Effects of Habitat Features and Landscape Composition on the Population Structure of a Common Aquatic Turtle in a Region Undergoing Rapid Development

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Abstract: *We investigated the demography of a common aquatic turtle* (Chrysemys picta) *along a gradient of urbanization in southeastern New Hampshire. Using a geographic information system and live trapping of turtles, we compared the proportion of males, the proportion of adults, and the relative abundance of turtles in 37 ponds. We used satellite images, aerial photographs, and field visits to describe pond-specific features and habitat composition up to 2000 m from the perimeter of each pond. The proportion of males was positively associated with the percentage of forest cover within 500 m, greater road density within 100 m, and an index of predator activity at a pond. The proportion of adults in a population was associated with road density within 250 m of the pond and the percentage of the pond perimeter that was forested. Abnormal population structures associated with greater road densities did not necessarily result in lower abundances of turtles in ponds. Turtle abundance increased as the distance to neighboring wetlands decreased and the amount of nesting habitat near pond edges increased. Pond-specific features also affected turtle abundance where populations were larger in ponds with organic substrates and abundant coverage by shoreline vegetation than in ponds lacking these features. Few turtles were encountered in ponds with an abundance of herbaceous emergent vegetation, and fewer turtles were captured during a summer with abundant precipitation. Suburban and urban developments, with dense road networks and abundant populations of generalist predators (especially the raccoon,* Procyon lotor), *can alter the structure of aquatic turtle populations. Although these alterations may not result in immediate changes in turtle abundance within a specific population, we suspect that the reduction in recruitment caused by habitat alterations will eventually reduce or eliminate local populations. Even though there are life-history differences among species of turtles, our results may provide new insight into the causes of recent declines of other turtles.*

Key Words: development, habitat fragmentation, population structure, roads, turtle

Efectos de las Características del Hábitat y la Composición del Paisaje sobre la Estructura Poblacional de una Tortuga Acuática Común en un Paisaje Bajo Desarrollo Rápido

Resumen: *Investigamos la demografía de una tortuga acuática común* (Chrysemys picta) *a lo largo de un gradiente de urbanización en el sur de New Hampshire. Por medio de un sistema de información geográfica y la captura de tortugas vivas, comparamos la proporción de machos, proporción de adultos y la abundancia relativa de tortugas en 37 charcas. Utilizamos imágenes de satélite, fotografías aéreas y visitas de campo para describir características específicas de cada charca y la composición del hábitat hasta 2000 m del perímetro de cada charca. La proporción de machos se asoció positivamente con el porcentaje de cobertura forestal hasta*

500 m, mayor densidad de caminos hasta 100 m y un índice de actividad de depredador en una charca. La proporción de adultos en una población se asoció con la densidad de caminos hasta 250 m de la charca y el porcentaje arbolado del perímetro de la charca. Estructuras poblacionales anormales asociadas con mayores densidades de caminos no resultaron necesariamente en menor abundancia de tortugas en las charcas. La abundancia de tortugas incrementó a medida que disminuía la distancia a humedales vecinos y aumentaba la cantidad de hábitat para anidar cerca de los bordes de las charcas. Las características específicas de las charcas también afectaron a la abundancia de tortugas donde las poblaciones fueron mayores en charcas con sustratos orgánicos y abundante cobertura de vegetación de borde que en charcas sin estas características. Encontramos pocas tortugas en charcas con abundancia de vegetación herbácea emergente, y capturamos menos tortugas durante un verano con abundante precipitación. Desarrollos urbanos y suburbanos, con densas redes de caminos y poblaciones abundantes de depredadores generalistas (especialmente el mapache, Procyon lotor), pueden alterar la estructura de las poblaciones de tortugas acuáticas. Aunque estas alteraciones pueden no resultar en cambios inmediatos en la abundancia de tortugas en una población específica, sospechamos que la reducción de reclutamiento causada por alteraciones de hábitat eventualmente reducirá o eliminará poblaciones locales. Aunque hay diferencias en la historia de vida entre especies de tortugas, nuestros resultados pueden proporcionar una nueva visión de las causas de declinaciones recientes de otras tortugas.

Palabras Clave: caminos, desarrollo, estructura poblacional, fragmentación de hábitat, tortuga

Introduction

Declines among reptile populations worldwide represent a conservation crisis (Gibbons et al. 2000). Reasons for these declines include habitat loss and degradation, introduced invasive species, environmental pollution, diseases, and overexploitation (Gibbons et al. 2000; Klemens 2000). Yet the consequences of habitat loss and fragmentation for reptiles have only recently been investigated (e.g., Curtin 1997; Sarre 1998; Kjoss & Litvaitis 2001; Gibbs & Shriver 2002). Among aquatic turtles, the loss, degradation, and fragmentation of wetland habitats can result in abnormal population structures (Dodd 1990; Reese & Welsh 1998) and population declines or extinctions (Gibbons et al. 2000). As wetlands are degraded or destroyed, sites occupied by remaining turtles become isolated, reducing the ability of individuals to successfully disperse, which eventually may result in lower genetic variability among populations (Gray 1995).

Loss and degradation of upland habitats may also have substantial effects on aquatic turtles. In addition to using these habitats while emigrating between wetlands and dispersing from drying ponds, female turtles require upland habitats for nesting. Females may travel long distances during nesting excursions (Obbard & Brooks 1980; Christens & Bider 1987; Joyal et al. 2001) and suffer substantial mortality when making frequent road crossings (Wood & Herlands 1997; Haxton 2000; Gibbs & Shriver 2002) or when exposed to terrestrial predators (Seigel 1980). Generalist predators, such as raccoons (*Procyon lotor*), are capable of limiting local populations of turtles (Christiansen & Gallaway 1984; Brooks et al. 1992). These predators benefit from supplemental foods associated with human-dominated habitats, and their populations have increased in many regions (Robinson & Wilcove 1994; Oehler & Litvaitis 1996). Additional mor-

talities of adult turtles in such modified landscapes can reduce the generally high adult survival rates upon which turtle populations depend (Garber & Burger 1995). However, the effects of landscape alterations and elevated populations of generalist predators may not be obvious for decades (Findlay & Bourdages 2000), especially if only the presence of turtles is considered (Klemens 2000).

For example, if female turtles are more vulnerable to upland mortality than males, a male-biased population might be predicted to occur in landscapes where the abundance of generalist predators and road density have increased (Stickel 1978). A reduction in the number of adult females may then result in a reduction in recruitment and a population structure that is heavily skewed to adults (Thompson 1983). Although the remaining (older) individuals may continue to persist, these populations may become functionally extinct because of the lack of juvenile recruitment (Klemens 1989). Supporting this conjecture, Garber and Burger (1995) documented the extirpation of wood turtles (*Clemmys insculpta*) at two sites following an increase in human recreational activities. During a 10-year study period, the number of juvenile and adult females decreased, mean age increased, and the abundance of turtles declined until both populations were extirpated (Garber & Burger 1995).

We examined the demographic responses of turtle populations exposed to different intensities of habitat loss and fragmentation. Although painted turtles (*Chrysemys picta*) are among the most well-studied aquatic turtles (Moll 1979), research examining the effects of terrestrial habitat fragmentation on populations of this species and many other aquatic turtle species has been limited. Additionally, the sample sizes needed to generate multifactor comparisons among populations of other rare species (e.g., spotted turtles [*Clemmys guttata*]) are difficult or impossible to obtain. Therefore, the painted turtle is a

model organism for examining the effects of habitat fragmentation on aquatic turtle populations.

Based on research on other taxa and consideration of the life-history characteristics of turtles, we predicted that the structure of painted turtle populations would be substantially altered in response to mortality factors attributed to landscape modifications. Specifically, we predicted (1) increased mortality of female turtles associated with developed landscapes, resulting in male-biased populations; (2) in substantially modified landscapes, a reduction in the number of mature females and increased mortality among turtle eggs and hatchlings, resulting in a greater proportion of adults; and (3) subsequent reductions in recruitment and adult survival, resulting in reduced abundance of turtles within developed landscapes in comparison with turtles in ponds in less modified landscapes.

Methods

Study Area

We studied an approximately 1400-km^2 portion of Strafford and Rockingham counties, New Hampshire, (U.S.A.). New Hampshire is largely forested (approximately 83%; Sundquist & Stevens 1999), but the southern portion of the state has undergone rapid development and increases in human population, and these changes are predicted to continue (Vogelmann 1995; Sundquist & Stevens 1999).

To facilitate our ability to adequately sample the turtle population of each pond, we selected ponds that were permanent water bodies within a restricted range of sizes. We selected 37 ponds that ranged from 0.3 to 5.2 ha. These ponds were isolated from one another, reducing the amount of landscape shared among them. Most selected ponds (35 of 37) were separated by ≥400 m, and many were >1 km from the nearest sample pond (33 of 37). Because we wanted ponds surrounded by a range of land uses, we selected them along a gradient of forest continuity where the intensity of development changed from west (less developed) to east (more developed), as summarized by Vogelmann (1995). Landscapes surrounding ponds consisted of a mosaic of forests, agricultural areas, fields, and developed areas. Dominant overstory species included American beech (*Fagus grandifolia* Ehrh.), maples (*Acer* spp.), oaks (*Quercus* spp.), eastern white pine (*Pinus strobus* L.), and eastern hemlock (*Tsuga canadensis* [L.] Carr.).

Within ponds, dominant submergent vegetation included coontails (*Ceratophyllum* spp.), bladderworts (*Utricularia* spp.), and waterweeds (*Elodea* spp.). Dominant floating vegetation included duckweeds (*Lemna*, *Wolffia*), lilies (*Nuphar*, *Nymphaea*), watershield (*Brasenia schreberi* Gmel.), and pondweeds (*Potamogeton* spp.). Dominant herbaceous emergents included pickerel-

weeds (*Pontederia* spp.), sedges (*Carex* spp.), bur-reeds (*Sparganium* spp.), three-way sedge (*Dulichium arundinaceum* [L.] Britt.), and cattail (*Typha latifolia* L.). Woody emergent vegetation included leather-leaf (*Chamaedaphne calyculata* [L.] Moench.) and buttonbush (*Cephalanthus occidentalis* L.).

Capture Methods

To assess the population structure of turtles within each sample pond, we used baited funnel traps (2.5-cm mesh; Lagler 1943) and a dip net to capture turtles during April–September 2000 and 2001. Although several other species of turtles were captured during this period (*Chelydra serpentina, C. guttata, Sternotherus odoratus*), *C. picta* represented >90% of the captures; therefore, we restricted our comparisons to this species.

We baited funnel traps with canned cat food and secured the traps along the shallow margins of ponds with stakes. A portion of all traps remained at least several inches above the surface of the water so turtles could breathe while in the traps. Traps were checked approximately 24 and 48 hours after they were set, and captured turtles were removed and released after data were recorded. We sampled several ponds during each 48-hour period, following which we rotated traps to a new set of ponds until all ponds had been sampled. We resampled ponds in a similar order until all ponds had been sampled for four 48-hour periods (8 days each). In most instances, we set five traps at a pond during each sample period. Some ponds differed in trapping intensity, however, because of drops in water level, loss of trap bait, and trap theft. Also, at each pond we conducted four 1-hour searches. During these searches, we used a canoe to navigate around ponds and a long-handled dip net to capture any turtle observed. Time required to process turtles was not included in 1-hour search periods. To maximize efficiency and reduce variation in capture rates due to weather, we conducted searches on warm, sunny days (mean ambient temperature = 26° C ± 3.5 SD). To eliminate variation among observers, all trapping and searches were conducted by the same individual. In addition to our standardized trapping and 1-hour searches, several turtles were captured when we were checking traps.

Once captured, we marked each turtle by filing a unique combination of marginal scutes with a triangular file (Cagle 1939). The soft, unossified shells of young turtles were notched with fingernail clippers. Additionally, we noted missing limbs and shell damage for all captured turtles. We measured maximum carapace length (CL) with calipers to the nearest millimeter. For those individuals with a CL of ≥90 mm, we also recorded gender (based on secondary sexual characteristics; Klemens 1993). Turtles with intermediate sexual characteristics were classified as unknown. Because plastron scutes were often smooth, we were unable to consistently determine

the age of turtles. As a result, we used a more conservative approach and grouped turtles into two size classes: CL < 90 mm, juveniles; CL ≥ 90 mm, adults. Although some female *C. picta* may reach maturity at a later age than males and have a CL of >90 mm (Mitchell 1988), we chose to use the same size cutoff for both males and females. Age at maturity varies between regions and possibly between ponds within a region (Zweifel 1989), so an assessment of growth rates would be required at each pond. Grouping turtles in size classes allowed for an assessment of the proportion of the population consisting of young versus old turtles.

For each capture method, we determined the number of captures per pond (including recaptures) and the number of unique turtles captured per pond. Because we were most interested in representing population structure rather than comparing various capture methods, we combined data for all captures. A combination of methods more likely represents the true population structure (Ream & Ream 1966; Ernst 1971), and any potential biases were consistent among ponds because all ponds were sampled similarly. In addition to captures in ponds, we recorded the gender and condition—especially noting injuries—of turtles incidentally encountered in upland habitats, including those found dead on roads. Capture efforts in upland habitats were not standardized, but all captures were made by the same individual who conducted pond captures and were only used to explore gender differences in the use of terrestrial habitats.

Pond Characteristics

Aquatic vegetation provides an important food source and structural component for aquatic turtles (Sexton 1959); therefore, we measured several types of vegetation within each pond. Percent coverage of aquatic vegetation was estimated within circular plots (85-cm-diameter plastic hoop). The number of plots per pond varied according to pond sizes (range, 30–90), and plots were distributed systematically along two transects at each pond. We visually estimated percent coverage of woody emergents (mostly buttonbush and leatherleaf), herbaceous emergents (grasses, sedges, and rushes), and floating submergent vegetation. Water clarity and substrate differed among ponds, so we estimated only submergent vegetation within 0.5 m of the surface of the water. Also, when floating vegetation (e.g., *Nuphar*) was abundant, it was difficult to determine the amount of submergent vegetation below the surface of the water. Viewed from above, vegetative coverage was recorded as the percentage of each plot with floating or submergent vegetation. We also estimated the percentage of shoreline covered by vegetation. Finally, dominant vegetation was noted for each plot and for shoreline vegetation.

Other physical features of ponds also were considered. Pond substrate was described at each pond and later col-

lapsed into one of two categories: organic (leaf litter, woody debris, muck) or inorganic (sand, stone, clay). Because basking is an important physiological behavior for turtles (e.g., thermoregulation), we estimated the number of potential basking sites (e.g., floating limbs, exposed rocks) at each pond and ranked them as follows: 0, sparse; 1, scattered; 2, common; and 3, abundant.

Landscape Habitat Variables

Most landscape habitat variables we used were created with a geographic information system (ArcView 3.2 and ArcInfo 8.1; Environmental Systems Research Institute, Redlands, California). We isolated ponds from the National Wetland Inventory layer and verified the size and shape of these ponds by examining 1998 digital orthophoto quads (1:12000) and making field visits. If there was a discrepancy among information sources, we digitized ponds from orthophotos. Landscape variables created within the geographic information system (roads, forest, wetland) were inventoried within five distances (100, 250, 500, 1000, and 2000 m) from pond perimeters. Turtles are likely to travel distances of ≤500 m from ponds. In our study area, the maximum distance that transmitter-equipped female painted turtles were observed from ponds during the nesting season was 273 m ($n = 20$; Baldwin et al. 2004). Such distances also may influence predator activity near ponds. Larger buffer distances (1000 and 2000 m) were used to incorporate landscapes more likely to influence predator abundances and represent the approximate daily cruising range of many mammalian predators, such as raccoons and foxes (*Vulpes vulpes*; Oehler & Litvaitis 1996) that are known to prey on adult turtles and their nests (Congdon et al. 1987; Maier et al. 2002).

We used a land-cover map produced by the Complex Systems Research Center at the University of New Hampshire to determine the land cover surrounding each pond. The 19-class land-cover map was produced from Landsat thematic mapper imagery (spatial resolution ca. 0.09 ha) taken between 1990 and 1996 (Rubin et al. 2001). We collapsed the 19 cover types to six—forest, wetlands, open water, developed, agricultural, and open or disturbed areas—further increasing the accuracy of the map (Rubin et al. 2001). For example, the seven forest-cover types that were classified in the land-cover map were condensed into forest. Because each pond had a unique shape, the area within a buffer of equal distance from pond edges was different. To standardize the area of each land-cover category among ponds, we calculated the percentage of buffer area consisting of a particular category. Because land-cover categories within each buffer were a percentage, categories were not mutually exclusive and many categories were therefore highly correlated. For example, developed land had a high negative correlation with percentage of forest.

We used New Hampshire Division of Transportation public- and private-road layers to assess road density surrounding ponds. We excluded public roads designated as unmaintained or not compact. We included gravel roads because at our sites these roads seemed to be associated with greater traffic and because several turtles were killed on gravel roads (M. M., personal observation). The type of road surface was not designated for the private-road layer; therefore, we conducted field surveys to determine the road surface for all roads within 2 km of ponds. Dirt roads and driveways were excluded. We combined the retained public and private roads, digitized missing roads on screen, and added active railroads. The total linear distance of roads (kilometers) was measured within each buffer distance and divided by the buffer size (square kilometers) to standardize among different areas. As an additional measurement of road effects, we determined the distance from pond perimeters to the nearest road. Roads occurring within 50 m of a pond perimeter were measured in the field to increase the accuracy of this measurement.

To determine whether the amount of potential turtle habitat surrounding ponds had an impact on the sampled populations, we calculated the amount of freshwater wetland (based on the National Wetland Inventory layer) within each buffer distance. Estuarine habitats and palustrine wetlands with a water regime of A (temporarily flooded), B (saturated), or C (seasonally flooded) were excluded. To determine whether isolation of wetland habitats had an impact on *C. picta* in sample ponds, we calculated the distance from sample pond perimeters to the nearest wetland that was >0.5 ha and then again for wetlands of >1.0 ha. This excluded small ponds that were not likely to provide permanent habitat for turtles.

In addition to the habitat variables derived from the geographic information system at the five buffer distances, we described land use within 30 m of the pond perimeters. Because satellite imagery could not be used at this scale, land uses were described in the field. Perimeter land-cover classes were similar to those used in the Landsat designations and were calculated as the percentage of the pond perimeter consisting of a particular land-cover class. We converted road and wetland variables into presence and absence data because of the large number of zeros. We also recorded the area within 30 m of pond perimeters that was suitable for nesting. Suitable nesting areas had open canopies and well-drained soils and included lawns, fields, roadsides, trails, and canopy gaps. Because many nesting areas were small, our estimate in the field provided a more realistic assessment of nesting habitat than could be determined with satellite imagery or aerial photographs.

As an assessment of predator activity in areas surrounding ponds, we included a variable that indexed the rate of nest predation based on the rate of predation of 40 artificial nests placed at 36 of the 37 ponds (Marchand & Litvaitis 2004). For each nest, three Bobwhite (*Colinus virginianus*) eggs were placed in an excavated nest chamber and covered with soil (Marchand et al. 2002). Because two ponds were in close proximity and had similar surrounding landscapes, we placed artificial nests at one pond and used the subsequent predation rate as an index of predator activity for both ponds.

Data Analysis

Prior to analyses, we screened all variables for normality, skewness, and kurtosis and conducted appropriate transformations. Arcsine transformations were applied to the percent coverage of aquatic vegetation (floating submergent, herbaceous emergent, woody emergent, and shoreline) within ponds, to forest coverage, to percent wetland habitat surrounding ponds, and to our index of predation rates at ponds. Pond surface area and the distance from pond perimeters to the nearest road were log-transformed. We calculated the square root of the following variables: road density, distance from pond perimeters to nearest wetland, and area (square meter) of potential nesting habitat within 30 m of pond edges.

We then used backwards-elimination (probability of F to remove ≥ 0.1) multiple linear regressions to generate models that explained variation in turtle abundance, proportion of males, and proportion of adults in turtle populations at each pond. An alpha value of >0.05 ensured that independent variables explaining variation in the dependent variable were not excluded (Tabachnick & Fidell 2001). To reduce redundant variables, we created a Pearson's correlation matrix and retained only one of a highly correlated pair of variables ($r \geq 0.7$). We entered landscape variables into the regressions only at the buffer distance that explained the greatest variability (r^2) in the dependent variable. Final models were assessed at $p < 0.05$. Ponds in which ≤ 10 unique *C. picta* were captured were eliminated from the regression examining the proportion of adults within ponds. For the regression examining the proportion of males, at least 10 individuals that had a carapace length of ≥ 90 mm and known gender were required for each pond. Additional univariate comparisons included chi-square goodness-of-fit tests (Zar 1999) to compare the proportion of male and female turtles encountered in upland habitats and to compare the proportion of injured turtles among genders. We used a Mann-Whitney test to compare the proportion of surface vegetation among ponds with organic versus inorganic substrates (Zar 1999). Finally, with a Spearman rank correlation (Zar 1999), we tested for a relationship among the number of injured turtles captured within ponds and the amount of urban area within 100 m of ponds. We used SPSS statistical software (version 11.0) for analyses (SPSS, Chicago).
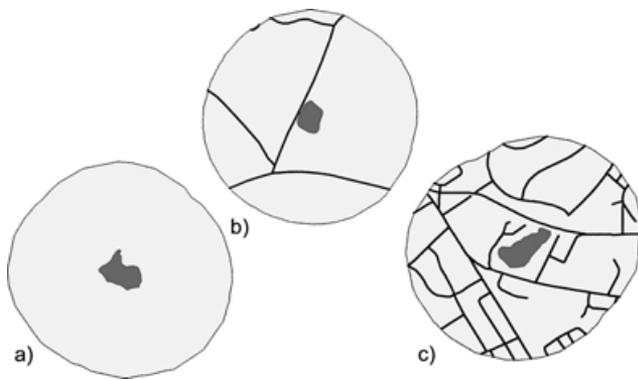
Figure 1. Variation in road density surrounding ponds used to examine the influence of landscape composition on population structures of painted turtles in southeastern New Hampshire, 2000–2001: at 500 m from pond edges (a) no roads (0 km/km²), (b) moderate road density (2.7 km/km²), and (c) high road density (9.5 km/km²).

Table 1. Backward linear regression models that explained variation in demographic characteristics of painted turtles (*C. picta*) in ponds in southeastern New Hampshire.

Demographic characteristic and variable	β	t	p	(sr²)*
Proportion males (*n* = 28)				
constant		−1.37	0.184	
forest coverage at 500 m	0.792	4.55	<0.001	0.407
road density at 100 m	0.770	4.18	<0.001	0.343
nest predation	0.583	3.65	0.001	0.261
Proportion adults (*n* = 29)				
constant		4.669	<0.001	
year	0.362	2.252	0.033	0.129
road density at 250 m	0.56	3.020	0.006	0.231
forest coverage along pond perimeter	0.458	2.452	0.022	0.152
Turtle abundance (*n* = 37)				
constant		3.419	0.002	
year	0.604	5.033	<0.001	0.296
substrate	−0.376	−2.596	0.014	0.079
herbaceous vegetation	−0.572	−4.651	<0.001	0.253
shoreline vegetation	0.281	2.03	0.051	0.048
nesting area	0.352	3.025	0.005	0.054
distance to nearest wetland of >0.5 ha	−0.247	−2.149	0.040	0.107

Represents the squared semipartial correlation.

Results

We sampled 18 ponds in 2000 and 19 in 2001. We captured 1746 *C. picta* (2000, 664; 2001, 1082); 1342 were unique individuals (2000, 504; 2001, 838). We eliminated ponds from a regression analysis when we had an insufficient number of turtles to calculate the proportion of males (9 ponds eliminated) or adults (8 ponds eliminated) within ponds.

Landscape composition varied greatly among ponds (Fig. 1). The amount of forest within 2 km of ponds averaged 61% ± 18 SD and ranged from 10% to 87%. The density of roads within 2 km of ponds averaged 2.3 km/km² and ranged from 0.5 to 11.1 km/km². Road density was highly correlated with urban area ($r > 0.7$) at each of the buffer distances. Because turtles are killed when crossing roads and the influence of the amount of developed areas on rates of predation seemed limited (Marchand & Litvaitis 2004), we eliminated urban habitat from consideration. Percent forest was retained to describe undisturbed areas with canopy closure. Percent forest, road density, and percent wetland habitat were eligible landscape variables, along with the distances to the nearest road and wetland, and the amount of suitable nesting habitat within 30 m of ponds. Most pond characteristics also were eligible for the three regression models. The number of basking sites and pond substrate were expected to affect all turtles in a pond similarly; therefore, we only included these variables in the regression model that considered turtle abundance.

Proportion Males

The proportion of males in ponds averaged 0.52 ± 0.13 and ranged from 0.33 to 0.86 among the 28 ponds considered. Nine variables were eligible to enter the regression model. Forest coverage within 500 m, road density within 100 m, and rate of predation on artificial nests were included in the final regression model that explained variation in the proportion of males among ponds (adjusted $R^2 = 0.47$, $F = 8.94$, df = 3, $p < 0.001$). A greater proportion of males was associated with greater forest coverage, a greater density of roads, and ponds with greater rates of nest predation (Table 1). During our population sampling, female turtles ($n = 33$) were observed in upland habitats more often than males ($n = 15$; $\chi^2_{0.05,1} = 6.75$, $p = 0.009$; Fig. 2). The majority of turtles observed in upland habitats were found dead on roads ($n = 32$), of which 21 were females ($\chi^2_{0.05,1} = 3.13$, $p = 0.077$).

Proportion Adults

The proportion of adults in ponds averaged 0.81 ± 0.12 SD and ranged from 0.60 to 1.00 among the 29 ponds considered. Twelve variables were eligible to enter the regression model. Year sampled, forest coverage along the pond perimeter, and road density within 250 m explained variation in the proportion of adults (adjusted $R^2 = 0.290$, $F = 4.1812$, df = 3, $p = 0.009$). All variables had positive associations with the proportion of adults among ponds (Table 1).

Abundance

The number of unique *C. picta* captured at ponds averaged 36 ± 33 SD and ranged from 0 to 145 among the 37 ponds examined. Sixteen variables were eligible
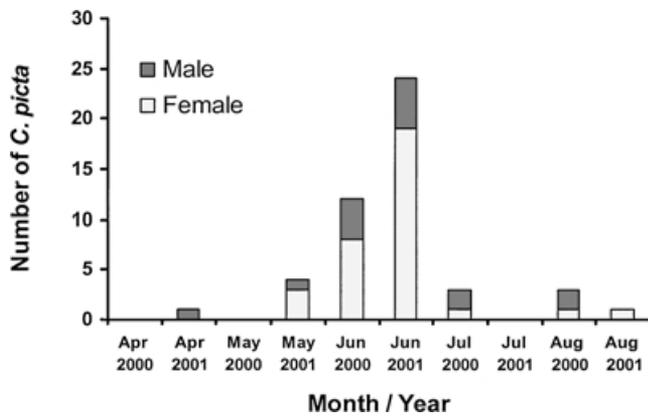
Figure 2. Frequency distribution of painted turtles encountered in upland habitats in southeastern New Hampshire. Overall, female turtles (n = *33*) *were observed in terrestrial habitats more often than males* (n = *15*).

to enter the regression model. Year sampled, pond substrate, herbaceous-emergent vegetation, shoreline vegetation, area of nesting habitat, and distance to nearest wetland ≥0.5 ha in size were retained in the final regression model that explained variation in turtle abundance (adjusted $R^2 = 0.580$, $F = 9.269$, df = 6, $p < 0.001$). More turtles were captured in 2001 than 2000, more turtles were captured in ponds with organic substrate than in ponds with inorganic substrate, shoreline vegetation and nesting areas were positively associated with turtle abundance, and herbaceous-emergent vegetation and isolation from other wetlands were negatively associated with turtle abundance (Table 1).

Discussion

Habitat features described at several spatial scales apparently influenced the demography of painted turtles. Pond characteristics, adjacent upland habitats, and surrounding landscape composition were associated with factors that affected life requisites, such as pond substrate, pond and shoreline vegetation, abundance of nesting area, and distance to nearest wetland, or had a direct effect on turtle survival, such as index of nest predation and road density in surrounding upland habitats. All landscape variables retained in our descriptive models included features ≤500 m from pond perimeters, supporting the 275-m buffer recommended by Burke and Gibbons (1995) to protect 100% of nesting and hibernation sites used by a South Carolina population of freshwater turtles.

Pond Characteristics Influencing Turtle Populations

The influence of study year is likely explained by variation in summer precipitation. In southeastern New Hampshire, 2000 was an extremely wet year, whereas 2001 was

a drought year. From May through September precipitation was 48.5 cm in 2000 compared with only 31.5 cm in 2001 (National Climatic Data Center, Epping, New Hampshire). It is possible turtles became more concentrated during 2001, making them easier to capture. Although most ponds sampled in 2000 retained water throughout 2001 field season, one pond dried out and all others had a noticeably reduced surface area and depth during 2001.

Other pond characteristics also influenced the abundance of turtles. Surface vegetation was less abundant in ponds with inorganic substrates than in ponds containing organic substrates (Mann-Whitney $U = 18$, $p < 0.001$). Besides providing suitable conditions for aquatic plant growth, organic substrate may provide more suitable hibernation and foraging opportunities than harder substrates. Herbaceous vegetation was negatively associated with turtle abundance. Black (2000) observed similar results for *C. picta* and *C. serpentina* and suggested that movements by turtles may be restricted by dense areas of vegetation, effectively reducing the suitability of such ponds.

Habitat and Landscape Features Influencing Turtle Populations

Supporting our predictions, greater road densities were associated with populations that contained a greater proportion of males and adult turtles. We encountered more females in terrestrial habitats (Fig. 2), and a greater proportion of females had severe injuries—missing limbs, stubbed tails, cracked or damaged shells, indents in shells, facial injuries—than males (43 vs. 25), when the overall sex ratio of captured turtles was adjusted for ($\chi^2_{0.05,1} = 6.49$, $p = 0.01$). These injuries likely resulted from a combination of encounters with automobiles and other machinery (e.g., lawn mowers) and predators. Thus, female turtles in our study area may indeed be more vulnerable to mortality in upland habitats than males. Similarly, female diamondback terrapins (*Malaclemys terrapin*) are more vulnerable than males to predation by raccoons (Seigel 1980) and to road mortality (Wood & Herlands 1997). However, Wilbur (1975) reported equal vulnerability to raccoon predation among male and female painted turtles.

In addition to the influence of road density, increased rates of predation for artificial nests were associated with a greater proportion of males within ponds when other variables (forest cover, road density) were controlled for. Although there is no logical reason to suspect that predators favored one gender of turtle within the nest chamber, vulnerability of nesting females to predators was probably greater where predator activity was greater.

Other studies support our observations that increasing alterations of terrestrial habitats can be detrimental to turtles. In an agricultural region of Québec, Canada, wood turtles had more shell injuries and slower growth rates

during their second decade of life than did turtles in a predominately forested region (Saumure & Bider 1998). Additionally, few juvenile turtles were encountered, and no turtles in the 0–4 age class were recorded at the agricultural site (Saumure & Bider 1998), indicating a reduction or elimination of recruitment. Ornate box turtles (*Terrapene ornata*) have larger home ranges and highly skewed age structures with little or no recruitment in a fragmented habitat compared with less disturbed habitats (Curtin 1997).

Road mortality among reptiles can be substantial in some areas, especially where roads bisect crucial habitats, such as wetlands and nesting habitats (Dodd et al. 1989; Ashley & Robinson 1996; Haxton 2000). Gibbs and Shriver (2002) used computer simulations to predict that road densities of >2 km/km^2 would increase adult mortalities among small-bodied turtles, including *C. picta*. Although road density did not explain significant variation in abundance, the number of injured turtles per pond was associated with increasing urban area (a consequence of dense road networks) within 100 m of ponds ($n = 35$, $r_s = 0.432$, $p = 0.010$). Some of these injuries were probably caused by predator attacks, whereas others were related to encounters with humans (e.g., automobiles, lawn mowers). Monitoring road mortalities alone may not provide sufficient insight into the factors affecting turtle demography in landscapes undergoing extensive development.

The amount of forest cover surrounding ponds was positively related to the proportion of males and adults within ponds. In most species of turtles, including *C. picta*, gender is determined by incubation temperature, with higher temperatures generally producing females (Ewert & Nelson 1991). It is possible that landscapes with abundant forest cover produced more males (Jackson & Walker 1997) because soil temperatures are lower. Also, female turtles depend on suitable nesting areas within upland habitats and males do not. Therefore, it also is possible that mature female turtles are more abundant where suitable nesting habitats—with an open canopy or no overstory vegetation—are in close proximity to ponds. Among our ponds, the amount of forest coverage along pond perimeters was inversely correlated with the amount of nesting habitat ($r_p = -0.67$). Areas with limited nesting opportunities may result in limited recruitment and subsequently a greater proportion of adults within such ponds. In support of this notion, the amount of suitable nesting area within 30 m of ponds was positively associated with turtle abundance. However, nesting areas often were associated with human-altered habitats such as residential lawns.

Although developed areas create hazards for turtles, they also may provide more open space for nesting. Many species of aquatic turtle regularly nest within residential lawns, roadside banks, and other human-altered habitats (Linck et al. 1989; Klemens 1993; Joyal et al. 2001). Ad-
ditionally, ponds in developed landscapes may be more eutrophied, a condition from which some turtles apparently benefit (*C. picta*: Knight & Gibbons 1968; Klemens 1993; *E. blandingii*: Graham & Doyle 1977). Even though turtle populations may benefit from some features associated with developed landscapes, recolonization of vacant habitats after local extinctions (e.g., caused by drought) may be more difficult in these areas. A combination of forested and wetland habitats to link habitats and pockets of open areas for nesting (with limited high-impact development) may provide the best long-term strategy for maintaining populations of aquatic turtles.

Implications for Turtle Conservation in Human-Dominated Landscapes

It is possible that low-intensity development may provide benefits to some turtle populations, including enhanced growth rates and additional nesting opportunities. Our results indicate, however, that even for a highly adaptable species such as painted turtles, population structure may be altered by other human-associated effects, especially dense road networks and abundant predator populations. Simply examining the abundance of turtle populations may be misleading because of a lag in their response to habitat alterations (Reese & Welsh 1998).

Understanding the biology of a species is important in making predictions about how population structure will be influenced by different landscapes. Some species (e.g., *M. terrapin*) are largely aquatic and rarely make extensive terrestrial journeys other than searches for nesting sites by females (Seigel 1980). Other species of turtle, including those that are rare, may differ in their life-history traits. For example, Blanding's, spotted, and wood turtles use upland habitats to a greater extent than *C. picta* (Joyal et al. 2001; Compton et al. 2002). Therefore, development of landscapes and isolation of necessary habitat features are likely to have a much greater effect on those species. If male turtles are traveling extensively in search of mates, then these populations may become female-biased as landscapes are altered. Populations that are heavily biased toward one gender or toward adults warrant further investigation. Examining turtle populations in landscapes where habitat conversions are just beginning may provide an early warning that populations are reacting and an opportunity to intervene before conservation actions become extremely difficult or too late to prevent local extinctions.

Acknowledgments

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