

Turtles outsmart rapid environmental change: The role of cognition in navigation

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Animals inhabiting changing environments show high levels of cognitive plasticity. Cognition may be a means by which animals buffer the impact of environmental change. However, studies examining the evolution of cognition seldom compare populations where change is rapid and selection pressures are strong. We investigated this phenomenon by radiotracking experienced and naïve Eastern painted turtles (*Chrysemys picta*) as they sought new habitats when their pond was drained. Resident adults repeatedly used specific routes to permanent water sources with exceptional precision, while adults translocated to the site did not. Naïve 1–3 y olds from both populations used the paths taken by resident adults, an ability lost by age 4. Experience did not, however, influence the timing of movement or the latency to begin navigation. This suggests that learning during a critical period may be important for how animals respond to changing environments, highlighting the importance of incorporating cognition into conservation.

Challenging environments tend to produce animals with advanced cognitive abilities.^{1–3} For example, food-caching birds from harsh climates possess better spatial memory and solve problems more quickly than those from mild climates.^{4–7} The rate of local environmental change also plays a role in the selection of enhanced cognition.⁸ How rapid environmental changes affect the cognitive abilities of animals is particularly important in light of global climate change.^{9,10,11} For example, cichlid fish raised with variable food availability perform better at cognitive tasks as adults than those raised under stable food regimes.¹² Although environmental challenges seem important for enhanced cognition, the effects of the current rapid rates of global climate change on species' abilities to adapt and respond are unknown.

Reptiles appear to be particularly susceptible to global climate change.^{13,14} They are currently facing marked population declines worldwide, perhaps reflecting their sensitivity to temperature and their reduced dispersal abilities (e.g.¹⁵). However, the ability of reptiles to use behavioral and cognitive abilities to buffer the impacts of environmental change is not well studied. While the use of spatial memory by reptiles remains equivocal,^{16–18} recent work on reptile cognition suggests that many species possess complex, spatially-related behavior (e.g.,¹⁹; see²⁰ for a review). For example, Burmese pythons (*Python bivittatus*) exhibit map- and compass-based navigation.²¹ Similarly, side-blotched lizards (*Uta stansburiana*) rely on memory to solve spatially-explicit tasks.²² Clearly, reptiles possess some specialized

cognitive abilities that could, in principle, aid them in mitigating the negative impacts of climate change.

Learning to Respond to Change

We recently investigated the ability of a population of Eastern painted turtles (*Chrysemys picta*) to learn navigation routes when responding to a unique form of human-induced rapid environmental change. This population is forced annually to search for new aquatic habitats when their ponds are drained for waterfowl management. We used 2 populations to demonstrate the importance of learning and experience in navigation, sampling animals from one year old to adult. Our main study population, which resides in ephemeral habitat (hereafter, the “resident” population) is an excellent model of rapid habitat change and may present a strong selective environment for learning. To examine the importance of experience during navigation, we also moved both juvenile and adult turtles to our resident site from a distinct donor site with permanent water (hereafter, the “translocated” population) about 20 km away.

We used radiotelemetry to track the movements of 76 resident and 48 translocated individuals as they left focal ponds during draining. All turtles were fitted with radiotransmitters and were located >3 times per h, for the entirety of their terrestrial movement. This enabled us to determine both the turtles' final

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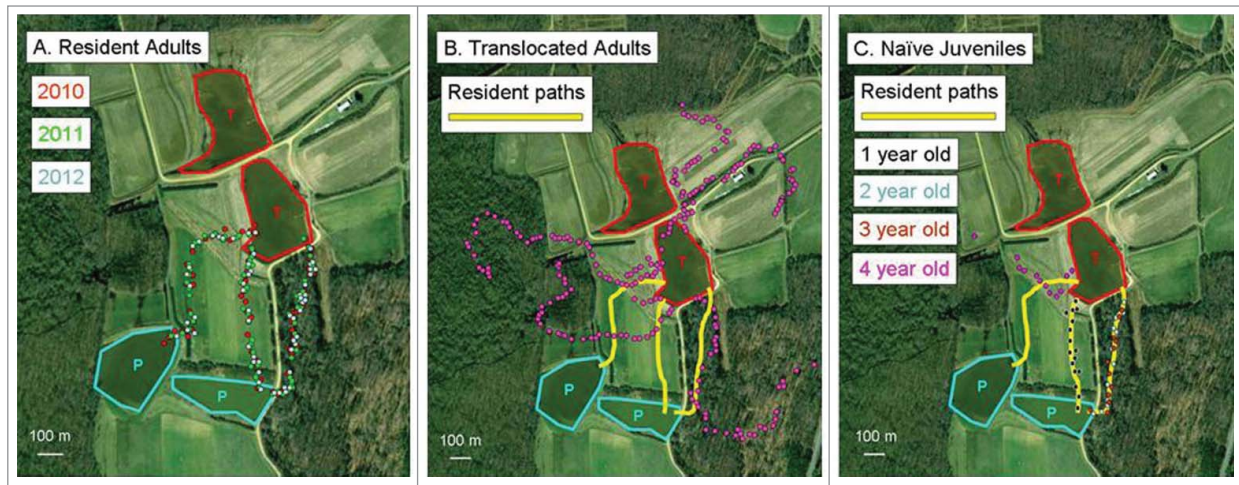


Figure 1. Representative samples (for clarity) of *C. picta* overland movements during habitat destruction. (A) Resident adults, (B) Translocated adults, (C) Naïve juveniles of ages 1–4 y. Resident adults and 1–3 yo naïve juveniles utilized well-established paths (yellow lines) to move from the temporary (T) to permanent (P) water sources. Translocated adults and naïve juveniles at age 4 could not navigate to water. Data from Roth and Krochmal.²³

destination, and more importantly, the specific routes taken for comparisons across individuals and years.

Adult resident turtles used complex and specific paths ($\pm 3.1\text{m}$) to alternative water sources (Fig. 1A);²³ routes were consistent across years, both within and among individuals. By contrast, adults from the translocated site failed to locate water (Fig. 1B).²³ Critically, naïve juvenile turtles (ages 1–3yo), both from the resident and translocated populations, successfully located permanent water using the same routes as experienced turtles (Fig. 1C); however, this ability deteriorated by age 4 (Fig. 1C).²³

How do Juveniles Learn?

Many taxa exhibit age-specific critical learning periods during which juveniles can acquire new information, but after which acquisition becomes difficult.²⁴⁻²⁶ In our system, juveniles must learn their paths by age 4 or they will not be able to successfully navigate. However, these turtles are not simply following experienced individuals. For example, the initiation of movement of turtles on paths is sporadic and we never observed animals moving in tandem ($> 3,000$ tracking hours).²³ Still, how they actually learn these movements is not clear.

Thus, we include here additional analyses comparing the movements of naïve animals to those of experienced ones. We examined the timing of movement of both groups and observed no differences between naïve turtles < 4 y old and experienced adults in latency to leave the pond after it drained ($t = 1.3201$, $df = 98$ $p = 0.1899$; Fig. 2). Further, turtles did not leave the pond uniformly across the day. Rather, both naïve and experienced turtles showed a bias toward midday departures and away from evening ones (naïve – $\chi^2 = 10.861$ $df = 2$, $P = 0.0044$; experienced – $\chi^2 = 22.800$, $df = 2$, $P = 0.0001$; Fig. 3).

Successfully navigating this landscape is clearly facilitated by experience, although the specific means by which naïve turtles learn remains unclear. We failed to find evidence that naïve turtles learn directly from experienced ones or that they follow each other as they leave the ponds. This, combined with the substantial size of our field site, its topography, and vegetation structure, suggests that juveniles learn these routes without direct influence from experienced animals.

Implication for Conservation

Our unique system provides the opportunity to better understand the role of cognition in how animals respond to changing environments and how this knowledge can help in conserving wild populations. Although some argue that integrating the fields

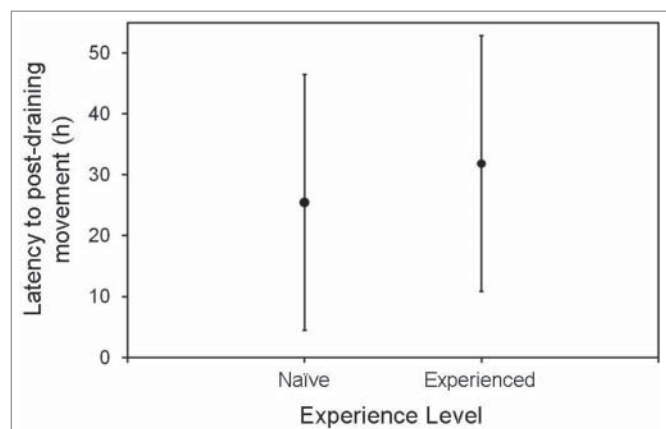


Figure 2. Latency to leave the drained pond does not depend on experience. Both naïve and experience turtles have comparable mean latencies to begin their navigations. Error bars denote one standard deviation.

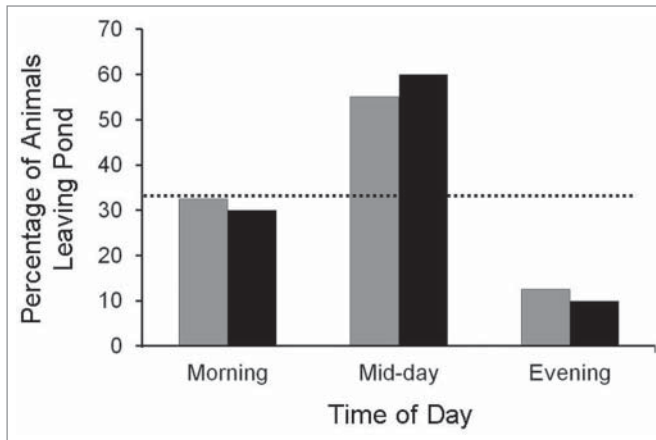


Figure 3. Timing of emergence from drained pond is not uniform and does not depend on experience. The percentage of naïve turtles departing the drained pond during morning (0700–1100h), mid-day (1100–1500h), and evening (1500–1900h) showed a significant deviation from uniformity and was biased toward midday and away from morning and evening, a preference shared with experienced turtles. Black bars represent experienced animals and gray bars represent naïve animals. Dotted line represents the null expectation of equal distribution of departures across the day.

of behavior and conservation is difficult and perhaps not feasible,^{27–29} we feel that our previous work²³ and the present analyses demonstrate the potential successes for uniting these 2 fields. By considering cognition and conservation together, we are better able to elucidate important, yet otherwise cryptic, aspects of

learning and cognition. Integrating studies of animal behavior and cognition with large-scale phenomena such as conservation will provide a more complete and relevant context in which to investigate behavior. We contend that given the severity of the biodiversity crisis and the strong cognitive and behavioral basis for much of the biology fundamental to conservation, careful consideration and inclusion of aspects of cognition is pivotal to understanding how animals respond to today's rapidly changing world.

Disclosure of Potential Conflicts of Interest

No potential conflicts of interest were disclosed.

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References

- Richerson PJ, Boyd R. Climate, Culture, and the Evolution of Cognition. In *Evolution of Cognition*, eds Heyes C, Huber L. Boston, MA: MIT Press 2000; 329–46
- Dukas R. Evolutionary biology of animal cognition. *Annu Rev Ecol Evol Syst* 2004; 35:347–74; <http://dx.doi.org/10.1146/annurev.ecolsys.35.112202.130152>
- Shettleworth SJ. The evolution of comparative cognition: is the snark still a boojum? *Behav Process* 2009; 80:210–7; PMID:18824222; <http://dx.doi.org/10.1016/j.beproc.2008.09.001>
- Roth TC, LaDage LD, Pravosudov VV. Learning capabilities enhanced in harsh environments: a common garden study. *Proc R Soc B* 2010; 277:3187–93; PMID:20519218; <http://dx.doi.org/10.1098/rspb.2010.0630>
- Roth TC, LaDage LD, Freas C, Pravosudov VV. Variation in memory and the hippocampus across populations from different climates: a common garden approach. *Proc R Soc B* 2012; 279:402–10; PMID:21715407; <http://dx.doi.org/10.1098/rspb.2011.1020>
- Pravosudov VV, Roth TC, LaDage LD, Freas CA. Environmental influences on spatial memory and the hippocampus in food-caching chickadees. *Comp Cogn Behav Rev* 2015; In press
- Pravosudov VV, Roth TC. Food hoarding and the evolution of memory and the hippocampus. *Ann Rev Ecol Evol Syst* 2013; 44(18):1–18.21
- Niemela PT, Vainikka A, Forsman JT, Loukola OJ, Kortet R. How does variation in the environment and individual cognition explain the existence of consistent behavioral differences? *Ecol Evol* 2013; 3:457–64; PMID:23467316; <http://dx.doi.org/10.1002/ecc3.451>
- Sih A, Ferrari MCO, Harris DJ. Evolution and behavioral responses to human-induced rapid environmental change. *Evol Appl* 2011; 4:367–87; PMID:25567979; <http://dx.doi.org/10.1111/j.1752-4571.2010.00166.x>
- Sol D, Bacher S, Reader SM, Lefebvre L. Brain size predicts the success of mammal species introduced into novel environments. *Am Nat* 2008; 172:S63–S71; PMID:18554145; <http://dx.doi.org/10.1086/588304>
- Sol D, Duncan RP, Blackburn TM, Cassey P, Lefebvre L. Big brains, enhanced cognition, and response of birds to novel environments. *Proc Natl Acad Sci USA* 2005; 102:5460–5; PMID:15784743; <http://dx.doi.org/10.1073/pnas.0408145102>
- Kotrschal A, Taborsky B. Environmental Change Enhances Cognitive Abilities in Fish. *PLOS Biol* 2010; 8:e1000351; PMID:20386729; <http://dx.doi.org/10.1371/journal.pbio.1000351>
- Araujo MB, Thuiller W, Pearson RG. Climate warming and the decline of amphibians and reptiles in Europe. *J Biogeograph* 2006; 33:1712–28; <http://dx.doi.org/10.1111/j.1365-2699.2006.01482.x>
- Chamaille-Jammes S, Massot M, Aragon P, Clobert J. Global warming and positive fitness response in mountain populations of common lizards *Lacerta vivipara*. *Global Change Biol* 2006; 12:392–402; <http://dx.doi.org/10.1111/j.1365-2486.2005.01088.x>
- Gibbons JW, Scott DE, Ryan TJ, Buhlmann KA, Tuberville TD, Metts BS, Greene JL, Mills T, Leiden Y, Poppy S, et al. The global decline of reptiles, Deje Vu amphibians. *BioScience* 2000; 50:653–66; [http://dx.doi.org/10.1641/0006-3568\(2000\)050%5b0653:TGDORD%5d2.0.CO;2](http://dx.doi.org/10.1641/0006-3568(2000)050%5b0653:TGDORD%5d2.0.CO;2)
- Day LB, Crews D, Wilczynski W. Spatial and reversal learning in congeneric lizards with different foraging strategies. *Anim Behav* 1999; 57:393–408; PMID:10049480; <http://dx.doi.org/10.1006/anbe.1998.1007>
- Jacobs LF, Schenk F. Unpacking the cognitive map: the parallel map theory of hippocampal function. *Psy Rev* 2003; 110:285–315; <http://dx.doi.org/10.1037/0033-295X.110.2.285>
- Jacobs LF. The evolution of the cognitive map. *Brain Behav Evol* 2003; 62:128–39; PMID:12937351; <http://dx.doi.org/10.1159/000072443>
- Powers AS, Houge P, Lynch C, Gattuso B, Lissek S, Nayal C. Role of Acetylcholine in negative patterning in turtles (*Chrysemys picta*). *Behav Neurosci* 2009; 123:804–9; PMID:19634938; <http://dx.doi.org/10.1037/a0016320>
- Broglio C, Martín-Monzón I, Ocaña FM, Gómez A, Durán E, Salas C, Rodríguez F. Hippocampal pallium and map-like memories through vertebrate evolution. *J Behav Brain Sci* 2015; 5:109–20; <http://dx.doi.org/10.4236/jbbs.2015.53011>
- Pittman SE, Hart KM, Cherkiss MS, Snow RW, Fujisaki I, Smith BJ, Mazzotti FJ, Dorcas ME. Homing of invasive Burmese pythons in South Florida: evidence for map and compass senses in snakes. *Biol Lett* 2014; 10:20140040; PMID:24647727; <http://dx.doi.org/10.1098/rsbl.2014.0040>
- LaDage LD, Roth TC, Cerjanic AM, Sinervo B, Pravosudov VV. Spatial memory: are lizards really deficient? *Biol Lett* 2012; 8:939–41; PMID:22933038; <http://dx.doi.org/10.1098/rsbl.2012.0527>
- Roth TC, Krochmal AR. The role of age-specific learning and experience for turtles navigating a changing landscape. *Curr Biol* 2015; 25:333–7;

- PMID:25578905; <http://dx.doi.org/10.1016/j.cub.2014.11.048>
24. Doupe AJ, Kuhl PK. Birdsong and Human Speech. *Annu Rev Neurosci* 1999; 22:567-631; PMID:10202549; <http://dx.doi.org/10.1146/annurev.neuro.22.1.567>
25. Tchernichovski O, Mitra PP, Lints T, Nottebohm F. Dynamics of the vocal imitation process: how a zebra finch learns its song. *Science* 2001; 291:2564-9; PMID:11283361; <http://dx.doi.org/10.1126/science.1058522>
26. Biro D, Inoue-Nakamura N, Tonooka R, Yamakoshi G, Sousa C, Matsuzawa T. Cultural innovation and transmission of tool use in wild chimpanzees: evidence from field experiments. *Anim Cogn* 2003; 6:213-23; PMID:12898285; <http://dx.doi.org/10.1007/s10071-003-0183-x>
27. Berger-Tal O, Polak T, Oron A, Lubin Y, Kotler BP, Saltz D. Integrating animal behavior and conservation biology: a conceptual framework. *Behav Ecol* 2011; 22:236-9; <http://dx.doi.org/10.1093/beheco/arq224>
28. Caro T, Sherman PW: Eighteen reasons animal behaviourists avoid involvement in conservation. *Anim Behav* 2013; 85:305-12; <http://dx.doi.org/10.1016/j.anbehav.2012.11.007>
29. Cooke SJ, Blumstein DT, Buchholz R, Caro T, Fernandez-Juricic E, Franklin CE, Metcalfe J, O'Connor CM, St. Clair CC, Sutherland WJ, et al. Physiology, behavior, and conservation. *Physiol Biochem Zool* 2014; 87:1-14; PMID:24457917; <http://dx.doi.org/10.1086/671165>