

Diet and Feeding Behaviour of Snapping Turtles (*Chelydra serpentina*) and Midland Painted Turtles (*Chrysemys picta marginata*) in Algonquin Provincial Park, Ontario

PATRICK D. MOLDOWAN¹, MATTHEW G. KEEVIL¹, PETER B. MILLS², RONALD J. BROOKS³, and JACQUELINE D. LITZGUS^{1,4}

¹Department of Biology, Laurentian University, 935 Ramsey Lake Road, Sudbury, Ontario P3E 2C6 Canada

²Algonquin Visitor Centre, Algonquin Provincial Park, Km 43 Hwy 60, P.O. Box 219, Whitney, Ontario K0J 2M0 Canada

³Department of Integrative Biology, University of Guelph, 50 Stone Road East, Guelph, Ontario N1G 2W1 Canada

⁴Corresponding author: jlitzgus@laurentian.ca

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We compare diet and feeding behaviour of Snapping Turtles (*Chelydra serpentina*) and Midland Painted Turtles (*Chrysemys picta marginata*) in Algonquin Provincial Park, Ontario, Canada. We observed young *Chelydra* and *Chrysemys* turtles feeding on insect and amphibian larvae in ephemeral ponds, adult *Chrysemys* terrestrially foraging on odonate larvae, and adult *Chelydra* consuming aquatic vegetation and seeds. These and other observations highlight the importance of seasonally available habitat and food for juvenile turtles. We also discuss the evidence for, and importance of, turtles as seed-dispersal agents for aquatic vegetation. Illustrative video recordings accompany our dietary observations.

Key Words: Amphibian larvae; Snapping Turtle; *Chelydra serpentina*; Midland Painted Turtle; *Chrysemys picta marginata*; diet; ephemeral pond; odonate; seed dispersal

Introduction

Snapping Turtles (*Chelydra serpentina*) and Painted Turtles (*Chrysemys picta*) are omnivorous and known to consume a wide variety of invertebrate, vertebrate, algae, and aquatic vascular plant species across their broad geographic ranges (Ernst and Lovich 2009). A long-term study on the life history and ecology of Snapping Turtles and Midland Painted Turtles (*C. p. marginata*) based out of the Wildlife Research Station in Algonquin Provincial Park, Ontario, has been ongoing since 1972. Here, we report observations of dietary and feeding behaviour collected during field research, principally between 2009 and 2014.

Methods

Data were collected using standard field methods, including haphazard mark–recapture surveys, nest site surveys, and radio telemetry, consistent with the long-term study (see Obbard and Brooks 1981 and Rollinson and Brooks 2007 for further details). Turtles were captured from canoe using a landing net, by baited hoop trap, and by hand and transported to a field laboratory at the Wildlife Research Station for measuring and marking. *Chelydra* were measured using tree calipers (to the nearest 0.05 cm) and *Chrysemys* were measured with Vernier or digital calipers (to the nearest 0.01 cm). Both species were weighed using an appropriately sized spring scale (Pesola AG, Baar, Switzerland). Juvenile turtles were marked with notches in the marginal scutes (Cagle 1939). Adults were notched and also received an aluminum tag bearing an alphanumeric identification code that was affixed to the posterior marginal scutes (Loncke and Obbard 1977). Turtles less than 1 year of

age were individually marked with nail polish on the plastral scutes for short-term identification. Adult *Chrysemys* were marked annually by painting a unique identification code on the carapace so that individuals could be identified from afar.

Observations and Discussion

Juvenile Diet and Feeding Behaviour

During spring and early summer 2011, frequent rains resulted in networks of ephemeral pools along low-lying areas of an old railway embankment at one of our main study sites, Wolf Howl Pond (45°34'N, 78°41'W). Parts of the embankment are the primary nesting areas for turtles in adjacent water bodies (Schwarzkopf and Brooks 1985; Rollinson and Brooks 2007). From 19 May to 24 June 2011, 33 juvenile *Chelydra* and 19 juvenile *Chrysemys* were found occupying these pools during daily checks. All were less than 1 year of age (2010 hatch year based on size and growth-ring counts): for *Chelydra*, straight midline carapace length = 2.90 ± 0.11 cm (mean ± SD), midline plastron length = 2.20 ± 0.10 cm, mass = 8.30 ± 0.96 g; for *Chrysemys*, straight midline carapace length = 2.76 ± 0.22 cm, midline plastron length = 2.62 ± 0.18 cm, mass = 4.82 ± 0.98 g.

Young turtles were observed foraging, swimming, and hiding among detritus in the shallow pools, which were 2–6 cm deep. Juvenile turtles were observed feeding on the abundant mosquito (Diptera: Culicidae) larvae present in these pools, and the two species used different behaviours to capture prey. Juvenile *Chelydra* remained motionless in ambush or exhibited a slow, stalking movement toward mosquito larvae with neg-

ligible water disturbance (see Video 1 under Supplementary Material; see also Vogt 1981 citing Bramble 1975). Prey were captured using a rapid strike and ram-feeding mechanism (Lauder and Prendergast 1992). In contrast, juvenile *Chrysemys* cued to movement of mosquito larvae and approached the prey directly. The mosquito larvae reacted by attempting to move away, and a chase would ensue (Video 2, Supplementary Material). Exploratory striking, prey disturbance, and chasing characterized the feeding strategy of *Chrysemys*, as also observed by Sexton (1959). The ambush strategy of juvenile *Chelydra* appeared to be more successful than the direct approach of juvenile *Chrysemys*, although we did not quantify putative differences in capture success. The seasonally abundant prey source and high-quality foraging opportunities provided by ephemeral pools may be important for the early growth of *Chelydra* and *Chrysemys* (Cosentino *et al.* 2010). Others report the use of seasonally flooded pools by *Chelydra* and *Chrysemys* for foraging and thermoregulation (DeGraaf and Rudis 1983; Kenney and Burne 2000; Calhoun and deMaynadier 2008; Ernst and Lovich 2009) and overwintering (MGK and PDM, personal observations of juvenile *Chelydra* in Algonquin Park).

On 27 August 2011, a yearling *Chelydra* was observed in shallow water along the shoreline of Wolf Howl Pond. The young turtle had grasped the left hind limb of a partly metamorphosed Mink Frog (*Lithobates*

septentrionalis) in its jaws and had partly eviscerated the frog during prey handling (Figure 1). Although only in its first growing season, this *Chelydra* demonstrated the aggressive feeding response typically associated with adults (Ernst and Lovich 2009) when it attempted to capture prey almost as large as itself.

Heavy and regular rainfall in summer 2014 resulted in the formation of ephemeral pools along Ramona Lake Road (45°29'N, 78°45'W), which leads to a waste transfer station and aggregate pit in Algonquin Park. In addition, rainwater pooled in a tarpaulin that was installed to inhibit the growth of Common Reed (*Phragmites australis* (Cavanilles) Trinius ex Steudel) and in low-lying areas with a silty substrate ("settled fine dust" left behind after heavy machine work). Young *Chrysemys* were observed in the pools throughout August. In one pool, measuring 10–12 m in diameter and 5 cm deep, Gray Treefrog (*Hyla versicolor*) larvae were observed. Wandering Glider dragonflies (*Pantala flavescens* (Fabricius) [Odonata: Libellulidae]) were also observed courting and depositing eggs at the pools. *Hyla* larvae were extremely abundant in one pool on 9 August 2014, and three young *Chrysemys* (fall 2013 hatchlings based on size and plastron growth-ring count) were observed preying on them. Visual inspection showed wide spacing between the natal scute (present at hatching) and first growth ring on the plastron of all three juvenile *Chrysemys*, suggesting rapid growth in their first active season (2014). A combina-



FIGURE 1. Yearling Snapping Turtle (*Chelydra serpentina*), 2010 hatch year, restraining a partly metamorphosed Mink Frog (*Lithobates septentrionalis*) by the left hind limb, 27 August 2011, Algonquin Provincial Park, Ontario, Canada. Photo: M. G. Keevil.

tion of shallow water, extreme exposure to sunlight, and (in the case of one series of pools) a dark underlying tarpaulin, likely resulted in warm water temperatures in these ephemeral pools. Such warm water conditions and access to an abundant prey source would account for rapid first-year growth of these juvenile *Chrysemys* relative to growth in other Algonquin populations (MGK, unpublished data). A juvenile *Chelydra* was also observed feeding on *Hyla* larvae in a flooded ditch adjacent to Highway 60 near Found Lake (45°33'N, 78°38'W) for at least 2 weeks during summer 2015.

Amphibian larvae exhibit a range of morphological and behavioural responses to predation risk (Relyea 2001, 2004). *Hyla* larvae display conspicuous red colouration of the caudal fin when developing in the presence of (odonate) predators (McCullum and Leimberger 1997). However, despite exposure to turtle predators, *Hyla* larvae found in the Ramona Lake Road pools and the roadside ditch did not display red colouration. Odonates and predacious diving beetles (Coleoptera: Dytiscidae) chew and shred larval anurans and thus broadcast alarm cues into the environment, whereas, in most cases, turtles swallow anuran larvae whole. Compared with predatory insects, turtles are likely less frequent and less predictable predators of anuran larvae. Perhaps the different feeding strategies and predation pressure exerted by aquatic insects and turtles would elicit different magnitudes of plastic (morphological or behavioural) response from anuran larvae. Future work should consider turtles as a predator in anuran larvae plasticity experiments.

Consumption of Aquatic Vegetation and Seed Dispersal

Aquatic vegetation makes up a large portion of the diet of adult *Chelydra* (Alexander 1943; Lagler 1943; Hammer 1969; Punzo 1975; Ernst and Lovich 2009) and *Chrysemys* (Raney and Lachner 1942; MacCulloch and Secoy 1983; Lindeman 1996; Rowe and Parsons 2000; Ernst and Lovich 2009; Padgett *et al.* 2010). In addition, watershields (*Brasenia* spp.) and water-lilies (*Nuphar* spp. and *Nymphaea* spp.) serve as food and cover for *Chelydra* (Obbard and Brooks 1981) and *Chrysemys* (Sexton 1959). Throughout the active season for turtles in Algonquin Park (May–August), *Chelydra* have been observed feeding on Watershield (*Brasenia schreberi* J. F. Gmelin).

On 29 May 2010, an adult male *Chelydra* (straight midline carapace length = 31.7 cm; mass = 8.9 kg) was video-recorded feeding on Watershield in Wolf Howl Pond (Video 3, Supplementary Material). *Chelydra* appear to locate Watershield visually and approach clusters of leaves at the water's surface. Watershield leaves are consumed one at a time by rapid forward extension of the neck and depression of the hyoid, akin to the ram-feeding/suction mechanism employed when feeding on animal prey (Lauder and Prendergast 1992; Summers *et al.* 1998). *Chelydra* may use their forelimbs and claws to sever the long trailing stem of

Watershield, just as when handling oversized prey (Punzo 1975). They may also use their forelimbs to drag a Watershield leaf under water before striking and consuming it. Examination of the gut of a road-killed adult male *Chelydra* (straight midline carapace length = 34.0 cm, mass = 9.0 kg), found on 21 August 1992 on Highway 60 in Algonquin Park, revealed very densely packed Watershield, essentially filling the entire alimentary tract from stomach to cloaca. This Watershield showed little sign of digestion, and even leaves near the cloaca appeared freshly eaten. Although the mucilage coating on Watershield deters insect predators (Thompson *et al.* 2014), it seemingly does not discourage consumption by *Chelydra*.

We have observed consumption of flowers and seed-pods of Variegated Pond-lily (*Nuphar variegata* Engelman ex Durand) by *Chelydra* directly, and indirectly in feces. The seeds of this plant are also abundant in feces of *Chrysemys* in Algonquin Park. *Chelydra* (Kimmins and Moll 2010) and *Chrysemys* (Raney and Lachner 1942; Padgett *et al.* 2010) appear to be important seed dispersers for aquatic plants. A literature review (Traveset 1998) and subsequent publications (e.g., Varela and Bucher 2002; Strong and Fragoso 2006; Griffiths *et al.* 2011; Blake *et al.* 2012) suggest that turtles (and other seed-eating reptiles) may help, or at least not hinder, the germination rates of seeds that pass through their digestive tracts. Seed dispersal has been described for numerous chelonian species: *Trachemys scripta elegans* (Kimmins and Moll 2010), *Terrapene carolina* (Braun and Brooks 1987; Liu *et al.* 2004), *Emys orbicularis* (Calvino-Cancela *et al.* 2007), *Chelodina longicollis* (Burgin and Renshaw 2008), *Elseya* spp. (Kennett and Russell-Smith 1993; Freeman 2010), *Gopherus polyphemus* (Carlson *et al.* 2003), *Chelonoidis chilensis* (Varela and Bucher 2002), *Geochelone nigra* (Blake *et al.* 2012), *G. carbonaria* and *G. denticulata* (Strong and Fragoso 2006; Guzmán and Stevenson 2008; Jerozolimski *et al.* 2009), *Gopherus agassizii* (Woodbury and Hardy 1948), *Testudo graeca* (Cobo and Andreu 1988), *Aldabrachelys gigantea* (Wickens 1979; Griffiths *et al.* 2011), and *Rhinoclemmys* spp. (Moll and Jansen 1995). Seed dispersal is also suspected in *Podocnemis expansa* (Kubitzk and Ziburski 1994), *Sternotherus odoratus* (Ford and Moll 2004), *Macrochelys temminckii* (Sloan *et al.* 1996), and numerous members of Old World Geoemydidae (Carlott 1998), among other species (Moll and Moll 2004). Given the relatively large number of species known to consume seeds, chelonians are of great potential importance as seed dispersers and contributors to aquatic and terrestrial ecosystem function.

Additional Dietary Observations of Adult Chrysemys and Chelydra

Other observations of *Chrysemys* and *Chelydra* related to diet and feeding have been recorded during the long-term research on these species in Algonquin Park. Most observations of feeding have been of the con-

sumption of plant material during mid-to-late summer when aquatic vegetation is abundant. However, turtles appear to be more carnivorous in spring when less vegetation is available and animal prey is more exposed (e.g., breeding and laying amphibians). On several occasions, adult *Chelydra* were observed pursuing and eating American Bullfrogs (*Lithobates catesbeianus*); these events typically involved a short, rapid chase by the turtle after which the frog was quickly dispatched. On one occasion in June, young Common Grackles (*Quiscalus quiscula*) prematurely exited their nest, which was in a hollow tree over a pond, and fell to the water surface where a large male *Chelydra* captured and ate them. Adult *Chelydra* are easily trained to take fresh fish from researchers in canoes, and they readily consume up to 10% of their body mass at a feeding (Brown and Brooks 1991).

On 7 May 2011, an adult female *Chrysemys* (straight midline carapace length = 14.79 cm, mass = 465 g) was observed feeding on a Spotted Salamander (*Ambystoma maculatum*) egg mass in Wolf Howl Pond. The turtle was captured and fragments of the gelatinous egg mass were observed in her mouth. On 22 May 2011, an adult female *Chrysemys* was seen climbing onto *Sphagnum* bog mats to catch emergent dragonfly larvae that were preparing to metamorphose (Video 4, Supplementary Material). The turtle appeared to search actively for terrestrial prey and to identify visually motionless dragonfly larvae. This turtle plucked dragonfly larvae from low-lying stems of bog vegetation and carried her prey back to water before feeding. Freshwater turtles have a soft, flattened eye lens that permits emmetropic (normal-sighted) vision and comparable focus in air and water (Walls 1942; Dudziak 1955; Granda and Dvorak 1977; Northmore and Granda 1991; Kröger and Katzir 2008), perhaps allowing efficient foraging in both media. *Chrysemys picta*, among other aquatic turtle species, can experience difficulty swallowing prey out of water (Bramble 1973; Bramble and Wake 1985), and turtles may return to the water to feed because aquatic suction enhances feeding efficiency (Stayton 2011) or because being in water may reduce exposure to predators. Dragonfly prey species were not identified, although 15 species of 10 genera and four families with spring emergence dates have been identified at Wolf Howl Pond (PBM, unpublished data). Sexton (1959) also reported *Chrysemys* foraging on mats of aquatic vegetation and pursuing odonate larvae. As noted above for mosquito and anuran larvae, the seasonally available dragonfly larvae, among other aquatic insects (Rowe and Parsons 2000), may be an important food source for turtles.

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Literature Cited

- Alexander, M. M.** 1943. Food habitats of the Snapping Turtle in Connecticut. *Journal of Wildlife Management* 7: 278–282.
- Blake, S., M. Wikelski, F. Cabrera, A. Guezou, M. Silva, E. Sadeghayobi, C. B. Yackulic, and P. Jaramillo.** 2012. Seed dispersal by Galapagos Tortoises. *Journal of Biogeography* 39: 1961–1972.
- Bramble, D. M.** 1973. Media dependent feeding in turtles. *American Zoologist* 13: 1342.
- Bramble, D. M.** 1975. Feeding mechanics and behavior in the snapping turtle, *Chelydra serpentina*. Presented at the American Society of Ichthyologists and Herpetologists, Williamsburg, Virginia, USA (cited in Vogt 1981).
- Bramble, D. M., and D. B. Wake.** 1985. Feeding mechanisms of lower tetrapods. Pages 230–261 in *Functional Vertebrate Morphology*. Edited by M. Hildebrand, D. M. Bramble, K. F. Leim, and D. B. Wake. Harvard University Press, Cambridge, Massachusetts, USA.
- Braun, J., and G. R. Brooks.** 1987. Box Turtles (*Terrapene carolina*) as potential agents for seed dispersal. *American Midland Naturalist* 117: 312–318.
- Brown, G. P., and R. J. Brooks.** 1991. Thermal and behavioral responses to feeding in free-ranging turtles, *Chelydra serpentina*. *Journal of Herpetology* 25: 273–378.
- Burgin, S., and A. Renshaw.** 2008. Epizoochory, algae and the Australian Eastern Long-Necked Turtle *Chelodina longicollis* (Shaw). *American Midland Naturalist* 160: 61–68.
- Cagle, F. R.** 1939. A system of marking turtles for future identification. *Copeia* 1939: 170–173.
- Calhoun, A. J. K., and P. G. deMaynadier.** 2008. Science and Conservation of Vernal Pools in Northeastern North America. CRC Press, Boca Raton, Florida, USA.
- Calvino-Cancela, M., C. A. Fernandez, and A. C. Rivera.** 2007. European Pond Turtles (*Emys orbicularis*) as alternative dispersers of “water-dispersed” waterlily (*Nymphaea alba*). *Ecoscience* 14: 529–534.
- Carlott, R. T.** 1998. Frugivory and seed dispersal by vertebrates in the Oriental (Indomalayan) Region. *Biological Reviews of the Cambridge Philosophical Society* 73: 413–448.
- Carlson, J. E., E. S. Menges, and P. L. Marks.** 2003. Seed dispersal by *Gopherus polyphemus* at Archbold Biological Station, Florida. *Florida Scientist* 66: 147–154.
- Cobo, M., and A. C. Andreu.** 1988. Seed consumption and dispersal by the spur-thighed tortoise *Testudo graeca*. *Oikos* 51: 267–273.
- Cosentino, B. J., R. L. Schooley, and C. A. Phillips.** 2010. Wetland hydrology, area, and isolation influence occupancy and spatial turnover of the Painted Turtle, *Chrysemys picta*. *Landscape Ecology* 25: 1589–1600.
- DeGraaf, R. M., and D. D. Rudis.** 1983. Amphibians and Reptiles of New England: Habitats and Natural History. University of Massachusetts Press, Amherst, Massachusetts, USA.

- Dudziak, J.** 1955. The visual acuity of *Emys orbicularis* L. in air and in water. *Folia Biologica* (Kraków) 3: 205–228.
- Ernst, C. H., and J. E. Lovich.** 2009. Turtles of the United States and Canada. Second edition. Johns Hopkins University Press, Baltimore, Maryland, USA.
- Ford, D. K., and D. Moll.** 2004. Sexual and seasonal variation in foraging patterns in the Stinkpot, *Sternotherus odoratus*, in Southwestern Missouri. *Journal of Herpetology* 38: 296–301.
- Freeman, A. B.** 2010. Saving a living fossil: identification and mitigation of threats to the conservation status of the freshwater turtle, *Elseya lavarackorum* (technical report). Department of Environment, Water, Heritage, and the Arts, Canberra, Australia.
- Granda, A. M., and C. A. Dvorak.** 1977. Vision in turtles. Pages 451–495 in *Handbook of Sensory Physiology: the Visual System in Vertebrates*. Edited by F. Crescitelli. Springer, New York, New York, USA.
- Griffiths, C. J., D. M. Hansen, C. G. Jones, N. Zuël, and S. Harris.** 2011. Resurrecting extinct interactions with extant substitutes. *Current Biology* 21: 762–765.
- Guzmán, A., and P. R. Stevenson.** 2008. Seed dispersal, habitat selection and movement patterns in the Amazonian tortoise, *Geochelone denticulata*. *Amphibia–Reptilia* 4: 463–472.
- Hammer, D. A.** 1969. Parameters of a marsh Snapping Turtle population Lecreek Refuge, South Dakota. *Journal of Wildlife Management* 33: 995–1005.
- Jerozolinski, A., M. B. N. Ribeiro, and M. Martins.** 2009. Are tortoises important seed dispersers in Amazonian forests? *Oecologia* 161: 517–528.
- Kennett, R., and J. Russell-Smith.** 1993. Seed dispersal by freshwater turtles in northern Australia. Pages 69–70 in *Herpetology in Australia: a Diverse Discipline*. Edited by D. Lunney and D. Ayres. Royal Zoological Society of New South Wales and Surrey, Beatty and Sons, Sydney, New South Wales, Australia.
- Kenney, L. P., and M. R. Burne.** 2000. A field guide to the animals of vernal pools. Massachusetts Natural Heritage & Endangered Species Program. Massachusetts Division of Fisheries & Wildlife and Vernal Pool Association, Westborough, Massachusetts, USA.
- Kimmons, J. B., and D. Moll.** 2010. Seed dispersal by Red-eared Sliders (*Trachemys scripta elegans*) and Common Snapping Turtles (*Chelydra serpentina*). *Chelonian Conservation and Biology* 9: 289–294.
- Kröger, R. H. H., and G. Katzir.** 2008. Comparative anatomy and physiology of vision in aquatic tetrapods. Pages 121–147 in *Sensory Evolution on the Threshold: Adaptations in Secondly Aquatic Vertebrates*. Edited by J. G. M. Thewissen and S. Nummela. University of California Press, Oakland, California, USA.
- Kubitzki, K., and A. Ziburski.** 1994. Seed dispersal in flood plain forests of Amazonia. *Biotropica* 26: 30–43.
- Lagler, K. F.** 1943. Food habits and economic relations of the turtles of Michigan with species reference to fish management. *American Midland Naturalist* 29: 257–312.
- Lauder, G. V., and T. Prendergast.** 1992. Kinematics of aquatic prey capture in the Snapping Turtle *Chelydra serpentina*. *Journal of Experimental Biology* 164: 55–78.
- Lindeman, P. V.** 1996. Comparative life history of Painted Turtles (*Chrysemys picta*) in two habitats in the inland Pacific Northwest. *Copeia* 1996: 114–130.
- Liu, H., S. G. Platt, and C. K. Borg.** 2004. Seed dispersal by the Florida Box Turtle (*Terrapene carolina bauri*) in pine rockland forests of the lower Florida Keys, United States. *Oecologia* 138: 539–546.
- Loncke, D. J., and M. E. Obbard.** 1977. Tag success, dimensions, clutch size, and nesting site fidelity for the Snapping Turtle, *Chelydra serpentina*, (Reptilia, Testudines, Chelydridae) in Algonquin Park, Ontario. *Journal of Herpetology* 11: 243–244.
- MacCulloch, R. D., and D. M. Secoy.** 1983. Demography, growth, and food of Western Painted Turtles, *Chrysemys picta bellii* (Gray), from southern Saskatchewan. *Canadian Journal of Zoology* 61: 1499–1509.
- McCollum, S. A., and J. D. Leimberger.** 1997. Predator-induced morphological changes in an amphibian: predation by dragonflies affects tadpole shape and color. *Oecologia* 109: 615–621.
- Moll, D., and K. P. Jansen.** 1995. Evidence for a role in seed dispersal by two tropical herbivorous turtles. *Biotropica* 27: 121–127.
- Moll, D., and E. O. Moll.** 2004. *The Ecology, Exploitation, and Conservation of River Turtles*. Oxford University Press, New York, New York, USA.
- Northmore, D. P. M., and A. M. Granda.** 1991. Ocular dimensions and schematic eyes of freshwater and sea turtles. *Visual Neuroscience* 7: 627–635.
- Obbard, M. E., and R. J. Brooks.** 1981. A radio-telemetry and mark-recapture study of activity in the Common Snapping Turtle, *Chelydra serpentina*. *Copeia* 1981: 630–637.
- Padgett, D. J., J. J. Carboni, and D. J. Schepis.** 2010. The dietary composition of *Chrysemys picta picta* (Eastern Painted Turtles) with special reference to the seeds of aquatic macrophytes. *Northeastern Naturalist* 17: 305–312.
- Punzo, F.** 1975. Studies on the feeding behavior, diet, nesting habits and temperature relationships of *Chelydra serpentina osceola* (Chelonia: Chelydridae). *Journal of Herpetology* 9: 207–210.
- Raney, E. C., and E. A. Lachner.** 1942. Summer food of *Chrysemys picta marginata* in Chautauqua Lake, New York. *Copeia* 1942: 83–85.
- Relyea, R. A.** 2001. Morphological and behavioral plasticity of larval anurans in response to different predators. *Ecology* 82: 523–540.
- Relyea, R. A.** 2004. Fine-tuned phenotypes: tadpole plasticity under 16 combinations of predators and competitors. *Ecology* 85: 172–179.
- Rollinson, N., and R. J. Brooks.** 2007. Proximate constraints on reproductive output in a northern population of painted turtles: an empirical test of the bet-hedging paradigm. *Canadian Journal of Zoology* 85: 177–184.
- Rowe, J. W., and W. Parsons.** 2000. Diet of the midland painted turtle (*Chrysemys picta marginata*) on Beaver Island, Michigan. *Herpetological Review* 31: 16–17.
- Schwarzkopf, L., and R. J. Brooks.** 1985. Sex determination in northern painted turtles: effect of incubation at constant and fluctuating temperatures. *Canadian Journal of Zoology* 63: 2543–2547.
- Sexton, O. J.** 1959. Spatial and temporal movements of a population of the Painted Turtle, *Chrysemys picta marginata* (Agassiz). *Ecological Monographs* 29: 113–140.
- Sloan, K. N., K. A. Buhlmann, and J. E. Lovich.** 1996. Stomach contents of commercially harvested adult Alligator Snapping Turtles, *Macrochelys temminckii*. *Chelonian Conservation and Biology* 2: 96–99.
- Stayton, C. T.** 2011. Terrestrial feeding in aquatic turtles: environment-dependent feeding behavior modulation and

- the evolution of terrestrial feeding in Emydidae. *Journal of Experimental Biology* 214: 4083–4091.
- Strong, J. N., and J. M. V. Fragoso.** 2006. Seed dispersal by *Geochelone carbonaria* and *Geochelone denticulata* in northwestern Brazil. *Biotropica* 38: 683–686.
- Summers, A. P., K. F. Darouian, A. M. Richmond, and E. L. Brainerd.** 1998. Kinematics of aquatic and terrestrial prey captures in *Terrapene carolina*, with implications for the evolution of feeding in cryptodire turtles. *Journal of Experimental Biology* 281: 280–287.
- Thompson, K. A., D. M. Sora, K. S. Cross, J. M. St. Germain, and K. Cottenie.** 2014. Mucilage reduces leaf herbivory in Schreber's watershield, *Brasenia schreberi* J.F. Gmel (Cabombaceae). *Botany* 92: 412–416.
- Traveset, A.** 1998. Effect of seed passage through vertebrate frugivores' guts on germination: a review. *Perspective in Plant Ecology, Evolution and Systematics* 1: 151–190.
- Varela, R. O., and E. H. Bucher.** 2002. Seed dispersal by *Chelonoidis chilensis* in the Chaco dry woodland of Argentina. *Journal of Herpetology* 36: 137–140.
- Vogt, R. C.** 1981. *Natural History of Amphibians and Reptiles in Wisconsin*. Milwaukee Public Museum, Milwaukee, Wisconsin, USA.
- Walls, G. L.** 1942. *The Vertebrate Eye and its Adaptive Radiation*. McGraw-Hill, New York, New York, USA.
- Wickens, G. E.** 1979. Speculations on seed dispersal and the flora of the Aldabra Archipelago. *Philosophical Transactions of the Royal Society of London, Biological Sciences* 286: 85–97.
- Woodbury, A. M., and R. Hardy.** 1948. Studies of the Desert Tortoise, *Gopherus agassizii*. *Ecological Monographs* 18: 145–200.

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SUPPLEMENTARY MATERIAL:

- VIDEO 1.** Young Snapping Turtle (*Chelydra serpentina*) preying on mosquito larvae (Diptera: Culicidae) in an ephemeral pool in Algonquin Provincial Park, Ontario, Canada. Note the stalking and ambush behaviour, in contrast with the feeding strategy of a young Midland Painted Turtle (*Chrysemys picta marginata*) in Video 2.
<https://www.youtube.com/watch?v=2Ea5xZIH5n8>
- VIDEO 2.** Young Midland Painted Turtle (*Chrysemys picta marginata*) preying on mosquito larvae (Diptera: Culicidae) in an ephemeral pool in Algonquin Provincial Park, Ontario, Canada. Note the active chase feeding behaviour, in contrast with the feeding strategy of young Snapping Turtle (*Chelydra serpentina*) in Video 1.
<https://www.youtube.com/watch?v=A0poVfMIEeY>
- VIDEOS 3A and 3B.** Adult male Snapping Turtle (*Chelydra serpentina*) feeding on Watershield (*Brasenia schreberi* J. F. Gmelin) at Wolf Howl Pond, Algonquin Provincial Park, Ontario, Canada.
<https://www.youtube.com/watch?v=G4up-fkXbss&feature=youtu.be>
<https://www.youtube.com/watch?v=WcNNiHO4tas>
- VIDEOS 4A and 4B.** Adult female Midland Painted Turtle (*Chrysemys picta marginata*) preying on emergent dragonfly larvae (Odonata: Anisoptera) preparing for metamorphosis at Wolf Howl Pond East, Algonquin Provincial Park, Ontario, Canada. Recorded by A. M. Bennett.
<https://www.youtube.com/watch?v=Z7LNdafj1HQ&feature=youtu.be>
<https://www.youtube.com/watch?v=ryZ6JSfXbno&feature=youtu.be>