

Pre- and post winter hibernation ecology of the eastern box turtle, *Terrapene carolina carolina*

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ABSTRACT - Thermal ecology of the eastern box turtle (*Terrapene carolina carolina*) was studied during the cooler months of the year (September to April) at the Mason Neck National Wildlife Refuge, Fairfax County, Virginia, USA. The research enlisted individual male and female turtles tracked by radio telemetry. Observations were made on behaviour and thermoregulation in relation to their effect as the turtles entered into hibernacula, moved during the winter, and emerged in the spring. We found extensive above ground movements were common through mid- to late December and ground movement from hibernacula to others were more frequent than expected. Turtles emerged in late March and early April and, depending on the spring warm-up, the turtles remained close to hibernacula before undertaking characteristic spring movement and activity. The observed thermal characteristics of microhabitats appeared to affect, and could predict, varied behaviours and movements. While turtles in geographic areas where temperatures fall below freezing enter hibernacula during the winter, our study found this to be a generalisation. The temperature profiles of specific microhabitats suggest a relationship between amount, type and degree of activity. In northern Virginia, we found turtles to be significantly more active than expected at temperatures that would otherwise suggest less movement. They entered hibernacula later, moved (relocated) dependent on environmental ambient temperatures, and seemed to be subject to freezing during the winter and emerged earlier.

INTRODUCTION

There are numerous studies on turtles of the genus *Terrapene*, but field research focused on their natural winter ecology and behaviour is generally lacking. Box turtles are a cold and freeze adapted (tolerant) reptile with observations indicating that they may remain active during winter time (see review in Ernst & Lovich, 2009). The focus of this study is to expand on current knowledge of the winter ecology and behaviour of *Terrapene carolina carolina*, the eastern box turtle, in northern Virginia during the cooler months of the year.

MATERIALS AND METHODS

Observations of box turtles were made on average every three days, with greater frequency during late autumn and late winter/early spring, at a 30-ha site on an Atlantic coastal plain peninsula of the Potomac River at the Mason Neck National Wildlife Refuge, Fairfax County, VA (38° 67' N, 77° 10' W; ~25-35 m elevation). The site was restricted and closed to the general public. The peninsula's vegetation is composed primarily of mixed deciduous upland forest. The length of the peninsula is bisected by a gravel road. The study area included five different habitats: (A), An old farmstead consisting of mixed hardwoods, grass plots and a parking area near the terminal point of the peninsula; (B), a ~3-ha field undergoing succession with the transecting gravel road to the west and surrounded

on the other three sides by woods; (C), a ~2-ha freshwater pond fed by a brook to the west, surrounded by woods on two sides, the gravel road to the east, and a brook flowing eastward to a tidal marshland; (D), a ~5-ha tidal-freshwater marsh along the Potomac River to the south; and (E), an extensive mixed second and third growth woods separating the other four habitats.

Turtle observations were made from September to mid-April of 1993-94 and 1994-95. Ten turtles (5 male / 5 female) were selected for the study each year. Sex was determined by visual inspection of the turtle using several sexually dimorphic traits; carapace shape, plastron shape, hind foot claw shape, tail length, tail width, position of vent on tail and iris colour (Ernst & Lovich, 2009). Turtles were fitted with radio transmitters (AVM, Type 2B, weighing 25 g) to track their movements. The transmitters were affixed to the carapace with PC-7 epoxy resin between the 3rd and 4th pleural scutes so as not to interfere with movement or the opening and closing of the plastron. The antennae were threaded through the marginal scutes, held in place by adhesive silicon sealant at the cervical scute. The antennae sat erect approximately 4 cm above the turtle but could fold backward against the carapace if individuals went under debris or entered a shallow form (pallet) or deeper hibernaculum.

Temperatures at both form and hibernaculum were recorded with Taylor Minimum/Maximum thermometers accurate to 0.1 °C that were placed on the ground surface and below the leaf litter adjacent to the form or hibernaculum.

Other temperature measurements were made with an Omega 22H electronic thermometer accurate to 0.1 °C equipped with constantin-tipped thermocouples. This was used to record air temperature (AT, 5 cm above the form/hibernaculum), surface temperature (ST, atop the leaf litter), and litter temperature (LT, below the leaf litter at the ground surface). It was also used to measure temperatures at the shallowest and deepest points of the hibernaculum based on the anterior and posterior positions of the turtle. Turtles were briefly removed from the hibernaculum to measure cloacal temperatures (CT) with a Schultheis cloacal thermometer accurate to 0.1 °C. Hibernaculum depth was measured at its shallowest (HDS) and deepest (HDD) points as determined by the anterior and posterior positions of the turtle. A 30 cm ruler, graduated in mm, was extended downward from directly above the hibernaculum to measure the distance between HDS/HDD and the ground surface.

RESULTS

Before hibernacula entry, extensive above ground movements at Mason Neck were observed as late as 30 December (1994). The majority of observations were of turtle forms, but because individuals were tracked by radio telemetry, locations could be marked and straight line distances and direction between vacated and occupied forms determined. The mean monthly distances travelled by all turtles between observations, and mean monthly CT, AT, ST, LT and form temperatures, are presented in Table 1. A Spearman Rank Correlation test (Spearman's Rho) showed that all comparative temperatures were significantly correlated ($p < 0.05$) and linear in their relationship. Thus, the overall influence of month on temperature and movement was analysed using a multivariate analysis of variance (MANOVA) with month as the independent variable and CT, AT, ST, LT and distance moved as dependent variables. The results indicated that, in addition to the trend noted above, monthly temperatures and distance moved were significantly different (Wilk's Lambda $F_{15,456} = 19.382$, $p < 0.0001$).

When box turtles finally entered hibernacula at Mason Neck, they favoured wooded areas with ample litter/detritus cover, downed trees, brush and logs, thick bushes (especially *Smilax* sp.) and rotting tree stumps. Of sixteen turtles that were tracked into hibernacula during this study, twelve (75%) selected this type of microhabitat. Two selected hibernacula on the ecotone between woods and an old field; one selected an open, less dense, wooded area; and another selected a depression that was either moist or water-filled. No hibernaculum site fidelity or multiple occupants of hibernacula were observed at Mason Neck, but multiple occupancy by *T. c. carolina* has been observed in Pennsylvania by Ernst (unpublished). Eight individuals included in the first year of this study, but not in the second year, could not be found using the probing method reported by Carpenter (1955) after searching a 314 m² area around their previous overwintering sites.

Of the sixteen turtles that entered hibernacula, five relocated. Eight did not move until they emerged in the late winter/early spring. The remaining three were removed

Table 1. Mean and range of monthly displacement (m) by *T. c. carolina* and mean monthly temperatures (°C)

	September	October	November	December
Mean displacement (m) (n)	50.61 (27)	34.28 (47)	23.95 (53)	12.68 (48)
Range	0 - 192	1.5 - 120	0.50 - 140	0.30 - 70
Mean Temperatures				
Air	18.48	13.64	11.70	6.83
Range	12.4 - 27.0	6.5 - 22.6	1.3 - 25.1	-3.8 - 13.20
Surface	18.30	13.76	11.57	7.24
Range	12.3 - 26.2	6.9 - 21.1	1.6 - 26.9	0 - 15.4
Litter	18.63	13.91	11.07	6.97
Range	13.8 - 24.8	9.0 - 19.7	5.4 - 21.1	1.5 - 14.3
Cloacal	17.99	13.47	11.57	7.45
Range	12.2 - 24.8	8.4 - 20.4	3.6 - 26.6	2.4 - 11.6
Form - Top	N.A.	N.A.	10.13	7.69
Range			6.4 - 14.5	3.4 - 12.0
Form - Bottom	N.A.	N.A.	10.22	7.49
Range			5.8 - 14.5	3.7 - 12.6

Table 2. Turtles relocating to different hibernacula during the hibernation period-initial dates of entry into hibernacula, dates of relocation, time elapsed between relocations, displacement differences between hibernacula, and final emergence date

Turtle ID	Date entered into Hibernaculum	Date Relocated	Elapsed Days (n)	Displacement (m)	Date Emerged
1044	10 December	13 March	93	15.0	4 April
1073	7 December	6 March	88	10.2	11 April
		15 March	97	22.0	
		19 March	101	18.5	
		3 April	116	0.45	
332A	18 December	6 March	77	12.3	13 March
4000	20 December	26 February	68	3.1	26 March
557	18 December	13 March	85	18.0	25 March

Table 3. Mean monthly hibernaculum depth (mm) at shallowest (HDS) and deepest (HDD) points

Month	HDS	Range	HDD	Range
December	62.18 ± 7.18	7 - 100	83.57 ± 6.25	25 - 150
January	67.62 ± 7.73	15 - 97	105.08 ± 7.57	36 - 187.5
February	74.82 ± 5.99	45 - 100	89.55 ± 7.58	36 - 187.5
March	61.49 ± 6.43	20 - 105	69.08 ± 4.56	20 - 140
April	38.31 ± 9.23	20 - 60	59.12 ± 5.96	30 - 80

from the research site before they emerged, because radio transmitter batteries had failed. Of the five that relocated, four relocated once and one moved three times. These relocating turtles all travelled similar distances and did not choose different hibernacula. Table 2 shows the dates of relocation and distance moved. The mean time elapsed between entry into a hibernaculum and the first relocation was 82.2 days and mean straight-line distance moved was 11.72 m (3.1 to 18 m).

Internally, hibernacula were slightly enlarged cavities, excavated by horizontal and/or vertical movement. On several occasions, up to 3 cm of lateral clearance was found between an individual and the side of the hibernaculum. This seemed to be related to soil temperatures because during colder periods (i.e., when temperatures near the surface were close to freezing) individuals were found snugly ensconced. A reduction in contact with air that might be slightly colder than the surrounding soil probably elicited such a change. Additionally, on several occasions, the top of the carapace was noted to be at or near the ground level, covered only by leaf litter or a thin layer of coarsely decomposed organic matter below leaf litter.

Tunnels excavated by turtles were found in hibernacula on 102 of 294 observations (34.7%) but not noted consistently or with any regularity. When a tunnel was present, the direction the turtle faced was mainly inward away from the opening surface of the hibernaculum (88 observations; 86.3%) rather than outward (14 observations; 13.7%). Above the hibernaculum, the depth of the leaf litter cover varied by individual location. The mean litter depth for all hibernacula was 75.53 ± 2.41 mm (30-120 mm). The mean difference between minimum and maximum litter/surface temperatures was calculated as minimum litter temperature 3.10 ± 0.39 °C warmer than minimum surface temperature and maximum litter temperature 5.11 ± 0.64 °C colder than maximum surface temperature.

Hibernacula were confined to the top soil horizon which extends downward to a depth greater than 100 mm at Mason Neck. At no time did hibernacula extend into the A Soil horizon (mineral layer). The mean maximum depth of hibernacula at Mason Neck was determined to be 85.47 ± 3.57 mm (20-187.5 mm) but monthly changes in hibernacula depth were observed (Table 3).

The mean carapace height of turtles in this study was 60.97 ± 2.34 mm, so at various times over the course of the winter some part of the carapace was either at or slightly below the ground surface and covered only by leaf litter. Minimum litter temperatures in both January and February fell to -7.0 °C and -6.0 °C, respectively, which indicates that on a number of occasions part of the carapace was subject to freezing, and several times ice was observed on the posterior and apex of the carapace and/or leaf litter was frozen to the carapace, indicating that at least part of the turtle's surface was frozen. The mean duration of hibernation was 103.46 ± 10.31 days (77 - 135 days). *T. carolina* can tolerate ice penetration throughout the body cavity and ice contents that can reach equilibrium values of more than 50% of total body water (Storey and Storey, 2004).

DeGregorio et al. (2017) reported that South Carolina *T. carolina* did not emerge from dormancy until the 5-day mean surface temperatures measured at hibernacula reached about 5 °C. Following emergence, our turtles entered an inactive period, here defined as movement and behaviour only undertaken within a 10 m radius of the hibernaculum (an area of 314 m²). In the turtles for which post-emergence data were recorded, emergence occurred between 6 March and 11 April (Table 4) and the number of days spent undertaking activity near the hibernacula varied considerably. During this time, the mean straight-line

Table 4. Dates of entry into and emergence from hibernacula

Turtle ID	Date of Entry	Date of Emergence	Length of Hibernation	
♀	107	26 November	11 April	135 days
	332A	18 December	13 March	85 days
	1081	30 December	18 March	77 days
	136	18 December	6 March	78 days
	303	28 November	26 March	117 days
	4000	20 December	26 March	96 days
♂	356	10 December	25 March	104 days
	92	29 November	5 April	126 days
	1044	10 December	4 April	114 days
	1073	7 December	3 April	116 days
	54	26 November	23 March	116 days
	557	18 December	25 March	97 days
	59	27 December	21 March	83 days

Table 5. Dates of emergence from, and movement away from, hibernaculum

Date Emerged	Turtle ID	Date Moved Away From Hibernaculum Site	Number of Days Close to Hibernaculum
4 April	1044	14 April	10
11 April	107	13 April	2
3 April	1073	4 April	1
6 March	136	12 April	37
13 March	332	7 April	25
25 March	557	11 April	15
25 March	350	5 April	13

Table 6. Numbers of *T. c. carolina* and frequency of their behaviours in sick and healthy individuals

	Basking	Thermal Regulating Under Leaf Litter	Form	Walking	Total
Healthy	20	21	41	1	83
%	(18.18)	(19.09)	(37.27)	(0.91)	(75.45)
Sick	16	9	1	1	27
%	(14.55)	(8.18)	(0.9)	(0.91)	(24.65)
Total	36	30	42	2	110
%	(32.73)	(27.27)	(38.18)	(1.82)	(100.00)

distance moved between observations (excluding no movement or zero distance measurements) was 0.81 m \pm 0.39 m ($n = 24$). Observed behaviours were walking (1), occupying form (23), basking (13) and behavioural thermal regulating under leaf litter (22).

Behavioural thermal regulation was a common activity after emergence, particularly under leaf litter, which has been unreported. This was characterised by an individual being located under a sparse covering of dead leaves (less than 10 mm in thickness), in full sunlight but with its head and/or limbs extended. Furthermore, it is considered herein

a modified form of thermal regulation because CT under leaf litter ($mean = 15.69\text{ }^{\circ}\text{C}$) was significantly higher than CT for form ($mean = 10.25\text{ }^{\circ}\text{C}$) (Unpaired t-test, $t = 3.389$, $df = 40$, $p = 0.0016$, $n = 42$), but was not significantly different from CT for traditional basking in sunlight ($mean = 18.67$) (Unpaired t-test, $t = 1.654$, $df = 32$, $p = 0.1080$, $n = 34$).

In all instances, either type of thermal regulation was within 64 mm of the form and on few occasions were individuals directly atop leaf litter or bare ground and exposed to full sun. Instead, in most observations turtles were encountered basking in the sun with the anterior portion of the carapace hidden under leaf litter, or in a tunnel of leaf litter, and the posterior end exposed to the sun. Physical evidence showed that individuals had backed out of their forms (which during this time of the year were often slight depressions covered only by leaf litter) to achieve this position. It was also noted, although less regularly, that on occasion turtles turned around in forms and basked with their heads facing outward.

Table 5 indicates that those individuals that emerged early in March spent more time near their hibernaculum than those that emerged later in April, and all individuals became active between 4-14 April. Once *T. c. carolina* were active at Mason Neck, straight-line distances travelled averaged 27.8 ± 6.80 m (0.2 - 87 m; $n = 43$) between observations. Behaviours noted were basking (23), walking (11), form (19) and thermal regulating under leaf litter (8).

No turtles were found dead within hibernacula, but three turtles were found to have respiratory infections as evidenced by a yellow discharge emanating from the nares (Boucher & Ernst, 2004). The behaviours of sick and healthy turtles, along with the number of observations are shown in Table 6. A Chi-square test of independence on these data indicated that behaviour was not independent of health ($\chi^2 = 20.019$, $df = 2$, $p = 0.0002$). Basking was observed much more often in sick turtles.

DISCUSSION

In the autumn, activity varied among individuals. Numerous observations (see review by Ernst & Lovich, 2009) indicate that *T. carolina* are often active during autumn, regardless of geographic location (Oklahoma: Carpenter, 1957; Ohio: Claussen et al., 1991; South Carolina: Congdon et al., 1989; Gatten, 1987; Tennessee: Dolbeer, 1971; New York: Madden, 1975), and turtles observed at Mason Neck were no exception. Their activity, however, was observed extending into late autumn and early winter, which has previously been rarely recorded. Hibernation by *T. carolina* has been reported to begin between mid-October and mid-November in Ohio (Claussen et al., 1991), by mid-November in Oklahoma (Carpenter, 1957), by late November in Illinois (Cahn, 1933), Indiana (Currylow et al., 2013), eastern Tennessee (Dolbeer, 1971), and from late October to late November in Maryland (Savva et al., 2010). The majority of box turtles studied at Mason Neck entered hibernacula in mid- to late December. The later hibernation dates in this study could possibly be explained

by thermal protection caused by the study site's proximity to the warmer Potomac River (land heats and cools faster than water). Biases in some of the previous studies may have been caused by keeping box turtles in enclosures, or by annual variations of entry into hibernacula caused by fluctuating temperature and the duration and severity of environmental conditions (Allard, 1935; Brisbin, 1972; Cahn, 1937; Carpenter, 1957; Claussen et al., 1991; Dolbeer, 1971; Doroff & Keith, 1990; Penn & Pottharst, 1940; Stickel, 1950).

Box turtles relocation of hibernacula at Mason Neck did not appear to be nearly as common as reported by Carpenter (1957), who reported that the average length of time between entry into a hibernaculum and relocations for *T. c. triunguis* in Oklahoma was 63.4 days and mean distance moved was 49.4 m (< 1 to 286.5 m). The apparent longer period between relocation reported for the Oklahoma box turtles may indicate a significant difference in their thermal ecology compared to those in northern Virginia. Carpenter (1957) also observed that *T. c. triunguis* were in their hibernacula by mid-November and this indicates, using the 63.4 day mean time (1-149 days) between relocation, that individuals moved hibernacula sometime between mid- to late January and early February. Hibernacula entered this early, once the extreme low temperatures of winter set in, might not offer enough protection and individuals may possibly be forced to relocate. Thus, the stimuli for relocation could be that a hibernaculum was too cold. At Mason Neck, because *T. c. carolina* enter hibernacula later in the year, they appear to select more sheltered locations which exhibit thermal stability and protection. This assumption would explain why fewer individuals were observed relocating hibernacula than expected. Table 5 shows that relocations occurred between 26 February and 13 March, on average 23.4 days before spring emergence. Relocation so late in the winter and so close to emergence suggests that individuals were actually emerging but found ATs still too cold and then returned to hibernacula until ATs moderated.

The mean maximum depth of hibernacula for *T. c. carolina* at Mason Neck agrees with the range of 20-100 mm reported for *Terrapene* in Oklahoma, Ohio, Missouri, New York and Tennessee (Carpenter, 1957; Claussen et al., 1991; Dolbeer, 1971; Grobman, 1990; Madden, 1975). It is substantially deeper than the 0-50 mm reported by Congdon et al. (1989), but this was noted in a South Carolina population subject to less severe winter temperatures. Currylow et al. (2013) reported an average depth of 100 mm in Indiana *T. carolina*, but reached 300 mm.

Hibernation at Mason Neck is shorter than at other locations. Studies on the duration of hibernation in *Terrapene carolina* report that it ranges from 141 to 216 days depending on taxon, geographic location and weather conditions (Claussen et al., 1991, in Ohio *T. c. carolina* - 142 days; Currylow et al., 2013, in Indiana *T. c. carolina* - 140 days [including emergence]; Madden, 1975, in New York *T. c. carolina* - 141 days; Stickel, 1950, in Maryland *T. c. carolina* - 168 days; Schwartz & Schwartz, 1974, in Missouri *T. c. triunguis* - 177 days; Doroff & Keith, 1990, in Wisconsin *T. ornata* - 216 days; Legler, 1960, in Kansas

T. ornata - 165 days). The dates of emergence at Mason Neck range between March and April and agree with the time of emergence reported elsewhere for *T. c. carolina* (Claussen et al., 1991; Currylow et al., 2013; Grobman, 1990; Madden, 1975; Stickel, 1950), so the short period of hibernation is a function of the late entry into hibernacula at Mason Neck.

Since basking was observed significantly more often in sick turtles than healthy turtles, they appeared to be simulating a pyrogenic response (sensu Monagas & Gatten, 1983).

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REFERENCES

- Allard, H.A. (1935). The natural history of the box turtle. *The Scientific Monthly* 41: 325-338.
- Boucher, T.P. & Ernst, C.H. (2004). *Terrapene carolina carolina* (eastern box turtle). Injuries. *Herpetological Review* 35: 56-57.
- Brisbin, I.L. (1972). Seasonal variations in the live weights and major body components of captive box turtles. *Herpetologica* 28: 70-75.
- Cahn, H.R. (1933). Hibernation of the box turtle. *Copeia* 1933: 13-14.
- Cahn, H.R. (1937). The turtles of Illinois. Illinois *Biological Monographs* 16: 1-218.
- Carpenter, C.C. (1955). Sounding turtles: a field locating technique. *Herpetologica* 11: 120.
- Carpenter, C.C. (1957). Hibernation, hibernacula and associated behavior of the three-toed box Turtle (*Terrapene carolina triunguis*). *Copeia* 1957: 278-282.
- Claussen, D.L., Daniels, P.M., Jiang, S. & Adams, N.A. (1991). Hibernation in the eastern box turtle, *Terrapene c. carolina*. *Journal of Herpetology* 25: 334-341.
- Congdon, J.D., Gatten, R.E. & Morreale, S.J. (1989). Overwintering activity of box turtles (*Terrapene carolina*) in South Carolina. *Journal of Herpetology* 23: 179-181.
- Currylow, A.F., MacGowan, B.J. & Williams, R.N. (2013). Hibernation thermal ecology of eastern box turtles within a managed forest landscape. *The Journal of Wildlife Management* 77: 326-335.
- DeGregorio, B.A., Tuberville, T.D., Kennamer, R.A., Harris, B.B. & Brisbin, I.L., Jr. (2017). Spring emergence of eastern box turtles (*Terrapene carolina*): Influences of individual variation and scale of temperature correlates. *Canadian Journal of Zoology* 95: 23-30.
- Dolbeer, R.A. (1971). Winter behavior of the eastern box turtle, *Terrapene c. carolina* L., in eastern Tennessee. *Copeia* 1971: 758-760.
- Doroff, A.M. & Keith, L.B. (1990). Demography and ecology of an ornate box turtle (*Terrapene ornata*) population in south-central Wisconsin. *Copeia* 1990: 387-399.
- Ernst, C.H. & Lovich, J.E. (2009). *Turtles of the United States and Canada*, 2nd ed. Baltimore, MD: Johns Hopkins University Press. 840 pp.
- Gatten, R.E. (1987). Cardiovascular and other physiological correlates of hibernation in aquatic and terrestrial turtles. *American Zoologist* 27: 59-68.
- Grobman, A.B. (1990). The effect of soil temperature on emergence from hibernation of *Terrapene carolina* and *T. ornata*. *American Midland Naturalist* 124: 366-371.
- Legler, J.M. (1960). Natural history of the ornate box turtle, *Terrapene ornata ornata* Agassiz. *University of Kansas Publications, Museum of Natural History* 8: 417-476.
- Madden, R.C. (1975). Home range, movements, and orientation in the eastern box turtle, *Terrapene carolina carolina*. Unpubl. Ph.D. Dissertation, City Univ., New York.
- Monagas, W.B. & Gatten, R.E., Jr. (1983). Behavioural fever in turtles *Terrapene carolina* and *Chrysemys picta*. *Journal of Thermal Biology* 8: 285-288.
- Penn, G.H., Jr. & Pottharst, K.E. (1940). The reproduction and dormancy of *Terrapene major* in New Orleans. *Herpetologica* 2: 25-29.
- Savva, Y., Swarth, C.W., Gupchup, J. & Szlavecz, K. (2010). Thermal environments of overwintering eastern box turtles (*Terrapene carolina carolina*). *Canadian Journal of Zoology* 88: 1086-1094.
- Schwartz, C.W. & Schwartz, E.R. (1974). The three-toed box turtle in central Missouri: its populations, home range, and movements. *Missouri Department of Conservation Terrestrial Series* 5: 1-4.
- Stickel, L.F. (1950). Populations and home range relationships of the box turtle *Terrapene carolina carolina* (Linnaeus). *Ecological Monographs* 20: 351-378.
- Storey, K.B. & Storey, J.M. (2004). Physiology, biochemistry and molecular biology of vertebrate freeze tolerance: the Wood Frog. In *Life in the Frozen State*, pp. 243-274. Benson, E., Fuller, B. & Lane, N. (Eds.). Boca Raton, Florida: CRC Press

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