|---|
| Model | Group | $\hat{S}$ | SE | Upper | Lower |
| $\{S(.)\}$ | — | 0.977 | 0.016 | 0.913 | 0.994 |
| $\{S(g)\}$ | Adults | 0.986 | 0.014 | 0.908 | 0.998 |
| | Juveniles | 0.933 | 0.064 | 0.648 | 0.991 |
| Model averaging | Adults | 0.980 | 0.015 | 0.908 | 0.996 |
| | Juveniles | 0.960 | 0.035 | 0.745 | 0.995 |

(.) = constant across months; (g) = group-dependent.

Table 3. Monthly survivorship ($\hat{S}$) estimates for 28 *Glyptemys insculpta* (22 adults, 6 juveniles) tracked via radio-telemetry from March - September 1999 at an agri-forest site in Québec, Canada.

| | | | | 95 % CI | |
|---|---|---|---|---|---|
| Model | Group | $\hat{S}$ | SE | Upper | Lower |
| {*S*(.)} | — | 0.979 | 0.012 | 0.937 | 0.993 |
| {*S*(g)} | Adults | 0.983 | 0.012 | 0.935 | 0.996 |
| | Juveniles | 0.961 | 0.038 | 0.772 | 0.995 |
| Model averaging | Adults | 0.980 | 0.012 | 0.936 | 0.994 |
| | Juveniles | 0.974 | 0.020 | 0.880 | 0.995 |

(.) = constant across months; (g) = group-dependent.

Table 4. Intersexual differences in mutilation rates of *Glyptemys insculpta* inhabiting an agri-forest landscape in Québec, Canada.

| | Male | | Female | | Juvenile | | Total | |
|---|---|---|---|---|---|---|---|---|
| | *n* | % | *n* | % | *n* | % | *n* | % |
| 1995[a] | 16 | 81.2 | 13 | 69.2 | 4 | 50.0 | 33 | 72.7 |
| 1998 | 10 | 90.0 | 11 | 90.9 | 2 | 50.0 | 23 | 86.9 |
| 1999 | 15 | 93.3 | 16 | 87.5 | 7 | 57.1 | 38 | 84.2 |

[a]Data from Saumure and Bider (1998)

Table 5. Injuries to the shell, limbs, and tail of *Glyptemys insculpta* inhabiting an agri-forest landscape in Québec, Canada.

| Year | Sample Size | Carapace | | Plastron | | Limbs | | Tail | |
|---|---|---|---|---|---|---|---|---|---|
| | | *n* | % | *n* | % | *n* | % | *n* | % |
| 1995[a] | 33 | 17 | 51.5 | 7 | 21.2 | 5 | 15.2 | 18 | 54.5 |
| 1998 | 23 | 15 | 65.2 | 6 | 26.1 | 4 | 17.4 | 14 | 60.9 |
| 1999 | 38 | 26 | 68.4 | 11 | 28.9 | 6 | 15.8 | 21 | 55.3 |

[a] Data from Saumure and Bider (1998)

Table 6. Comparison of Carapace Mutilation Indices for 66 *Glyptemys insculpta* inhabiting an agri-forest landscape in Québec, Canada.

| Groups | *U* | df | *P* |
|---|---|---|---|
| Males vs. Females | 2.44 | 1 | 0.118 |
| Males vs. Juveniles | 7.04 | 1 | 0.008* |
| Females vs. Juveniles | 2.40 | 1 | 0.121 |

* indicates statistically significant difference

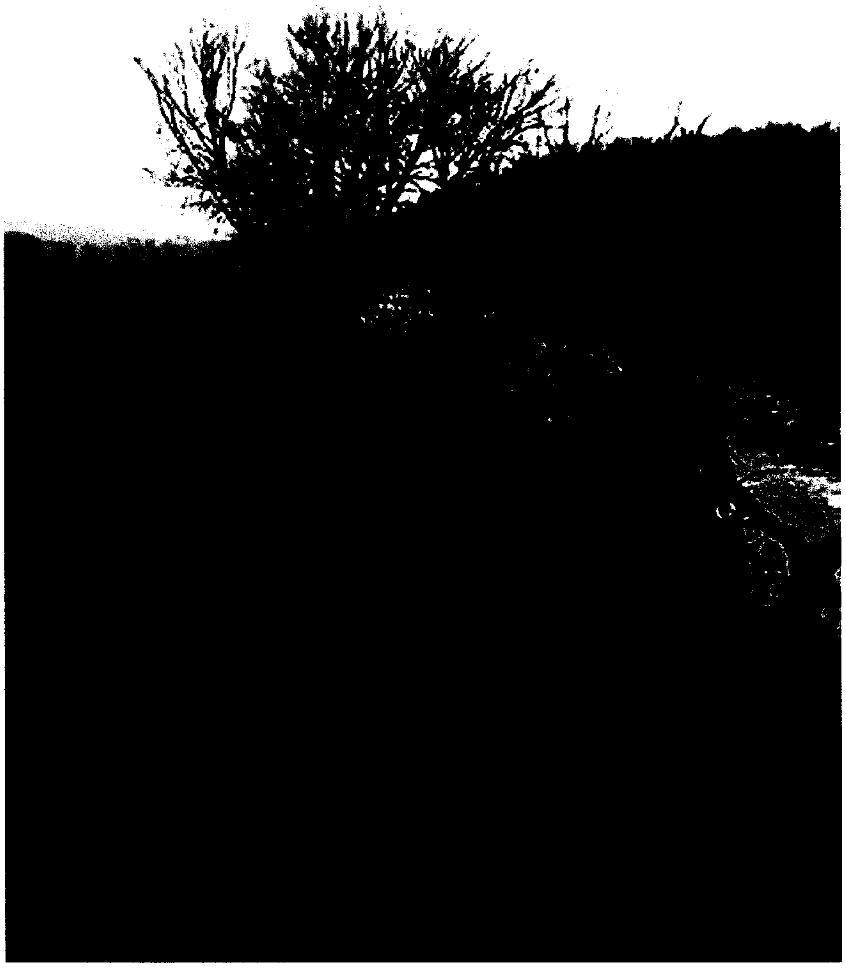
Figure 1. Extensive erosion of riverbanks along a pasture in Brome County, Québec, Canada.

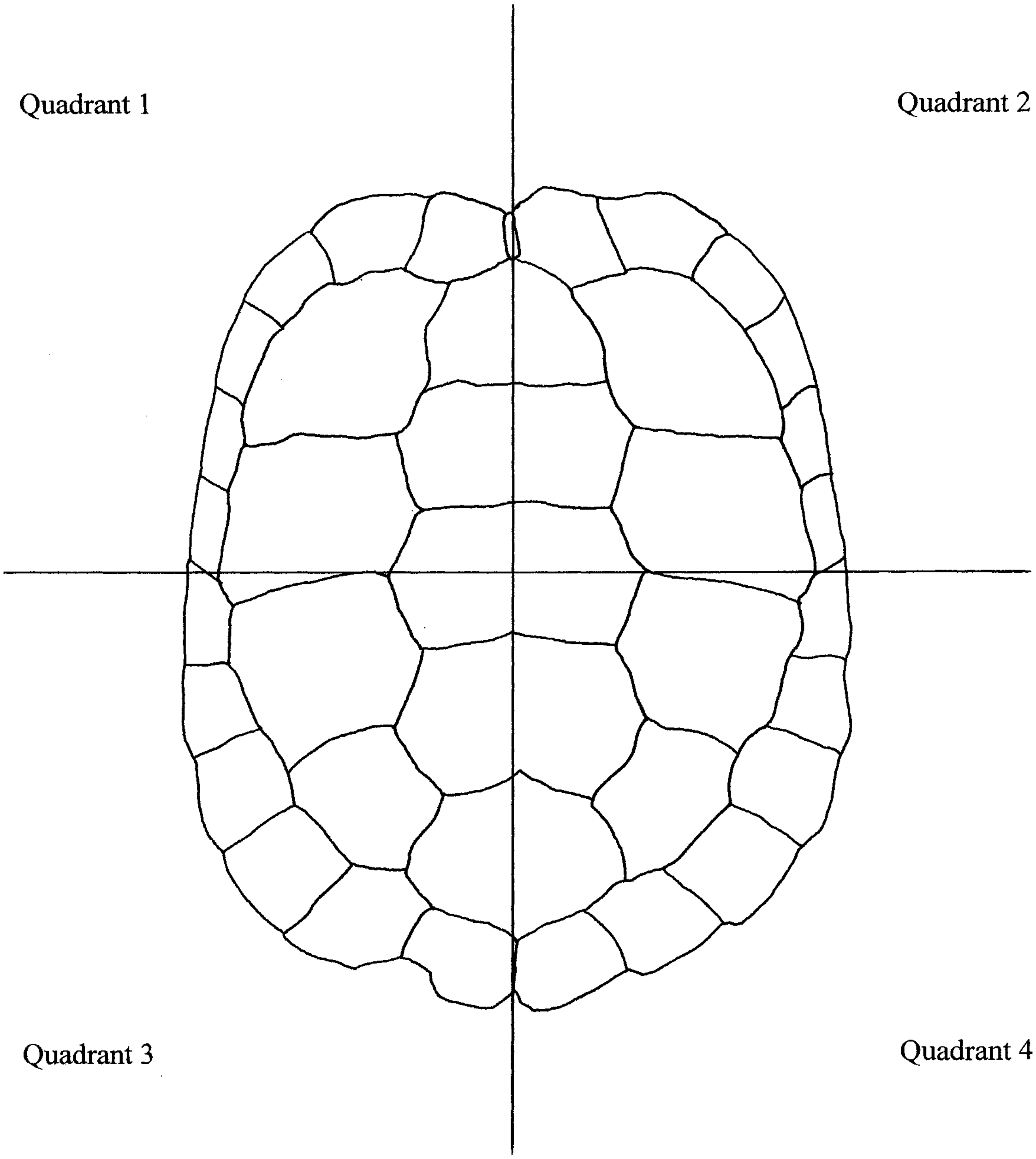
Figure 2. Temporary stabilization of hayfield riverbank with gravel dredged from the riverbed in Brome County, Québec, Canada.

Figure 3. Carapace Mutilation Index quadrants for calculating the severity of injuries sustained by turtles.

Figure 4. Tedder used to decrease drying time of cut hay and the source of some *Glyptemys insculpta* turtle mutilations.

Figure 5. Severely mutilated adult male *Glyptemys insculpta* (CMNAR # 35442) recovered from recently harvested hayfield in Brome County, Québec, Canada that clearly exhibits the dorso-lateral path of a disc mower blade.




Quadrant 1
Quadrant 2
Quadrant 3
Quadrant 4

# CONNECTING TEXT

The preceding chapter documented unsustainable rates of mortality and mutilation for a population of *Glyptemys insculpta* inhabiting a fragmented agri-forest landscape. No less than 20% of our subjects were at the wrong place, at the wrong time. In Chapter 3, we examine the spatial ecology of the turtles that survived. We compare the ranges of *G. insculpta* populations inhabiting areas with different levels of landscape alteration. To do so however, we explicitly defined standardized ranges. Moreover, the range sizes of our subjects were examined for correlations with turtle mass, length and injury intensity. Knowledge of which parameters influence the spatial ecology of *G. insculpta* will benefit future conservation initiatives.

# CHAPTER 3

## Beyond Home Ranges: Integral, Statistical, and Linear Ranges as Applied to the Wood Turtle, *Glyptemys insculpta*

> *"The diligent farmer plants trees,*
>
> *of which he himself will never see the fruit."*
>
> Marcus Tullius Cicero

# INTRODUCTION

Knowledge of the spatio-temporal distribution of wildlife is a fundamental component of conservation initiatives. One concept which has enabled biologists to quantify wildlife movements is home range (Burt, 1943). Home-range size is thought to be strongly correlated with energetic requirements and therefore, the spatio-temporal distribution of essential resources (McNab, 1963). Exogenous landscape alterations, however, have modified the natural distribution of these resources. Thus, wildlife residing within altered landscapes may adjust their movements in order to meet energetic requirements. McIntyre and Hobbs (1999) identify intact, variegated, fragmented, and relictual landscapes as four states along a continuum of destruction.

The North American wood turtle, *Glyptemys insculpta* (Le Conte, 1830), is ideal for research on the effects of anthropogenic disturbances due to its longevity, site fidelity, low vagility, and distribution (Garber and Burger, 1995). Wood turtles are semi-aquatic riparian obligates with a wide, yet patchy, distribution in the northeastern United States and southeastern Canada (Ernst et al., 1994). We believe the species is best characterized as disturbance-dependent; openings in the forest canopy are required for thermoregulation, egg incubation, and some foraging (Kaufmann, 1992; Compton et al., 2002; Arvisais et al., 2004). Today, such a propensity to occupy disturbed terrestrial habitats exposes *G. insculpta* to significant risk. For millennia, *G. insculpta* have relied on the protection afforded them by an armoured shell; an adaptation quickly becoming obsolete in a world of passenger vehicles and agricultural machinery (Ernst and McBreen, 1991; Saumure and Bider, 1998; Gibbs and Shriver, 2002; Chapter 2). Currently, *G. insculpta* are endangered in Iowa, threatened in Minnesota, New Jersey, Virginia, Wisconsin, and of special concern in all four Canadian provinces within their range (Levell, 2000).

Several authors have suggested that home-range size in *G. insculpta* may be positively correlated with increasing latitude, turtle density, or exogenous disturbances (Arvisais et al., 2002; Smith, 2002). Such analyses, however, are hampered by a lack of standardized methodologies for defining and estimating home ranges (Foscarini and Brooks, 1997; Smith, 2002; Tuttle and Carroll, 2003). The objectives of this paper are threefold: (*i*) to standardize methodologies for estimating ranges, (*ii*) to investigate the relationship between level of exogenous landscape alteration and range size, and (*iii*) to ascertain if correlations exist between range size and turtle mass, length and injury intensity.

## MATERIALS AND METHODS

*Study Site.*—This study took place from 7 May 1998 to 26 February 2000 at a site in Brome County, Québec, Canada. The site is ~ 150 km south of another intensively studied Québec population (i.e. Arvisais et al., 2002; 2004; Walde et al., 2003). Precise locality data for the imperilled *Glyptemys* are no longer divulged, as a direct consequence of the illicit live-animal trade. Research was conducted along 6.3 km of meandering river, of which ~ 1.5 km (24%) was dredged illegally in 1999 to temporarily alleviate bank erosion. The river was paralleled to the west by a rural two-lane highway and to the east by a railroad. Eleven tributary streams flowed into this river valley. The study area encompassed 330 ha of fragmented agri-forest landscape (*sensu* McIntyre and Hobbs, 1999; Jobin et al., 2003) comprising the following land classes: dairy farming 165 ha

(50%); forest 103 ha (31%); anthropogenic 18 ha (5%); cash crop 12 ha (3.5%); wetland 8 ha (2.5%); other 24 ha (8%). Briefly, dairy farming included hayfields, pastures, and old fields. Forest consisted of 40 remnant patches that ranged from 0.08 – 39.1 ha. The anthropogenic class includes housing, roads, and urban development. Cash crop is defined as cereals, cornfields, and ploughed fields. Wetlands were any water body including bogs, marshes, oxbows, rivers, sloughs, or swamps. Lastly, 'other' included the remaining unclassified areas. Detailed descriptions of this research site can also be found in Daigle (1997), Saumure and Bider (1998), and Chapter 2.

*Radio-telemetry.*—Wood turtles were captured opportunistically, marked, measured, and sexed following previously established protocols (Saumure and Bider, 1998; Chapter 2). An attempt was made to equip equal numbers of males, females, and juveniles with one of 30 radio-transmitters. A detailed description of the radio-telemetry equipment and methodology is given in Chapter 2. Turtles were located once or twice a week from 7 May to 25 September 1998 and from 29 March to 27 September 1999. Tracking was accomplished by two and four investigators in 1998 and 1999, respectively. In most cases, turtles were sighted but not physically handled. Sampling was sporadic during late fall and winter (23 Nov, 6 Dec 1998, 31 Jan 1999, 26 Feb 2000), with the sole objective of determining the location of dormant subjects / hibernacula. Capture sites were mapped on a 1:20,000 scale Government of Québec topographic map included on each field data sheet. Capture locations were subsequently plotted on 1:40,000 aerial orthophotograph base maps with ArcView® GIS 3.2a and Spatial Analyst (Environmental Systems Research Institute, Inc., California, USA). From these locations, ranges were calculated using the ArcView Animal Movement Extension (Hooge and Eichenlaub, 1997). Ranges were calculated only if ≥ 13 locations were recorded; which was sufficient to include at least one capture from each activity area (Springer, 1982).

*Ranges.*—Although not new concepts *per se*, three ranges are specifically named and defined: integral, statistical, and linear. An integral range is defined as a range that includes all locations recorded, regardless of whether such locations represent migration, emigration, or seemingly unusual movement. The integral range (*i*) is calculated with the minimum convex polygon (MCP) method (Mohr, 1947), (*ii*) can incorporate areas not known to be used by a given species, and (*iii*) is restricted to one complete annual cycle of activity, corresponding to a biologically relevant period for the organism under investigation (Powell, 2000). For temperate species such as *G. insculpta*, we define the annual cycle of activity to be between dormancy periods. This temporal constraint ensures that annual variability is not concealed by pooling data from several years. The statistical range differs from the integral range by excluding from calculations the ~ 5% of locations most distant from the harmonic mean. When 5% of locations represent < 1, one point is removed nonetheless. The linear range is defined as the straight-line distance between the two most widely-separated capture locations of all those recorded. All three range types clearly violate even the most concise biological definition of home range, which is "the area in which an animal normally lives, exclusive of migrations, emigrations, or unusual erratic wanderings" (Brown and Orians, 1970). Integral and statistical ranges include forays that are beyond or between home ranges, whereas linear range does not actually measure area.

*Spatial Ecology.*—Several factors, including sex, body size, and injuries may account for intrapopulation variability in range sizes. Turtles were sexed according to standard diagnostic features, as described in Saumure and Bider (1998). The most appropriate indices of body size in *G. insculpta* are mass and carapace length (CL) (Peters, 1983; Lovich et al., 1990). These data were recorded upon first capture of a given subject in 1998 or 1999. Mass is the more variable of the two measures, given that females are not necessarily gravid in consecutive years (Walde, 1998). Limb amputations and carapace mutilations were used as indices of injury in analyses of adult range-size variability. Juveniles were excluded from these analyses because of significantly lower mutilation rates compared to adults (Chapter 2). The ranges calculated for a single subject with a limb amputation were compared to the mean of sample ranges, following the method described in Sokal and Rohlf (1995). As the frequency distributions of these ranges were skewed to the right, all data were log transformed prior to analysis. To assess the impact of injuries that do not directly affect mobility, the range sizes of individuals with a Carapace Mutilation Index (CMI) $\geq 0.25$ were compared to those $< 0.25$ (Chapter 2).

## RESULTS

*Subjects.*—Thirty *G. insculpta* (13 males, 12 females, 5 juveniles) were tracked by radio-telemetry for periods of 51 to 507 days in 1998 – 99. Five subjects (2 males, 1 female, 2 juveniles) died during the study as a result of farming activities (see Chapter 2). Of note, one juvenile was entombed by the collapse of an eroding riverbank, whereas the second was buried during dredging operations to stabilize them. Only 24 subjects (11 males, 11 females, 2 juveniles) were recaptured $\geq 13$ times (Table 1). Of these, 14 were recaptured a sufficient number of times to allow range comparisons between years (Table 1). Juveniles # 104 and # 111a were 11 and 9 years old, respectively, in 1999.

Among adults, CL and mass of males exceeded those of females (Student's *t* CL = - 5.727, df = 20, $P < 0.0005$; mass = - 4.903, df = 19.6, $P < 0.0005$). Males first captured in 1998 were similar in size to those first captured in 1999 ($t = 1.679$, df = 8.9, $P = 0.128$).

Only two *G. insculpta* (1 male, 1 female) with amputated limbs were captured during the 1998 – 1999 study period. Male # 127b was captured first on 2 August 1998 and killed in early July 1999 (Chapter 2). Thus, too few capture locations were recorded in either year for accurate range estimates to be compiled. The female subject (# 19) had a posterior right limb amputated below the femur, an injury inflicted prior to 1995 (Saumure and Bider, 1998). This subject was tracked successfully in both years.

*Ranges.*—Integral, statistical, and linear ranges of the 22 adult and 2 juvenile turtles were calculated for each year (Table 1). In 1999, inclusion of the ranges of male # 102 resulted in skewness and kurtosis values exceeding 3 and 11. Thus, ranges in 1999 were not normally distributed, being skewed to the right and leptokurtic. This outlier subject was included in all statistical analyses nonetheless, as nonparametric statistical methods were used whenever possible. Previous investigators have included outlier subjects when compiling mean home-range sizes (Arvisais et al., 2002; Smith, 2002).

The mean ± SD of adult ranges are presented with the results of previous radio-telemetry studies of *G. insculpta* (Table 2 – 4). Median, dispersion, and skewness values are presented on a logarithmic scale with boxplots (Fig. 1, 2). There were no intersexual differences in range size in 1998 (Mann-Whitney *U*-test: Integral $U = 13.0$, $P = 0.205$; Statistical $U = 13.0$, $P = 0.205$; Linear $U = 9.0$, $P = 0.072$) or 1999 (Integral $U = 41.0$, $P = 0.324$; Statistical $U = 36.0$, $P = 0.181$; Linear $U = 32.0$, $P = 0.105$). Given the absence of intersexual differences, range data for all 24 subjects were pooled for inter-range comparisons. Integral ranges differed from statistical ranges in that the latter excluded a single outlier recapture point. As expected, this exclusion resulted in integral ranges being significantly larger than statistical ranges in 1998 (Wilcoxon signed ranks $Z = -3.059$, $P = 0.002$) and 1999 ($Z = -4.015$, $P = 0.0005$). Of note however, was that integral ranges were significantly smaller in 1998 than 1999 ($Z = 1.977$, $P = 0.048$); whereas, statistical ranges did not differ between years ($Z = 1.642$, $P = 0.101$). There was no yearly difference in linear range ($Z = 0.594$, $P = 0.552$).

Pearson product-moment correlations of adult turtle ranges vs CL and mass were compiled (Table 5). Significant correlations were detected among all three ranges and CL in 1998, but only for linear ranges in 1999. The Hadi multivariate outlier detection algorithm removed outliers prior to correlation analyses of 1999 range data (SPSS, 2000). A significant correlation between mass and 1998 linear ranges was also detected.

Range size did not vary with degree of carapace mutilation in 1998 (Integral $U = 30.0$, $P = 0.482$; Statistical $U = 33.0$, $P = 0.277$; Linear $U = 21.0$, $P = 0.655$) or 1999 (Integral $U = 69.0$, $P = 0.324$; Statistical $U = 68.5$, $P = 0.342$; Linear $U = 51.0$, $P = 0.778$). Moreover, the ranges of a female (#19) with an amputated posterior limb did not differ significantly from those of turtles with intact limbs. Analyses revealed that more than 5% of all ranges were as far from the mean as the 1998 (Integral $t = -0.2768$, Statistical $t = -0.4406$, Linear $t = -0.3854$; df = 13; $P > 0.05$) and 1999 (Integral $t = -0.3654$; Statistical $t = -0.2976$; Linear $t = -0.3815$; df = 21; $P > 0.05$) ranges of this female.

A comparison of reported integral and statistical ranges suggests that range size may be negatively correlated with degree of landscape alteration (Fig. 1, 2). When our statistical ranges for adults were compared to those presented in Arvisais et al. (2002), no significant difference in the distribution of adult ranges were detected for the first ($U = 153.5$, $P = 0.296$) or second year ($U = 245.0$, $P = 0.361$). However, a comparison of adult integral ranges from Smith's intact landscape (Smith 2002; unpubl. data) and those from our fragmented landscape revealed a significant difference ($U = 353.0$, $P = 0.022$).

## DISCUSSION

*Range Concept.*—From its inception, the definition of home range has been problematic. Home ranges are simply two-dimensional approximations of wildlife movements and thus, constructs of the human mind (Sanderson, 1966; Liro and Szacki, 1987). The borders of home ranges represent probability distributions (Hayne, 1949). Consequently, one cannot determine what might constitute "sallies outside the home range" (Burt, 1943) while simultaneously trying to define the home range itself (Liro and Szacki, 1987). The concept of normality is equally ambiguous, as one cannot objectively determine what normal is (Dice and Clark, 1953; White and Garrott, 1990; Blundell et al., 2001). Such inadequacies have led to a fundamental shift away from the biological home-range, which has been superseded by a statistical one: the utilization distribution. This statistical interpretation of home range is defined as the smallest area which accounts for a given animal's location 95% of the time (Jennrich and Turner, 1969). Regardless, several authors consider the home-range concept obsolete (White and Garrott, 1990; Gautestad and Mysterud, 1995).

The selection of an appropriate estimator of home-range size is critical to an accurate assessment of an animal's spatial requirements. Current estimators are numerous and consist of the following: quadrat summation (Haugen, 1942); minimum convex polygon (Mohr, 1947); harmonic mean (Dixon and Chapman, 1980); Fourier transform (Anderson, 1982); and kernels (Worton, 1989; Seaman and Powell, 1996). Only the MCP and kernel estimators are still widely used. Unfortunately, the various methods used to calculate home ranges are neither comparable nor transformable (Mohr, 1947; Hayne, 1949; Jennrich and Turner, 1969; Anderson, 1982; Rose, 1982; Lawson and Rodgers, 1997). Nonetheless, researchers often draw inferences from comparisons of studies that use different estimators (e.g. Arvisais et al., 2002; Smith, 2002). The validity of such an approach is questionable. Instead, we chose to define three ranges based on commonly used methodologies in order to ensure the validity of comparisons between studies. The nonparametric 100% MCP method has fallen into relative disfavour, being regarded as a mediocre estimator that is most appropriate for a quick estimate (Anderson, 1982; Boulanger and White, 1990). Others, however, advocate its use because of the unequivocal within-study repeatability and between-study comparability (Rose, 1982; Kazmaier et al., 2002). The main disadvantage of the MCP is the sample size bias (e.g. Anderson, 1982). For instance, although no inter-year differences were detected for either statistical or linear ranges, analyses revealed that integral ranges were smaller in 1998 than 1999. As this was a pair-wise comparison, the additional subjects tracked in 1999 did not affect the analysis. Dahle and Swenson (2003) noted a relationship between number of locations recorded and size of 100% MCP, but not 95% MCP. Thus, the significant difference in integral ranges is most likely the result of fewer locations being recorded in 1998. No other inter-year differences in ranges were detected.

The ranges defined herein provide three distinct measures of the spatial ecology of *G. insculpta*. Integral ranges reveal the total estimated spatial requirements of individual turtles. Contrary to home ranges, integral ranges may include: (*i*) short-duration, long-distance, movements to nesting sites, (*ii*) forays to seasonal food patches, (*iii*) seasonal migrations to hibernacula, and/or (*iv*) long-distance aquatic patrols of males. By definition, all such movements are excluded from home ranges (*sensu* Burt, 1943). Integral ranges are well-suited for studies of imperilled species because they include all habitats critical to the survival of individuals and populations. Although integral ranges may include areas little used by individual turtles, such habitats may be critical for certain life stages.

Ranges should not be construed as being independent of the landscape. Sanderson (1966) stressed that to evaluate the effects of habitat on an animal's movements, researchers must know what lies adjacent to that habitat. Interestingly, Powell (2000) notes that patches without food resources are rarely, if ever, visited specifically "because of the animal's familiarity with them". Consequently, unused patches within ranges should be viewed as impact areas, which are areas "through which an animal travels and on which its presence impacts occasionally" (Springer, 1982). The inclusion of impact areas within ranges is supported by ecological processes such as landscape complementation, supplementation, connectivity, source-sink dynamics, and neighbourhood effects (Dunning et al., 1992; Taylor et al., 1993). We stress, however, that range studies should not be interpreted as *de facto* studies of habitat selection.

Statistical ranges differ from integral ranges by the exclusion of ~ 5% of outlier points, i.e. one outlier point per statistical range in this study. Nevertheless, statistical ranges are conceptually different, as they are a statistical approximation of the area within which one has an approximately 95% chance of encountering a given turtle. Whereas *G. insculpta* integral ranges displayed significantly different size distributions between years, statistical ranges did not. This suggests that the exclusion of ~ 5% of outlier points, in this case a single location, imparts a measure of stability to inter-year comparisons. Dahle and Swenson (2003) made a similar observation for *Ursus arctos* and concluded that the exclusion of outlying capture locations rendered 95% MCP home range estimates less dependent on sample sizes. Although we believe integral ranges are ideal for conservation applications, statistical ranges seem more appropriate for within and possibly between study comparisons. We agree that the spatial ecology of a species might be better understood by using more than a single measure of range to quantify movements (Sanderson, 1966; Anderson, 1982; Tiebout and Cary, 1987).

The purpose of a linear range is to estimate the breadth of an animal's movements. Given the propensity of *G. insculpta* to use rivers and streams as movement corridors, linear ranges may be particularly useful as estimators of aquatic habitat requirements. For instance, linear ranges can be used to establish the length of proposed 300 m wide riparian protection zones (Burke and Gibbons, 1995; Compton, 1999; Arvisais et al., 2002; Semlitsch and Bodie, 2003). As a one-dimensional measurement, linear ranges also assist in deciphering the annual variability observed in integral or statistical ranges.

White and Garrott (1990) note that biological definitions of home range are inadequate because they fail to include a time frame. Tuttle and Carroll (2003) suggest a minimum of one full season to estimate home range size in *G. insculpta*. Conversely, others propose that the time required to delimit a home range can be determined empirically, based on the minimum number of capture locations required to obtain an asymptotic cumulative area curve (e.g. Rose, 1982; Tiebout and Cary, 1987). Springer (1982), however, demonstrates that the number of capture locations *per se* is not as important as including at least one point from each activity area. Thus, by definition, we stipulate that integral, statistical, and linear ranges are to include a complete cycle of annual activity, i.e. between dormancy periods. We believe this to be the most appropriate "biologically meaningful period of time", as admonished by Powell (2000). The absence of such a logical temporal restriction in the past has led to the compilation of *G. insculpta* "home ranges" based upon extremes of two months and up to five years of data (i.e. Ross et al., 1991; Kaufmann, 1995). Given the well-documented inter-annual variability of wood turtle home ranges (Kaufmann, 1995; Arvisais et al., 2002), such comparisons are not likely to be valid. We believe that the ranges described herein meet the criteria of objectivity and repeatability stipulated by Powell (2000).

*Morphology.*—Home-range size is believed to be positively correlated with energetic requirements, and thus body size, in certain mammals, birds, and lizards (McNab, 1963; Peters, 1983). As *G. insculpta* exhibit sexual size dimorphism in favour of males (Harding and Bloomer, 1979; Lovich et al., 1990), one would expect males to have larger home ranges. Previous home-range studies on *G. insculpta*, however, have not supported this hypothesis (e.g. Kaufmann, 1995; Arvisais et al., 2002; Tuttle and Carroll, 2003). Likewise, we did not detect intersexual differences in the size of integral, statistical, or linear ranges during our investigation. Compton et al. (2002) propose that the selection of resources by the omnivorous *G. insculpta* is a learned response, constrained by high site fidelity and relatively low vagility. Thus, the distributions of preferred food resources are likely strong determinants of individual range size. Indeed, habitat selection studies confirm that individual wood turtles exhibit strong habitat preferences (Kaufmann, 1992; Compton et al., 2002). It is perhaps not surprising then, that investigators have not detected significant correlations between home range and mass (Kaufmann, 1995; Arvisais et al., 2002) or carapace length (Tuttle and Carroll, 2003). Our study, however, revealed positive correlations between adult carapace length and the size of integral, statistical, and linear ranges in 1998. This correlation, however, held only for linear ranges in 1999. We suggest that this temporal disparity reflects landscape alterations that occurred during the second year of our study. Specifically, a quarter of the main aquatic corridor used by *G. insculpta* for ranging movements was dredged in an attempt to shore up the highly eroded banks. The impact of such large-scale habitat destruction is compounded further by annual habitat alterations at this site, which temporarily displace and restrict turtle movements, i.e. haying operations (Chapters 2, 4).

The single correlation between mass and linear ranges in 1998 likely reflects three factors. Firstly, the linear ranges of adult males were longer, on average, than those of females (Table 4). This discrepancy was not as great in 1999, presumably because of the destruction of the riparian corridor. Secondly, female nesting migrations do not necessarily occur in consecutive years, further exacerbating between-year comparisons (Table 1). Walde (1998) found that only the largest *G. insculpta* nested in consecutive years during a two-year study. Lastly, we reiterate that although female mass was recorded in both years, we used female mass upon first capture for analyses. Thus, these data include the masses of both gravid and non-gravid females.

*Injuries.*—Harding (1985) observed that the recapture rate of *G. insculpta* with amputated limbs was significantly lower than for intact specimens. One might be inclined to attribute this decrease in survivorship to decreased mobility. Indeed, Claussen et al. (1997) have noted that the complete amputation of the posterior right limb of a *Terrapene ornata* affected path sinuosity, length, and turning angles. Although our sample size was limited, the ranges of the single female with a partial posterior limb amputation did not differ from those of the non-impaired sample population. Moreover, Smith (2002) tracked a female with a completely amputated posterior left limb for 51 days and reported a "home range" of 110 ha. Previously, Quinn and Tate (1991) documented a maximum "activity area" of 115 ha for an intact specimen from the same area. These observations demonstrate that posterior limb amputations do not necessarily decrease mobility. The buoyancy afforded such turtles by water may assist them when travelling long-distances in aquatic corridors.

The range sizes of turtles with relatively high indices of carapace mutilation did not differ from those with only minor or no injuries. This suggests that the movements of *G. insculpta* exposed to sub-lethal shell trauma are not curtailed, at least not in the long-term. We note, however, that subjects with severe injuries were completely healed at the onset of our study, some of which were known to have occurred prior to 1995 based on the data of Daigle (1997) and Saumure and Bider (1998). Thus, the mutilated turtles tracked during our study represent only the movements of those which had fully recovered from their injuries. Nichols (1939) briefly described that a *Terrapene carolina* recovered from unspecified, but serious, injuries by confining its movements to a swamp during a protracted period of convalescence.

*Populations.*—Morrow et al. (2001) suggested that increases in bog turtle (*Glyptemys muhlenbergii*) home range size might indicate a degradation of site quality. Indeed, when our site was degraded further by dredging operations, range sizes increased. Our analyses suggest a negative relationship between range size and degree of landscape alteration (Tables 2, 3; Fig.1, 2). The mean integral ranges for the adult *G. insculpta* from our fragmented agri-forest landscape fall between those of relictual and intact landscapes (Table 2). As suggested by McCurdy (1995) and Arvisais et al. (2002), relictual landscapes likely inhibit widespread terrestrial movements by *G. insculpta*. Indeed, reciprocally transplanted *G. insculpta* in Nova Scotia have shown that home-range size is site-dependent (McCurdy, 1995). Turtles with large home ranges at a variegated boreal forest site immediately restricted their movements when displaced to a relictual agricultural landscape. Conversely, those from the agricultural landscape wandered extensively when translocated to the forest. Range size in *G. insculpta* may be primarily determined by the distances between essential resources (i.e. foraging areas, hibernacula, water, and nesting sites). In bank voles (*Clethrionomys glareolus*), a small woodland species, movements are more extensive in heterogeneous farmland (Kozakiewicz et al., 1993). This may be a result of essential resources being more widely distributed among smaller forest patches (Dunning et al., 1992). As a disturbance-dependent species, the opposite is true for *G. insculpta*. Compton et al. (2002) recently demonstrated that habitat selection in wood turtles is scale-dependent. At a watershed scale, *G. insculpta* activity areas are close to flowing water, possess moderate forest cover, and are relatively dry. Within activity areas, however, the species selects non-forested areas with low canopy cover that are close to water. Thus, using a simplistic patch-matrix analogy, we propose that the dense canopy of an intact forest represents the matrix. Patches of suitable habitat within this matrix will occur primarily at riparian ecotones and openings created by natural processes such as fire, flooding, wind, and/or ecosystem engineering by beavers (*Castor canadensis*). Recent habitat selection studies support this contention (Compton et al., 2002; Arvisais et al., 2004). Due to the stochastic spatio-temporal nature of such processes, larger ranges are expected for *G. insculpta* populations residing within intact forests, as opposed to those in fragmented or relictual agricultural landscapes. This is precisely what we documented when comparing integral ranges from fragmented and intact landscapes (Fig. 2). However, we did not detect a significant difference in the distribution of statistical ranges in variegated and fragmented landscapes (Fig. 1). Several factors may explain this result. Firstly, Arvisais et al. (2002) specifically state that they did not randomly select their radio-telemetry subjects. Instead, subjects were selected based on capture location, which likely introduced a sampling bias. Secondly, the disturbance-dependent *G. insculpta* may not perceive a difference between these two arbitrarily described levels of landscape alteration. Finally, the available data are quite limited, with only one population for each level of landscape alteration.

Kaufmann (1995) suggested that *G. insculpta* inhabiting relatively nutrient-poor northern forests may be forced to travel farther in order to fulfil their energetic requirements. However, net primary productions in wetland habitats, temperate coniferous, temperate deciduous, and cultivated land are 2,500, 1,300, 1,200, and 644

$g/m^2/yr$, respectively (Smith, 1990). A review of the literature reveals that wetlands are relatively abundant in variegated and intact riparian habitats (Saumure and Bider, 1998; Arvisais et al., 2002; Smith, 2002) but are relatively rare in fragmented or relictual agricultural sites (Foscarini, 1994; Saumure and Bider, 1998). Thus, net primary productivity may be greater at northern sites, as these have experienced fewer exogenous disturbances. Historically, shallow wetlands were some of the first riparian habitats to be drained and exploited for their rich organic soils. In fact, agricultural development is primarily responsible for the loss of 54% of the wetlands in the United States (Goudie, 1990). The higher net productivity of intact and variegated landscapes may also account for the significantly larger *G. insculpta* encountered at northern sites (e.g. Daigle, 1997; Saumure and Bider, 1998; Walde et al., 2003). Further research is required to test this hypothesis.

Arvisais et al. (2002) noted a tendency for mean home-range sizes to increase with latitude. The data presented herein do not refute this alternative hypothesis. Indeed, a latitudinal trend is apparent for the limited number of integral and statistical ranges compiled thus far. However, the variability in range size within populations appears to be greater than between them. Within any given *G. insculpta* population, there appears to be both relatively sedentary and somewhat nomadic individuals. For instance, Arvisais et al. (2002) noted a subgroup of four females which had mean home ranges almost four times greater than the remaining female subjects. Interestingly, these females travelled the farthest and frequented the portion of the study site most impacted by anthropogenic landscape alterations.

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Table 1. Integral, statistical and linear ranges of 24 *Glyptemys insculpta* inhabiting a fragmented agri-forest landscape in southern Québec, Canada.

| Turtle | Sex | Carapace Length (mm) | Mass (g) | No. of Locations | | Integral Range (ha) | | Statistical Range (ha) | | Linear Range (m) | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | 1998 | 1999 | 1998 | 1999 | 1998 | 1999 | 1998 | 1999 |
| 2 | M | 197.65 | 1125 | — | 18 | — | 9.1 | — | 8.4 | — | 528 |
| 6 | M | 205.20 | 1225 | 18 | 21 | 31.2 | 69.9 | 22.6 | 43.1 | 1982 | 2440 |
| 7 | M | 203.00 | 1150 | 13 | 5 | 34.6 | — | 32.1 | — | 1430 | — |
| 9 | M | 201.50 | 1175 | 6 | 19 | — | 31.1 | — | 28.8 | — | 1387 |
| 25 | M | 199.95 | 1150 | 14 | 23 | 10.1 | 14.9 | 10.1 | 12.8 | 651 | 724 |
| 102 | M | 192.85 | 1100 | 2 | 21 | — | 173.7 | — | 170.7 | — | 5160 |
| 106 | M | 193.20 | 1050 | — | 20 | — | 13.7 | — | 13.5 | — | 767 |
| 111b | M | 196.60 | 1175 | 20 | 25 | 4.7 | 4.4 | 2.9 | 4.4 | 800 | 760 |
| 116 | M | 193.90 | 935 | 6 | 20 | — | 10.2 | — | 9.0 | — | 510 |
| 121 | M | 206.45 | 1225 | 16 | 22 | 16.2 | 13.2 | 16.0 | 11.9 | 1642 | 1688 |
| 130 | M | 206.00 | 1225 | — | 24 | — | 19.5 | — | 19.1 | — | 1344 |
| 8 | F | 190.15 | 990 | — | 17 | — | 5.7 | — | 3.5 | — | 440 |
| 12 | F | 172.85 | 730 | 16 | 24 | 3.2 | 7.5 | 3.1 | 7.4 | 481 | 717 |
| 19 | F | 192.45 | 980 | 18 | 29 | 7.8 | 11.5 | 5.8 | 9.6 | 709 | 739 |
| 20 | F | 177.10 | 1040 | 11 | 18 | — | 34.6 | — | 31.0 | — | 1052 |
| 23 | F | 181.50 | 1025 | 18 | 26 | 2.0 | 8.7 | 2.0 | 7.4 | 400 | 649 |
| 24 | F | 187.15 | 940 | 17 | 24 | 19.8 | 20.4 | 19.5 | 19.5 | 727 | 649 |
| 26 | F | 175.40 | 875 | 13 | 27 | 5.7 | 5.5 | 5.7 | 2.7 | 617 | 517 |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 110 | F | 193.90 | 970 | 19 | 20 | 27.6 | 5.4 | 14.4 | 3.1 | 1248 | 627 |
| 112 | F | 188.20 | 1050 | 19 | 22 | 23.3 | 25.9 | 21.5 | 25.1 | 884 | 805 |
| 117 | F | 185.00 | 960 | 16 | 24 | 9.4 | 10.7 | 9.3 | 10.7 | 707 | 678 |
| 118 | F | 171.10 | 800 | 17 | 21 | 5.5 | 44.3 | 5.4 | 23.5 | 895 | 1898 |
| 104 | J | 151.65 | 505 | 19 | 27 | 5.8 | 15.9 | 3.9 | 11.1 | 711 | 797 |
| 111a | J | 154.20 | 440 | — | 20 | — | 32.4 | — | 12.5 | — | 1283 |

Table 2. Integral ranges (mean ± SD) of adult *Glyptemys insculpta* from three populations with different degrees of exogenous landscape alteration.

| Location | Land Use | Year | n | No. of Locations | Sex | Integral Range (ha) | Citation |
|---|---|---|---|---|---|---|---|
| Québec (45°N) | Agri-Forest (fragmented) | 1998 | 5 | 81 | M | 19.4 ± 13.1 | This Study |
| | | | 9 | 153 | F | 11.6 ± 16.4 | |
| | | 1999 | 9 | 213 | M | 36.0 ± 51.9 | |
| | | | 11 | 252 | F | 16.4 ± 13.3 | |
| | | 1998 | 14 | 234 | M&F | 14.4 ± 11.1 | |
| | | 1999 | 20 | 465 | M&F | 25.7 ± 37.4 | |
| Ontario (43°N) | Agriculture (relictual) | 1991 | 6 | — | M | 5.0 ± 2.9 | Foscarini (1994) |
| | | | 4 | — | F | 6.4 ± 3.7 | |
| Ontario (46°N) | Forest (intact) | 2000 | 24 | 687 | M&F | 31.8 ± 30.6 | Smith (2002) |

Table 3. Statistical ranges (mean ± SD) of adult *Glyptemys insculpta* from two Québec populations with different degrees of exogenous landscape alteration.

| Latitude | Land Use | Year | n | No. of Locations | Sex | Statistical Range (ha) | Citation |
|---|---|---|---|---|---|---|---|
| 45°N | Agri-Forest (fragmented) | 1998 | 5 | 81 | M | 16.7 ± 11.3 | This Study |
| | | | 9 | 153 | F | 9.6 ± 7.2 | |
| | | 1999 | 9 | 213 | M | 32.2 ± 50.0 | |
| | | | 11 | 252 | F | 13.0 ± 10.0 | |
| | | 1998 | 14 | 234 | M&F | 12.2 ± 9.1 | |
| | | 1999 | 20 | 465 | M&F | 22.2 ± 35.6 | |
| 46°N | Forest (variegated) | 1996 | 4 | 90 | M | 32.1 ± 38.7 | Arvisais et al. (2002) |
| | | | 14 | 311 | F | 25.9 ± 32.9 | |
| | | 1997 | 6 | 125 | M | 29.1 ± 20.0 | |
| | | | 14 | 324 | F | 29.4 ± 37.8 | |
| | | 1996 | 17 | 401 | M&F | 27.2 ± 33.1 | |
| | | 1997 | 20 | 449 | M&F | 29.3 ± 32.9 | |

Table 4. Linear ranges (mean ± SD) of adult *Glyptemys insculpta* inhabiting a fragmented agri-forest landscape in southern Québec, Canada.

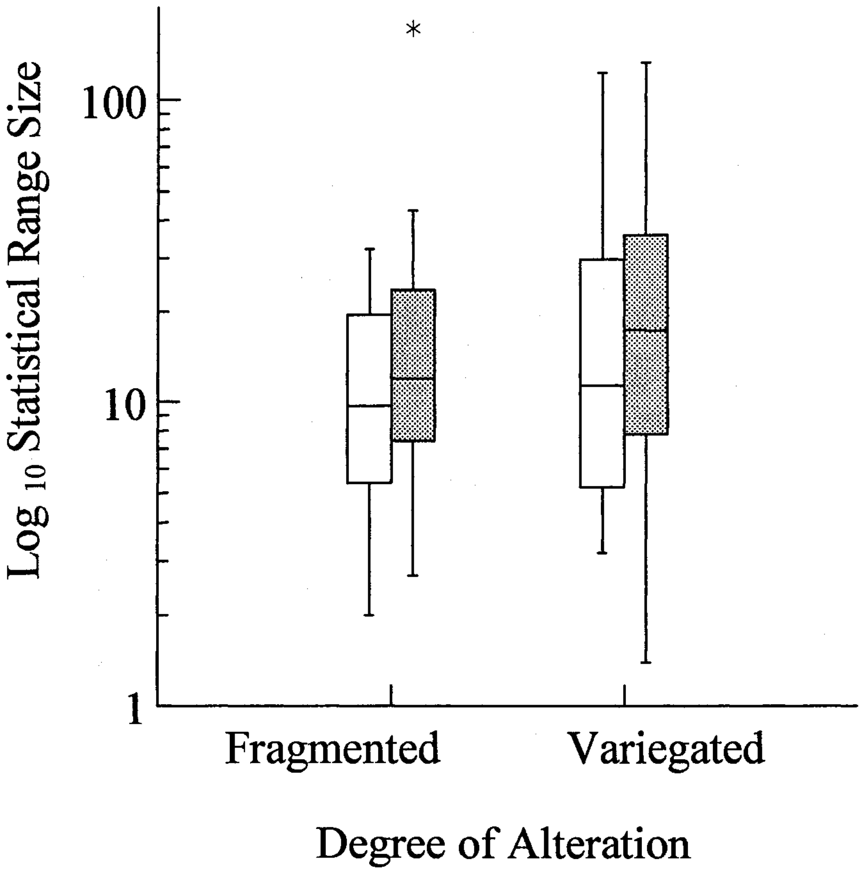
| Location | Land Use | Year | n | No. of Locations | Sex | Linear Range (m) |
|---|---|---|---|---|---|---|
| Québec | Agri-Forest | 1998 | 5 | 81 | M | 1301 ± 564 |
| | | | 9 | 153 | F | 741 ± 251 |
| | | 1999 | 9 | 213 | M | 1531 ± 1412 |
| | | | 11 | 252 | F | 797 ± 397 |
| | | 1998 | 14 | 234 | M&F | 941 ± 463 |
| | | 1999 | 20 | 465 | M&F | 1147 ± 1057 |

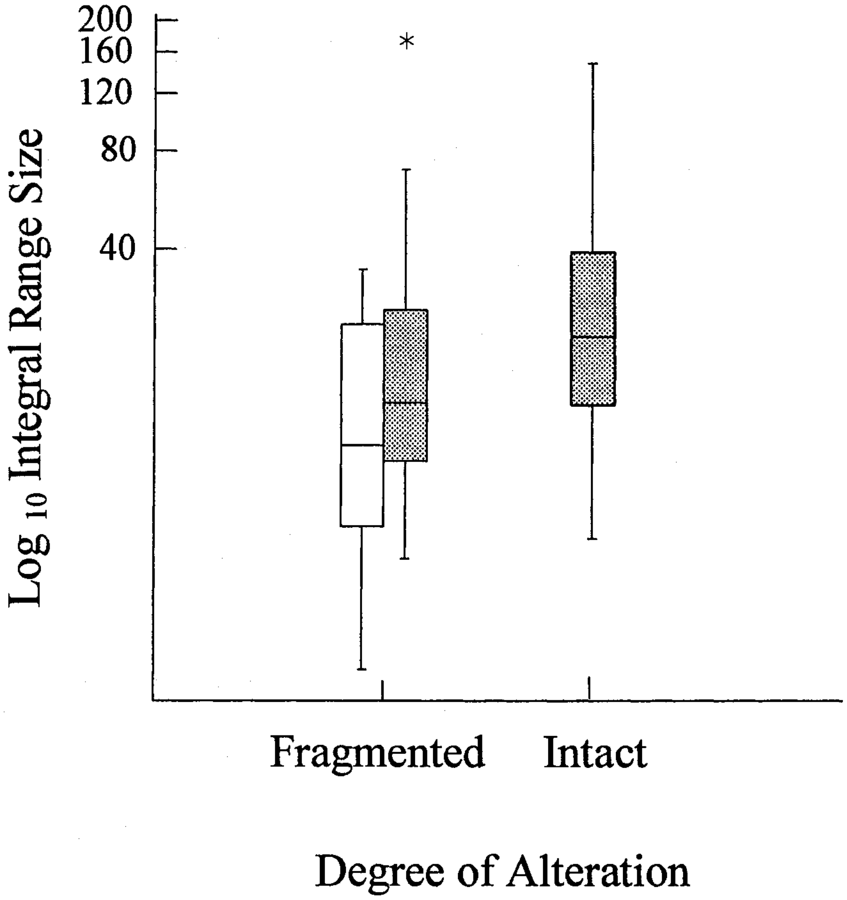
Table 5. Pearson product-moment correlations ($r$) between annual integral, statistical, and linear ranges and carapace length (CL) and mass of *Glyptemys insculpta* inhabiting a fragmented agri-forest landscape. ($r_h$) Hadi multivariate outlier detection algorithm removed outliers prior to correlation analyses in 1999. (*) denotes a significant correlation.

| | Integral | | Statistical | | Linear | |
|---|---|---|---|---|---|---|
| | 1998 | 1999 | 1998 | 1999 | 1998 | 1999 |
| CL | $r = 0.626$ | $r_h = - 0.214$ | $r = 0.597$ | $r_h = 0.164$ | $r = 0.712$ | $r_h = 0.511$ |
| | $P = 0.017$* | $P = 0.351$ | $P = 0.024$* | $P = 0.476$ | $P = 0.004$* | $P = 0.018$* |
| Mass | $r = 0.473$ | $r_h = 0.319$ | $r = 0.482$ | $r_h = 0.332$ | $r = 0.616$ | $r_h = 0.213$ |
| | $P = 0.087$ | $P = 0.159$ | $P = 0.081$ | $P = 0.141$ | $P = 0.019$* | $P = 0.354$ |

Figure 1. $\text{Log}_{10}$ statistical range sizes of *Glyptemys insculpta* populations from fragmented (this study) and variegated (Arvisais et al., 2002) landscapes in southern Québec, Canada. Clear and shaded boxes indicate first and second years of study, respectively.

Figure 2. $\text{Log}_{10}$ integral range sizes of *Glyptemys insculpta* populations from fragmented (this study) and intact (Smith, 2002) landscapes. Clear and shaded boxes indicate first and second years of study, respectively.


Log 10 Statistical Range Size
100
10
1
*
Fragmented
Variegated
Degree of Alteration


200
160
120
80
40
Log 10 Integral Range Size
*
Fragmented
Intact
Degree of Alteration

## CONNECTING TEXT

Although we determined the ranges of *Glyptemys insculpta* in a fragmented agri-forest landscape, relatively little is known about the fine-scale movements of the species. In Chapter 4, an experimental approach is used to elucidate the effects of patch size and habitat structure on path sinuosity, turning angle, and move length of translocated male *G. insculpta*. In addition, the hayfield patch-matrix design allowed us to examine paths for any discernable movement patterns.

# CHAPTER 4

## Effects of Patch Size and Habitat Structure on the Movements of Adult Male Wood Turtles, *Glyptemys insculpta*

*"Behold the turtle:*

*He only makes progress when he sticks his neck out."*

James Bryant Conant

## INTRODUCTION

Knowledge of wildlife movement patterns within fragmented ecosystems is essential for the success of conservation efforts (Taylor et al., 1993; Harrison and Fahrig, 1995). Since the early 17th century, deforestation has resulted in the loss of an estimated 160 million ha of natural forest in temperate North America (Goudie, 1990). Since 1994, Canada alone has harvested over one million ha of forest per year (Environment Canada, 2003). For threatened and endangered species exposed to such exogenous disturbances (i.e. of recent, often human-induced, origin), a detailed understanding of landscape connectivity is vital. Taylor et al. (1993) defined landscape connectivity as "the degree to which the landscape facilitates or impedes movement among resource patches".

One particularly well-suited organism for experimental studies on the effects of exogenous landscape alterations is the North American wood turtle, *Glyptemys insculpta* (Garber and Burger, 1995). Wood turtles are semi-aquatic riparian obligates which range widely throughout the northeastern United States and Canada (Harding and Bloomer, 1979). They are a disturbance-dependent species, requiring openings in the forest canopy for foraging and thermoregulation (Harding and Bloomer, 1979; Compton et al., 2002). Thus, *G. insculpta* are often encountered in agricultural landscapes, with individuals frequenting pastures, hayfields, and other croplands such as cornfields (Kaufmann, 1992; Niederberger and Seidel, 1999; Ernst, 2001; Chapter 2). However, movement within these habitats exposes *G. insculpta* to agricultural machinery, which results in unsustainable levels of mutilation and mortality (Saumure and Bider, 1998; Chapter 2).

The lack of research specifically addressing the effects of patch size and habitat structure on turtle movements has prompted us to examine how such landscape variables affect the movement patterns of *G. insculpta*. A hayfield patch-matrix design was deemed most appropriate due to: (*i*) the prevalence of hayfields throughout the species' range, (*ii*) the documented use of hayfields by wood turtles, and (*iii*) the high mortality and mutilation rates documented therein. The objectives of our study were twofold: (*i*) to ascertain whether adult male wood turtles translocated to a hayfield patch-matrix exhibit discernable movement patterns, and (*ii*) to determine the effects of habitat structure and patch size on path sinuosity, turning angle, and move length (*sensu* Turchin, 1998). We hypothesized that wood turtle path characteristics were independent of patch size and habitat structure (i.e. patch vs. matrix).

## MATERIALS AND METHODS

*Subjects.*—Wood turtles (*Glyptemys insculpta*) were obtained from an agricultural site in southern Québec from 20 July to 15 August, 2000. This source population has been described in detail elsewhere (Daigle, 1997; Saumure and Bider, 1998; Chapter 2). Our experiment was conducted with male subjects only, thus eliminating intersexual effects and avoiding disturbances to mature females. Moreover, current theory suggests that males frequently have enhanced spatial abilities as a result of greater mobility (Gaulin and FitzGerald, 1989; Gibbons et al., 1990; Williams et al., 1990; Roof and Havens, 1992). Turtles with potentially debilitating injuries were excluded, since amputations can affect path length, sinuosity, and turning angles (Claussen et al., 1997). Turtles were displaced for periods up to, but not exceeding, seven days.

*Study site.*—Turtles were translocated approximately 100 km NW to two contiguous hayfields comprised of 6.2 ha at the Macdonald Campus Farm Field Unit of McGill

University in Ste-Anne-de-Bellevue, Québec. Both were composed of a mixture of smooth brome (*Bromus inermis*) and reed canary (*Phalaris arundinacea*) grasses. The hayfields also contained cow vetch (*Vicia cracca*) and scattered common milkweed (*Asclepias syriaca*). The fields are considered quasihomogeneous, which is defined as a scale of heterogeneity that is less than the scale of the subject's dispersal (Turchin, 1998). At the onset of experimentation, hay height varied from approximately 0.66 – 1.00 m.

*Techniques.*—Dense vegetation invariably hampers the sighting, and thus capture, of turtles in mid-summer (Lovich et al., 1992). However, our subjects were captured readily since they had been equipped with radio-telemetry transmitters as part of a previous study. At the onset of experimentation, turtles were captured at the agricultural site and held temporarily in large cotton bags during field transport. Subjects were transferred to large 68 L Rubbermaid® containers upon reaching a vehicle. Each container was filled with water, to a depth of approximately 5 cm, in order to ensure that subjects were hydrated. We then transported the turtles to the experimental site. Once on site, subjects were equipped with a thread-trailing device (Breder, 1927; Schwartz and Schwartz, 1974). Previous research has demonstrated that thread-trailers do not significantly affect the movements of box turtles (*Terrapene c. carolina*), a smaller terrestrial species (Stickel, 1950). We used a thread-trailer model that was very similar to that of Claussen et al. (1997). Different colors of thread were used for each turtle to avoid confusion during data recording. The compilation of thread-trail data was performed at the conclusion of the experiment rather than after each set of trials, as the act of mapping the paths could seriously disturb the structure of the hayfield. Thread-trailers and transmitters were removed at the conclusion of trials. Turtles were then returned to their respective points of origin within the source population. Our mapping procedures were similar to those of Claussen et al. (1997). Paths were plotted for analyses using ArcView® GIS software (Environmental Systems Research Institute, Inc., Redlands, Calif. USA).

*Patch Experiment.*—The patch experiment was designed to determine the importance of patch size and habitat structure on the fine-scale movements of wood turtles. Patches are defined as areas with relatively high probability of encountering resources surrounded by areas where the probability is essentially nil (Bell, 1991). This latter non-habitat area is classically referred to as 'the matrix', characterized by low structural complexity and viewed as an ecologically neutral area (Wiens, 1995). Turtles were released in the center of two circular patches (one 30 m diameter, one 15 m diameter) of uncut hayfield surrounded by a harvested area, i.e. the matrix. A circular shape was chosen to ensure a constant radial distance to the patch perimeter, enabling comparisons of movements in any direction. The 30 m diameter patch was the largest that could be created while still leaving ≥ 8 m of mowed matrix. The other was 15 m, half the diameter of the larger patch.

Subjects were placed in each patch for one experimental trial. In order to limit the effects of prior exposure, turtles were randomly assigned to their initial patch. Trials began by placing a turtle equipped with a thread-trailer at the center of each patch. Subjects were then permitted to move undisturbed for 24 hours. Choice of this time period reflected: (*i*) thread spool length limitations, (*ii*) patch sizes, and (*iii*) known mean displacement of 108 ± 90 m per 24-hour period (Strang, 1983). Path end points were staked and marked with flagging tape at the end of each trial. A move is defined as "a segment of a path between two consecutive stopping points" (Turchin, 1998). Thus, move length is simply the length of a given path segment.

*Statistics.*—Wood turtle paths were analyzed by several statistical methods. Sinuosity was estimated by the ratio of $d/L$; where $d$ is the greatest distance between any two points on a given path, and L is the total path length. This index produces a numerical value ranging from 0 to 1, with increasing values indicating straighter paths. This measure of sinuosity is particularly suited for the analyses of paths of homing and/or transient animals (Claussen et al., 1997). When comparing the effects of habitat structure (i.e. patch vs. matrix) on path sinuosity, a constant L value was used, as recommended by Claussen et al. (1997). As a result, in most cases only a portion of the path data beyond the perimeter of each patch was used. This portion of path corresponded exactly to the length of the path laid down within the patch. Sinuosity and move length data were compared using paired-sample *t*-tests.

Turning bias in the initial five post-release moves was calculated *a posteriori*. To calculate turning bias, right and left turning angles were designated as positive and negative, respectively. These signed turning angles were summed and their mean was calculated (Bell, 1991). Contingency tables for analyses of overall directional biases in turning angles were analyzed with the adjusted G-tests of independence ($G_{adj}$) using William's correction (Sokal and Rohlf, 1995; Turchin, 1998). Common statistical analyses were accomplished using version 10 of SYSTAT® (SPSS Inc., Chicago, Ill. USA). Statistical tests were set at $\alpha = 0.05$.

## RESULTS

*Subjects.*—Six adult male wood turtles of similar size were used in our trials. Mean measurements, expressed as mean ± SD (range), were: Carapace Length = 197.8 ± 3.10 mm (193.8 – 201.9 mm); Carapace Width = 148.5 ± 4.54 mm (141.9 – 154.1 mm); Plastron Length = 176.9 ± 4.62 mm (171.7 – 184.0 mm); Mass = 1104.2 ± 29.2 g (1075 – 1150 g).

*Analysis of movements.*—Most paths were characterized by an initial series of relatively short moves that produced an arc away from the release point (Fig. 1, 2). A *posteriori* examination of initial turning bias (i.e. the first five moves) revealed a negative (left) turning bias in 8 of 11 (72.7%) of the paths (Table 1). One perfectly straight path was excluded from turning bias calculations. Although there were significantly more left turns within patches (right:left = 0.705:1, $N = 133$, $X^2 = 3.98$, $P < 0.05$) (Fig. 3), there was no significant difference in turning frequencies for moves beyond the patches (right:left = 0.724:1, $N = 50$, $X^2 = 1.28$, $P > 0.05$) (Fig. 4). However, a comprehensive analysis of all turning angles within the 15 and 30 m patches revealed an absence of 1st order serial autocorrelations in turning angles ($G_{adj} = 2.36$, $P > 0.05$). Moves beyond the two patches were also sequentially independent ($G_{adj} = 0.50$, $P > 0.05$). Interestingly, turning angles within patches were as wide as 150° (Fig. 3); whereas, those in the matrix only reached 120° (Fig. 4). We observed that the arced portions of paths ended abruptly and were followed by a series of unidirectional zigzag moves. None of the turtles chose to remain within the experimental patches and none crossed their own paths during a trial.

*Structural complexity.*—We compared path sinuosity for movements within and beyond the perimeter of 15 m and 30 m un-mowed hayfield patches (Table 2). A definite trend towards straighter paths beyond the perimeter of the 15 m patch was detected ($t$ = - 2.371, $P$ = 0.064). Paths beyond the perimeter of the 30 m patch were significantly straighter than those within ($t$ = - 8.865, $P$ = 0.001). Mean move lengths within vs. beyond the 15 m patch did not differ significantly ($t$ = - 1.792, $P$ = 0.133) (Table 3). Conversely, mean move lengths made beyond the 30 m patch were significantly longer than those within it ($t$ = - 5.022, $P$ = 0.004) (Table 3).

*Patch size.*—Fine-scale movements of each turtle were plotted (Fig. 1, 2). A comparison of within-patch sinuosity (d/L) between 15 m and 30 m patches revealed no significant difference ($t$ = 1.081, $P$ = 0.329) (Table 2). Moreover, no differences were detected in path sinuosity beyond the perimeter of the two patches ($t$ = 0.562, $P$ = 0.598) (Table 2). A comparison of mean lengths for moves within the 15 and 30 m patches revealed no significant differences ($t$ = 0.749, $P$ = 0.488) (Table 3). Similarly, no differences in mean lengths for moves beyond the two patches were detected ($t$ = - 0.066, $P$ = 0.950) (Table 3).

## DISCUSSION

The paths we observed can be classified into three previously described movement phases: (*i*) agitation dispersal, (*ii*) local search, and (*iii*) ranging (Bell, 1991; Turchin, 1998). Herein, we define agitation dispersal as innate movement in response to a stressor, i.e. a classic flight response. Agitation dispersal manifested itself as an arc in the initial post-release path of a given wood turtle (Fig. 1, 2). Such post-release arcs have been noted during other studies of *Glyptemys insculpta* (Barzilay, 1980; McCurdy, 1995). Barzilay (1980) suggested that the arcs resulted from initial periods of disorientation in unfamiliar environments. McCurdy (1995), however, disputed the disorientation hypothesis because his subjects had not been translocated, and were thus still within their activity areas. Rather, he interpreted arcs as an initial flight followed by topographic orientation (Jander, 1975). Our interpretation that taxis is a manifestation of agitation dispersal, however, corroborates both of the aforementioned theories: an innate flight response precludes orientation, where orientation is defined as the mechanism responsible for the recognition and maintenance of direction (Bell, 1991). Cabanac and Bernieri (2000) recently demonstrated that, despite appearances, wood turtles experience tachycardia as a result of even short-term gentle handling. Researchers desiring to reduce agitation dispersal movements might benefit from using the release method described in Yeomans (1995). This method uses a rudimentary pulley system to release subjects from beneath buckets after a predetermined period.

Our analyses of path turning characteristics revealed that turtles exhibited a left turning bias within patches (Fig. 3). Moreover, this bias was real and not the result of serial autocorrelations in turning angles. Casteel (1911) first described the development of right or left turning bias in painted turtles (*Chrysemys picta*) used in behavioural experiments that employed mild electric shock as negative reinforcement. The shock, or anticipation thereof, might be sufficient to result in the expression of an innate movement bias. Subsequent research on the same species, but without electrical stimulation, did not detect any turning bias (Ortleb and Sexton, 1964). Claussen et al. (1997) did not detect a turning bias in the paths of *in situ* ornate box turtle, *Terrapene ornata*. Intuitively, a bias in taxis must result from a series of asymmetrical movements. We propose two mechanisms, acting alone or in combination, that may account for such results. Firstly, wood turtles *in situ* exhibit 'handedness' (unpubl. data), a phenomenon recorded previously in frogs, lizards, and even snakes (Dill, 1977; Willard, 1977; Deckel, 1995; Oseen et al., 2001; Roth, 2003). This is perhaps not surprising given the ability of *G. insculpta* to manipulate food with their forelimbs (Carr, 1952; Babcock, 1971; Harding and Bloomer, 1979). Behavioural asymmetry is thought to be a result of hemispheric specialization, a tangible expression of the lateralization of the nervous system (McKeever, 1991). Recent research has found that turtles have shared neural circuitry for two non-related functions (i.e. scratching and swimming), which suggests other movements may also be linked (Berkowitz, 2002). Secondly, *G. insculpta* are the only species of turtle known to possess a diagonal sequence gait (Hildebrand, 1966; Zug, 1971; pers. obs.). Gait has been shown to influence the fine-scale paths of cockroaches (Bell, 1991; Turchin, 1998). During agitation dispersal, innate biases in gait are expressed.

Once physiological stress responses have abated, wood turtles enter a local search phase. Transition between the first two movement phases is quite pronounced (Fig. 1, 2). *G. insculpta* movements during the local search phase were characterized primarily by unidirectional series of zigzag moves. Similar unidirectional movements have also been observed in homing experiments with the terrestrial eastern box turtle, *Terrapene c. carolina* (Lemkau, 1970). Zigzagging is thought to be a mode of movement used when physical orientation cues are absent (Bell, 1991; Andreassen et al., 1996*a*). Additionally, it is likely to be more effective at producing forward movement than attempting to move in a perfectly straight line (Bell, 1991). Functionally, zigzag movements may have been the result of: (*i*) deflection by the patchy distribution of hay stems (Goodwin and Fahrig, 2002), (*ii*) visual obstruction produced by the vertical structure of a mature hay crop, and (*iii*) an artifact of gait (Bell, 1991; Turchin, 1998). However, one wood turtle (# 25, Fig.1) transected the radius of the 15 m patch without deviation or deflection, regardless of the structural complexity of the intervening vegetation (Fig. 1). This individual may simply have by-passed the agitation dispersal phase of movement. Intraspecific differences in post-handling behaviour have long been recognized in turtles (e.g. Casteel, 1911; Gould, 1957; Belinky and Belinky, 1974). Thus, it is not surprising that turtle # 25, as well as another specimen, began two additional paths in the local search phase (# 119, Fig. 1; # 25, Fig. 2). Although these paths comprised seemingly broad arcs, a closer examination reveals that these 'arcs' each contained a series of unidirectional zigzag movements, but in two different directions. In these cases, handling stress may not have resulted in flight, but rather in the chelonian 'refuge strategy' (i.e. withdrawal into relative safety of the shell). Once the stress had abated, the turtles then became active. Tinklepaugh (1932) observed that a male wood turtle withdrew for periods ranging from minutes to hours. Direct observations of wood turtle movements during further experiments may reveal how turtles react to perceived threats. If wood turtles do not flee a rapidly approaching disc mower, for instance, such inaction may have fatal consequences and thus, direct conservation implications. Such information is particularly relevant since the source population, from which our turtles originated, experiences extremely high mortality and mutilation rates (Saumure and Bider, 1998; Chapter 2).

Our results are consistent with the null hypothesis that path characteristics of adult male *G. insculpta* are independent of patch size. One could argue that an insufficient difference existed between the two patch diameters to elicit a change in search strategies. Animals in unfamiliar areas, however, move to maximize the likelihood of locating resources, while minimizing the probability of revisiting previously searched areas (Bell, 1991). This is precisely what we observed, as none of our subjects crossed their own paths and both patches were evacuated within the 24 hour trial periods. In the absence of information on patch size, our translocated turtles probably defaulted to predetermined search phenotypes. Our results demonstrate the consistency of path characteristics within quasi-homogeneous patches up to 30 m in diameter. Such a patch represents a diameter 150 times that of the mean CL of our subjects. This scale is consistent with the distance wood turtles will venture away from 'edge' habitats into hayfields in agricultural areas (Tuttle, 1996; unpubl. data).

Bell (1991) defined 'ranging' as movements beyond a patch or resource while in search of another, regardless of the orientation mechanism used. Ranging is characterized by a decrease in local search movements (*sensu* Bell, 1991) and an increase in linear displacement. Current theory suggests that changes in habitat structure will produce noticeable changes in movement patterns of animals (Wiens et al., 1985; Bell, 1991). Indeed, our data refute the null hypothesis that path characteristics of adult male *G. insculpta* are independent of structural complexity. When paths within and beyond the 30 m patch were compared, paths through the mowed matrix were straighter and mean move lengths were longer. Although a similar trend was observed in the 15 m patch trials, the lack of statistical significance may be attributed to limitations imposed by the patch size itself. Specifically, sample sizes were smaller because turtles required fewer moves to reach the patch perimeter. Nonetheless, a behavioural response to the change in habitat structure was observed. Voles, snakes, and insects have also been shown to exhibit changes in movement patterns when crossing through exposed or resource-poor habitats (Heinrich, 1979; Tiebout and Cary, 1987; Andreassen et al., 1996*b*; Gillis and Nams, 1998; Berggren et al., 2002). Since ranging can be interpreted as a form of area-avoidance behaviour, recently harvested hayfields can be viewed then as a 'temporal matrix'. Researchers have only just begun to investigate the effects of temporal variability on landscape connectivity in agricultural landscapes (Baudry et al., 2003).

Our findings demonstrate that translocated adult male wood turtles venture into, and cross, a harvested hayfield despite the presence of a high boundary contrast, or 'hard edge'. Moreover, the absence of back-tracking or deflection at patch perimeters indicates that this occurs without any hesitation (Fig. 1, 2). Thus, the boundary permeability of our experimental hayfield patch-matrix was 100%. Given that boundary permeability was absolute, one might suggest that wood turtles do not regard the mowed hayfield as a non-habitat matrix. However, the combination of straighter paths, longer moves, and observations of turtles *in situ* (Chapter 2) indicate otherwise.

Typically, organisms that are foraging successfully perform large dimension turns when they encounter a patch border (Bell, 1991). This implies that *G. insculpta* were not foraging, at least not successfully, within our patches. Moreover, our initial handling and presence likely inhibited foraging (Hassell and Southwood, 1978). We believe that our translocated subjects were exhibiting predator-avoidance behaviour. Although handling the wood turtles may have induced the movement patterns we observed, prior experience may have also been a factor. The wood turtles used in our experiment had survived biannual haying operations unscathed. Wood turtles *in situ* have been observed to evacuate hayfields at the onset of haying (Chapter 2). Although neither the auditory cues nor the ground vibrations emanating from mowing machinery in close proximity were present during our experimental trials, wood turtles may have detected the distinct odour of cut hay. Barzilay (1980), using anosmic and control animals, found that wood turtles rely primarily on their sense of smell to home. Olfaction appears to be well developed and an important cue in the movements of several turtle species (Chelazzi and Delfino, 1986; Graham et al., 1996; Quinn and Graves, 1998). Thus, we suspect that prior experience with agricultural machinery rendered our subjects highly motivated to evacuate our experimental patch-matrix.

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Table 1. Initial bias in right (+) and left (-) turning angles of adult male *Glyptemys insculpta* moving away from a central release point within 15 m and 30 m diameter hayfield patches. The (*) indicates that the turtle was randomly selected to undergo the first trial in the 15 m patch.

| Turtle # | 15 m patch | 30 m patch |
|---|---|---|
| 2 | - 37.4° | - 12.0° |
| 15 | + 6.4° | - 4.6° |
| 25* | no bias | + 14.2° |
| 102* | - 32.0° | - 27.2° |
| 111 | - 12.4° | - 51.8° |
| 119* | - 14.2° | + 1.4° |

Table 2. Path sinuosity (*d*/L) of adult male *Glyptemys insculpta* moving within and beyond the perimeter of 15 m and 30 m diameter un-mowed hayfield patches. The (*) indicates turtles that were randomly selected to undergo the first trial in the 15 m patch.

| Turtle # | 15 m patch |  | 30 m patch |  |
|---|---|---|---|---|
|  | Within | Beyond | Within | Beyond |
| 2 | 0.745 | 0.929 | 0.833 | — |
| 15 | 0.864 | 0.990 | 0.887 | 0.995 |
| 25* | 0.995 | 1.000 | 0.368 | 0.510 |
| 102* | 0.801 | 0.963 | 0.806 | 0.976 |
| 111 | 0.892 | 0.836 | 0.617 | 0.832 |
| 119* | 0.611 | 0.746 | 0.659 | 0.849 |

Table 3. Mean length of moves for adult male *Glyptemys insculpta* moving within and beyond the perimeter of 15 m and 30 m diameter hayfield patches. Number of moves indicated by N.

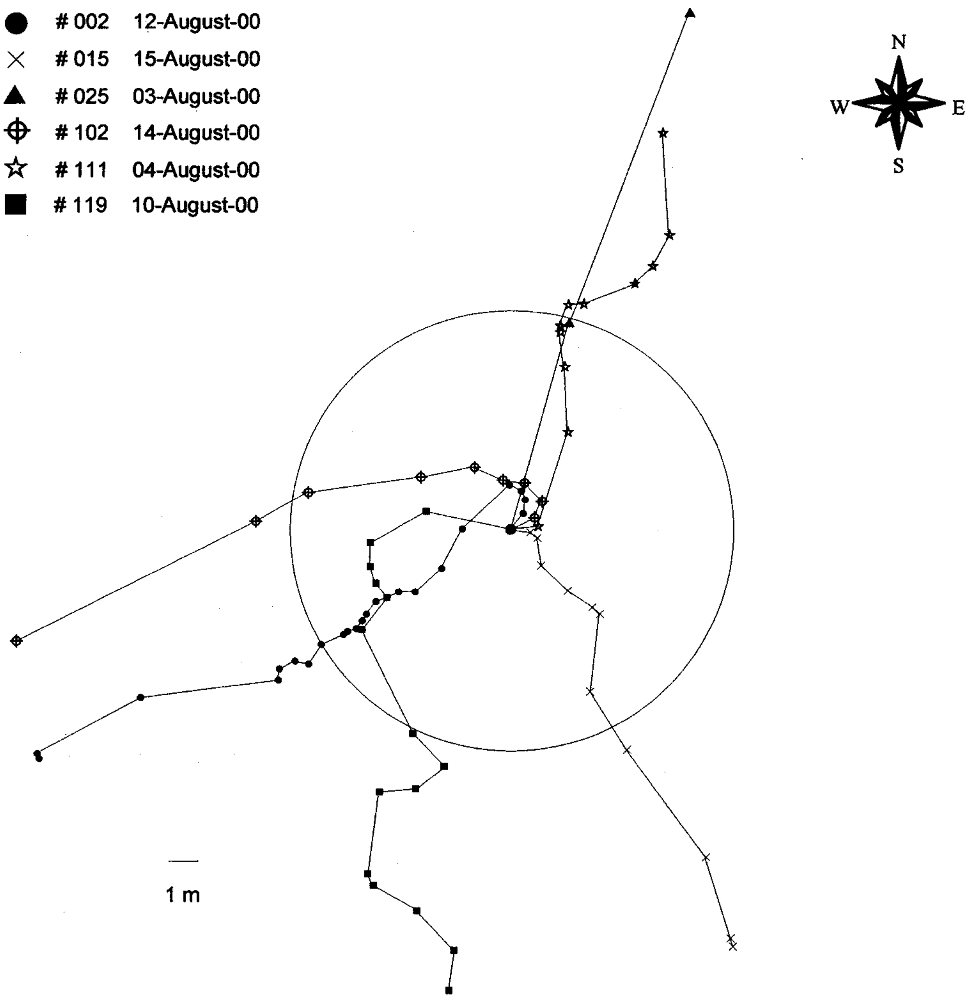
| | 15 m patch | | | | 30 m patch | | | |
|---|---|---|---|---|---|---|---|---|
| Turtle # | N | Within (cm) | N | Beyond (cm) | N | Within (cm) | N | Beyond (cm) |
| 2 | 15 | 75.8 | 7 | 165.1 | 9 | 200.0 | 1 | 555.0 |
| 15 | 8 | 123.5 | 3 | 316.0 | 12 | 134.1 | 2 | 862.0 |
| 25 | 1 | 745.0 | 1 | 1,150.0 | 22 | 190.9 | 7 | 565.3 |
| 102 | 8 | 153.7 | 1 | 1,210.0 | 21 | 81.0 | 5 | 430.6 |
| 111 | 6 | 148.7 | 5 | 182.0 | 15 | 231.7 | 7 | 384.0 |
| 119 | 7 | 181.7 | 8 | 169.4 | 17 | 139.5 | 8 | 485.2 |

Figure 1. Paths of six adult male *Glyptemys insculpta* within and beyond a 15 m diameter hayfield path-matrix. Perimeter of hay patch indicated by circle.

Figure 2. Paths of six adult male *Glyptemys insculpta* within and beyond a 30 m diameter hayfield path-matrix. Perimeter of hay patch indicated by circle.

Figure 3. Frequency of right (+) and left (-) turning angles of six adult male *Glyptemys insculpta* moving within 15 m and 30 m hayfield patches.

Figure 4. Frequency of right (+) and left (-) turning angles of six adult male *Glyptemys insculpta* moving through the matrix beyond 15 m and 30 m hayfield patches.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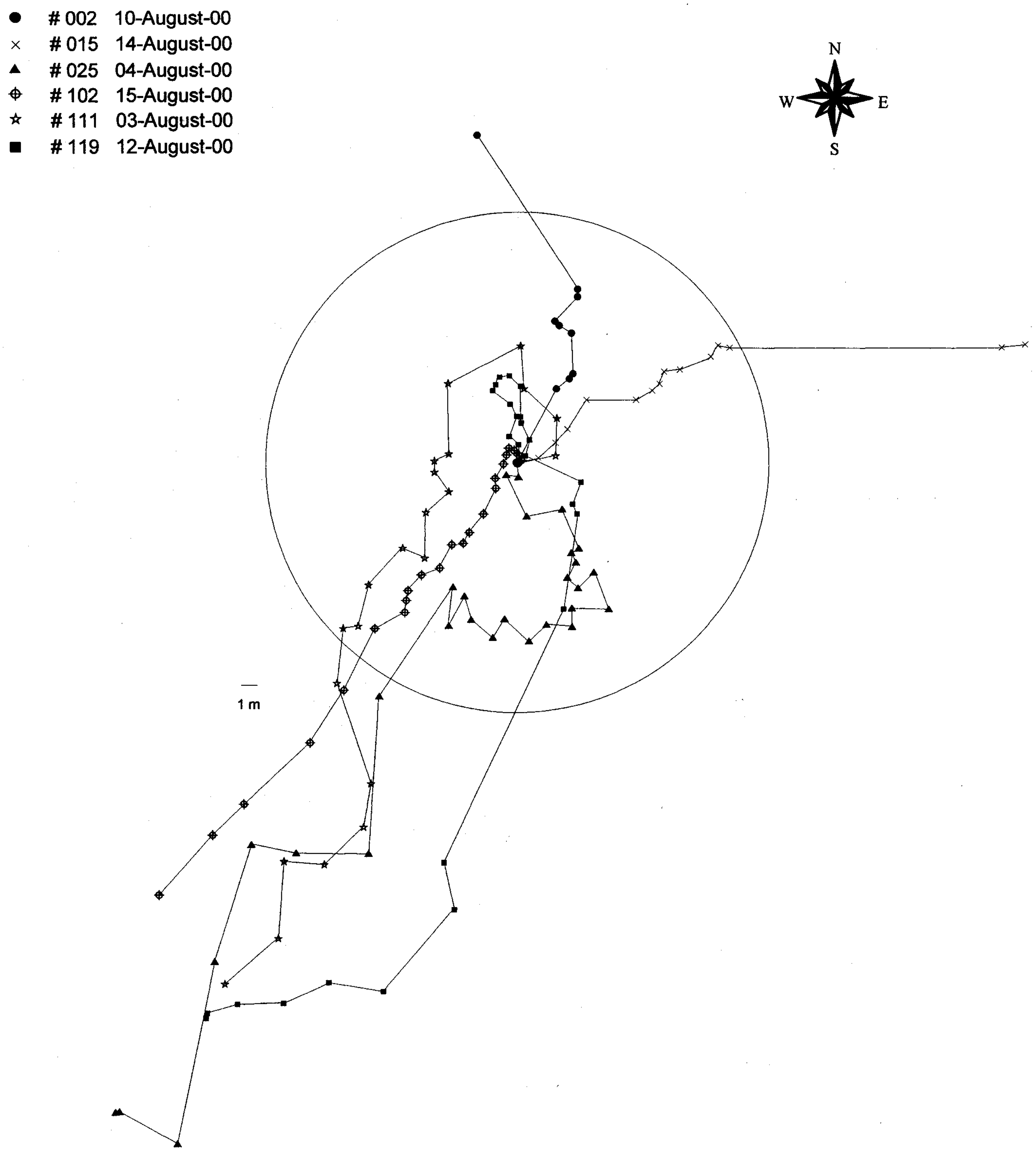
× # 015 15-August-00
▲ # 025 03-August-00
⊕ # 102 14-August-00
☆ # 111 04-August-00
■ # 119 10-August-00
N
W
E
S
1 m



● # 002 10-August-00
× # 015 14-August-00
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⊕ # 102 15-August-00
☆ # 111 03-August-00
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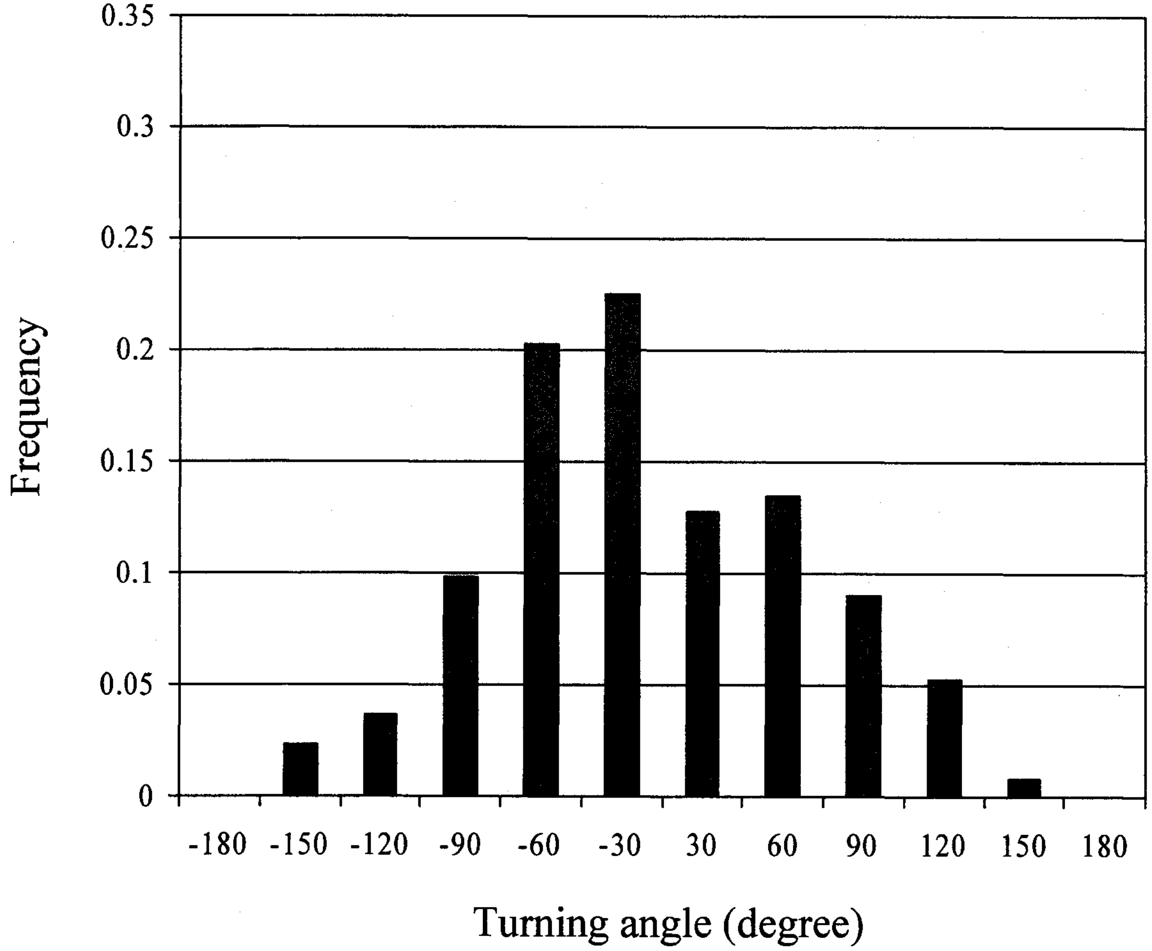
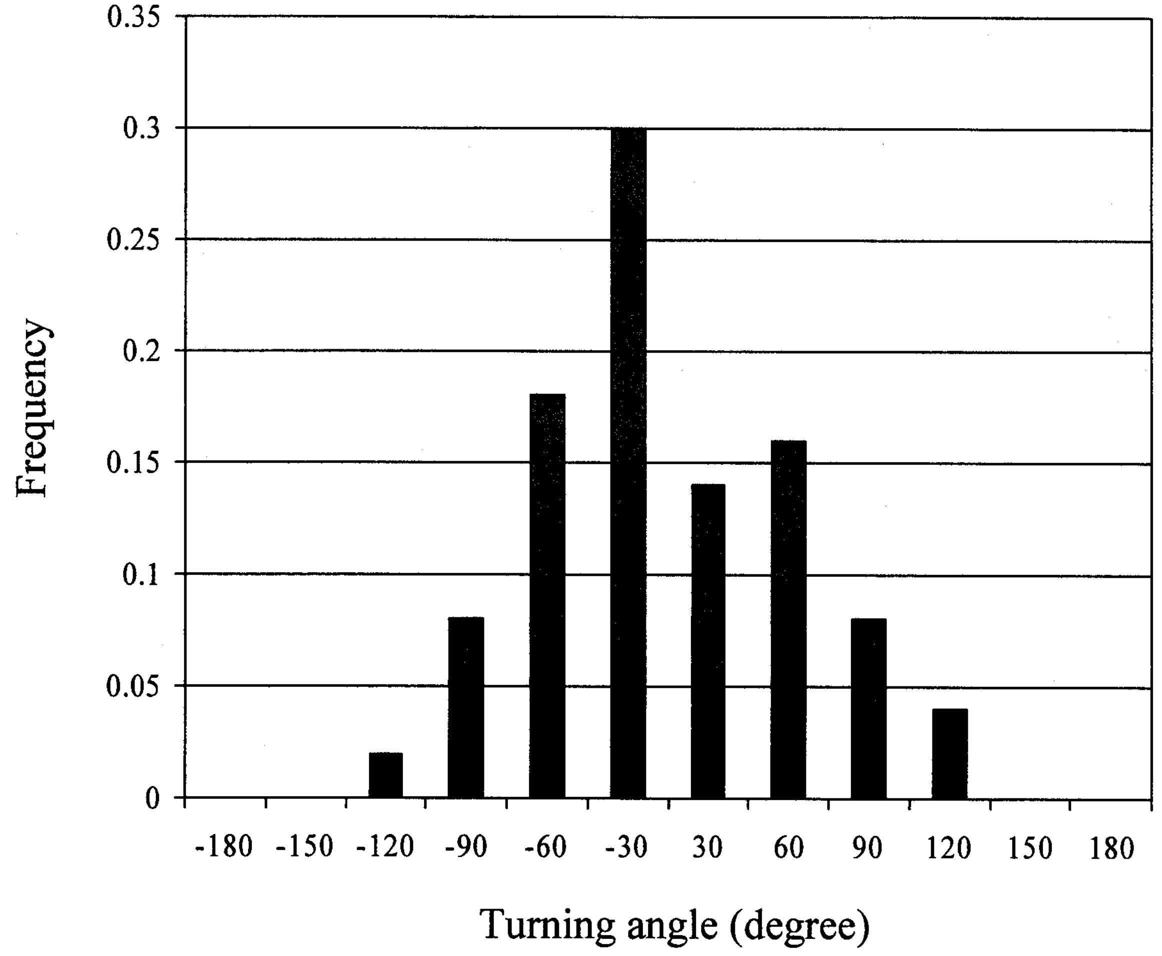
N
W
E
S
1 m


Frequency
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
-180
-150
-120
-90
-60
-30
30
60
90
120
150
180
Turning angle (degree)


0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
Frequency
-180
-150
-120
-90
-60
-30
30
60
90
120
150
180
Turning angle (degree)

# CHAPTER 5

# SUMMARY AND CONCLUSIONS

This study provides new information on the spatial ecology and conservation of *Glyptemys insculpta*. As a disturbance-dependent species, *G. insculpta* populations are often encountered in agricultural landscapes, where they are exposed to a variety of anthropogenic activities and their consequences. Within a two year period, one in five *G. insculpta* inhabiting our fragmented agri-forest landscape in southern Québec died due to agricultural practices and/or machinery. Most of the surviving turtles bore scars, testimonies to the pervasive nature of the threat.

A probable scenario describing the relationship between *G. insculpta* and agriculture over the last few centuries is suggested as follows. Historically, *G. insculpta* populations were likely confined to open areas created by beaver activity and/or forest fires. The species may have profited also from farming activities of certain Native American cultures that created large openings in forests. Agricultural development was subsequently expanded with the arrival of European colonists, which one can only presume benefited a disturbance-dependant turtle species. Meanwhile, beavers were extirpated from large parts of their North American range due to the bourgeoning demand for their pelts. Within the last century, most jurisdictions have put in place forest-fire suppression programs, while expanding logging operations. Thus, most *G. insculpta* populations now seem dependent upon agriculture and logging operations to create suitable foraging and nesting habitats. During the mid 1970s, the revolutionary disc mower began to be marketed in North America. Farmers slowly began to replace aging sickle cutterbar mowers with the more efficient rotary disc mowers. Consequently, many adult *G. insculpta* were killed or injured.

At our research site, annual survivorship of *G. insculpta* is insufficient to maintain a stable population; without changes in agricultural practices, the population will be extirpated. Wildlife managers should note that recruitment into *G. insculpta* populations does not necessarily indicate healthy populations nor ensure survival. Juveniles were not affected by disc mowers at our site. These same turtles however, will be at risk due to increased shell height once they reach reproductive size. Consequently, disc mower operators should be encouraged to: (*i*) set blade cutting height to 100 mm, (*ii*) leave an unharvested buffer strip of at least 10 m wide along hayfield edges adjacent to rivers, and (*iii*) begin mowing at the point farthest from the river. Furthermore, wildlife biologists should remember that the absence of detectable mortality does not negate its occurrence. Were it not for radio-telemetry, 10% of *G. insculpta* mortalities recorded in the present study would not have been documented. Turtles were entombed during ploughing and dredging operations, as well as by the collapse of an eroding river bank. Consequently, conspicuous declines in populations of *G. insculpta* inhabiting agricultural landscapes should not be attributed automatically to the illicit live animal trade, particularly if large numbers of mutilated turtles are present.

This study provides a new system of standardized ranges that can be implemented for most, if not all wildlife species. Integral, statistical, and linear ranges resolve issues of repeatability, estimator selection, and temporal constraints. Integral ranges are advocated for studies of imperilled species, particularly those that migrate or make short-term forays to critical resources. Such movements are excluded from traditional home ranges, yet such habitats are crucial to the survival of the species. Moreover, integral ranges embrace principles of landscape ecology such as complementation, connectivity, and supplementation rather than discard seemingly unused patches as irrelevant. Statistical ranges are more stable and are ideally suited for within- and between-study comparisons. Linear ranges also have a practical application, as they can be used to establish the length of proposed 300 m wide riparian protection zones. These riparian protection zones should be considered management zones however, as *G. insculpta* populations can be extirpated or displaced by natural forest succession. In every population of *G. insculpta* studied thus far, a few individuals migrate considerably farther than the remainder of the population. Thus, linear ranges are also critical for estimating degree of isolation and potential gene flow between populations.

Integral, statistical, and linear range size were correlated with body size in the first year of the study, whereas few correlations held in the second. These annual differences likely reflected the magnitude of landscape alterations during the second year of the study, which included the illegal dredging of a quarter of the main aquatic corridor. There is some indication that range size in *G. insculpta* may be negatively correlated with degree of exogenous landscape alteration but additional studies are required.

The fine-scale movements of translocated adult male *G. insculpta* reveal much about how this species perceives its environment. Although patch size had no effect on move length or path sinuosity, habitat structure did. Not surprisingly, paths were generally straighter and move lengths longer in the harvested portion of a hayfield. Paths also revealed that hayfield boundary permeability was absolute; suggesting that wood turtles will enter and exit hayfields freely. Ranging movements, however, imply that recently harvested hayfields are unsuitable habitats for *G. insculpta*. Thus, large portions of the agricultural landscape become unsuitable for about two weeks post-harvest. Such spatio-temporal resource limitations could have a negative effect on *G. insculpta*, particularly if harvests occur several times per summer. Moreover, agricultural intensification reduces the extent of refuge habitats such as fallow and oldfields or riparian buffers.

How *G. insculpta* react to perceived threats is crucial to their survival. One third of our subjects bypassed the agitation dispersal phase in at least one trial, favouring the typical chelonian refuge strategy. This adaptive response reduces the probability of limb amputations when attacked in terrestrial habitats by a mammalian predator, such as a raccoon. Similarly, a quick withdrawal into the shell was likely sufficient to survive an encounter with a sickle cutterbar mower because of the attached blade guards. Such inaction during the approach of a disc mower however, can have fatal consequences.

Although the increased habitat heterogeneity of agricultural landscapes may once have benefited *G. insculpta*, our investigation clearly documents that current agricultural practices and machinery are having an adverse effect. Such knowledge is essential for the conservation of an imperilled species that presently depends upon exogenous landscape alterations.

# CONTRIBUTIONS TO ORIGINAL KNOWLEDGE

1. This study is the first to quantify the effects of agricultural practices and farm machinery on a population of wood turtles, *Glyptemys insculpta.* Moreover, specific recommendations to alleviate the impact of disc mowers while increasing crop yield are made.

2. The Carapace Mutilation Index (CMI) provides the first standardized method to permit researchers to quantify and analyze mutilation patterns. This study is also the first to document a bilateral asymmetry of turtle injuries.

3. Three discrete measures of range are explicitly defined. Integral, statistical, and linear ranges are introduced as conceptually distinct but complementary estimators of wildlife movements. These measures of animal movement and occupation of space are proposed to update the concept of home range, which several authors consider obsolete.

4. This is the first study of *G. insculpta* to document a correlation between range size and morphology.

5. This study is the first to investigate the effects of patch size and habitat structure on the path sinuosity, turning angle, and move length of a turtle.

6. Three distinct movement phases are documented for the first time in a turtle: agitation dispersal, local search, and ranging. The agitation dispersal phase revealed a left-turning bias that was not the result of a serial autocorrelation of turning angles. This study is the first to suggest that arced paths may be the result of handedness and/or diagonal sequence gait.

# APPENDIX I