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ACTIVITY PATTERNS IN AUSTRALIAN ELAPID SNAKES (SQUAMATA: SERPENTES: ELAPIDAE)

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ABSTRACT: This study compares activity patterns of Australian elapids with those of North American and European snakes. Six species of elapids (*Austrelaps superbus, Hemiaspis signata, Notechis scutatus, Pseudechis porphyriacus, Pseudonaja textilis*, and *Unechis gouldii*) were studied in the eastern highlands of Australia. Major findings are: (1) elapids overwinter singly in shallow hibernacula, usually under logs or rocks; (2) reproduction profoundly affects activity patterns of female elapids, gravid snakes being sedentary, basking for long periods, reducing food intake, and (in *P. porphyriacus*) aggregating in small groups; (3) most elapids are diurnal (with some crepuscular activity) and have relatively high preferred body temperatures (30–35°C); and (4) day-to-day movements are extensive, except in gravid females.

Key words: Activity; Australia; Elapidae; Reproduction

ALTHOUGH squamate life-history strategies have attracted increasing scientific attention, most research has been concentrated on only a small proportion of squamate groups (see Fitch, 1970). Abundant data are available on North American iguanid lizards (e.g., Tinkle, 1967, 1969, 1972; Tinkle et al., 1970) and colubrid snakes (e.g., Fitch, 1963*a,b*, 1965, 1975; Parker, 1974), but other groups are much less well known. In particular, the ecology of large venomous snakes remains almost unstudied, except for work on North American crotalids (Fitch, 1949, 1960; Klauber, 1956; Wharton, 1966, 1969) and European viperids (Prestt, 1971; Saint Girons, 1952, 1957; Viitanen, 1967). This dearth of information hinders attempts to generalize about squamate life-history strategies. The present paper is part of a larger study on the ecology of six sympatric species of Australian elapid snakes (Shine, 1975, 1977*a,b,c*, 1978; Shine and Bull, 1977). In it, I consider the following aspects of elapid activity patterns:

(1) *Overwintering*.—Do the Australian elapids hibernate in large communal dens, as do many North American and European snakes?

(2) *Reproductive activities*.—How does reproduction affect general behavior patterns (e.g., movements, feeding, basking, sociality) in the elapids?

(3) *Daily activity cycles*.—Are the elapids mainly diurnal, crepuscular, or nocturnal? What are the preferred body temperatures?

(4) *Activity ranges*.—How extensive are day-to-day movements in the elapids?

MATERIALS AND METHODS

Fieldwork was conducted within 80 km of Armidale, N.S.W., in the New England region of eastern Australia. The terrain is hilly (800–2,000 m elevation), and the climate is relatively mild (Table 1). Most specimens were collected by hand from grassland country, usually near streams and lagoons among sheep pastures. *Notechis*

TABLE 1.—Climatic data for the New England area of N.S.W., Australia. Mean values courtesy of Australian Government Bureau of Meteorology. Letters are abbreviations for months of the year.

Locality	Variable	J	F	M	A	M	J
Armidale (30°31′S, 151°39′E), elevation 980 m	Daily max air temp (°C)	26.6	26.2	24.2	21.2	16.5	13.9
	Daily min air temp (°C)	13.5	13.6	11.5	7.7	3.5	1.7
	Precipitation (mm)	101	87	67	46	42	61
Guyra (30°13′S 151°40′E), elevation 1320 m	Daily max air temp (°C)	22.8	22.6	20.8	17.9	13.3	11.0
	Daily min air temp (°C)	11.4	11.6	9.5	6.0	2.7	0.9
	Precipitation (mm)	110	90	74	49	48	67
		J	A	S	O	N	D
Armidale (30°31′S, 151°39′E), elevation 980 m	Daily max air temp (°C)	12.7	14.2	17.5	21.1	24.0	26.1
	Daily min air temp (°C)	0	1.4	3.5	7.1	9.7	12.7
	Precipitation (mm)	50	51	53	69	80	88
Guyra (30°13′S 151°40′E), elevation 1320 m	Daily max air temp (°C)	10.1	11.3	13.6	17.9	19.1	21.9
	Daily min air temp (°C)	–1.0	0.7	2.6	6.5	7.8	10.5
	Precipitation (mm)	61	59	58	84	87	102

scutatus was collected at the Uralla Lagoons, 15 km south of Armidale; *Austrelaps superbus* at the Llangothlin Lagoon, 40 km north of Armidale and close to Guyra, N.S.W.; and *Hemiaspis signata* and *Unechis gouldii* at Chiswick, 10 km south of Armidale. *Pseudechis porphyriacus* and *Pseudonaja textilis* were collected throughout the wider study area. Detailed habitat data are given by Shine (1977*c*). Body sizes of the species studied are given in Table 2.

Most data in this paper resulted from field observations. Body temperatures and movements were recorded by implanting thermal-sensitive radiotelemeters (Mini-mitters®, 3.5 × 1.5 cm, 10.5 g) in seven individuals (3 species) and releasing snakes at the sites of initial capture. These units averaged 2.9% of the body weight of the seven animals used. After sealing, calibrating to ± 0.1°C, and sterilizing, the telemeters were inserted midway down the body of the snake through a ventral incision 5–8 scutes wide (Brown and Parker, 1976). Snakes were cooled to approximately 5°C before the operation, and were restrained in a clear glass tube. No anaesthetic was used. All snakes were released within 72 h

TABLE 2.—List of elapid species studied and locations where overwintering animals were discovered.

Species	Vernacular name	n	Mean snout–vent length of adult ♂♂ (cm)	Active specimens (winter)	hibernacula[b]				
					In rockpile	Under rock	Under log	In burrow	In haystack
Austrelaps superbus	copperhead	110	76.6	—	2	2	2	1	—
Hemiaspis signata	swamp snake	53	43.1	—	—	—	—	—	—
Notechis scutatus	tigersnake	174	81.6	—	—	1	3	—	1
Pseudechis porphyriacus	blacksnake	225	111.6	3	1	3	1	2	1
Pseudonaja textilis	brownsnake	53	126.3	—	—	2	—	—	—
Unechis gouldii	Gould's snake	129	36.2	2[a]	—	8	4	—	—

[a] See text.
[b] Locations of inactive snakes collected May–Aug.

of initial capture. The effective range for monitoring signals (Tokai receiver) was 100 m. Telemeter failures resulted in highly variable duration of trials. All specimens were active and apparently healthy at the conclusion of field tracking.

Statistical tests used are from Siegel (1956). Results were considered significant when $P < .05$.

OVERWINTERING

Many North American and European snake species migrate to and from deep communal hibernacula in autumn and spring. This behavior is especially marked in areas with severe winters (Klauber, 1956; Parker and Brown, 1973, 1974). Snakes in relatively warm areas overwinter singly in shallow hibernacula (Fitch, 1949; Wharton, 1966), presumably because there is less danger of freezing. Snakes are active year-round in very warm climates. Which pattern do the New England elapids show?

The only elapid species recorded as active during winter (Jun–Aug) was *Pseudechis porphyriacus* (3 snakes basking; Table 2). *Unechis gouldii*, a secretive fossorial species, must also have been active during this period, because stomachs of two individuals collected in winter contained freshly-ingested food items. Low thermal preferenda (Heatwole, 1976), small body size, and shallow hibernacula probably facilitate winter activity in *U. gouldii*. Mature males and females of this species were found together on two occasions during winter, suggesting that mating may also occur during this season. *Unechis gouldii* is known to mate in both autumn and spring (Shine, 1977*a*).

Several elapid hibernacula were discovered (Table 2). Most were within 100 m of water, on slightly raised ground. Any available cover seems to be used, with rocks and logs being the most common sites (Table 2). Worrell (1958) found *Notechis scutatus* overwintering inside logs, and Ormsby (1951) found that elapids would overwinter under artificial shelter (concrete, flat iron). I found elapids almost always overwintering singly: among 33 snakes discovered, 27 were hibernating alone. Small aggregations have been reported in *Pseudechis porphyriacus* (Ormsby, 1951) and *Notechis scutatus* (Worrell, 1958).

A likely reason for the use of shallow hibernacula by hibernating elapids is the mild Armidale climate (Table 1). Soil temperatures 10 cm deep at Laureldale Station, Armidale, did not fall below 2°C during winter of 1975 (official Laureldale records, University of New England). Because Armidale winters are more severe than those over most of mainland Australia (Gentilli, 1971), communal hibernation and

TABLE 3.—Frequency of basking and feeding in gravid and nongravid female elapid snakes. Values are numbers of snakes collected Oct–Feb, and percentage of each sample basking and not basking (upper), and feeding and not feeding (lower). Significance levels based on chi-square with one degree of freedom; null hypotheses are that gravid females bask no more frequently than nongravid females, and that gravid females feed no less frequently than nongravid females.

	Gravid		Nongravid			
Species	Basking	Not basking	Basking	Not basking	χ^2	P
Notechis scutatus	11 (69%)	5 (21%)	4 (29%)	10 (71%)	3.35	< .05
Pseudechis porphyriacus	11 (85%)	2 (15%)	7 (29%)	17 (17%)	8.28	< .001
	Food in stomach	No food in stomach	Food in stomach	No food in stomach		
Notechis scutatus	2 (14%)	12 (86%)	6 (60%)	4 (40%)	—	< .05[a]
Pseudechis porphyriacus	7 (30%)	16 (70%)	14 (78%)	4 (22%)	7.26	< .001

[a] Based on Fisher Exact Probability Test because $n < 30$ (Siegel 1956).

long-distance spring and autumn dispersal are likely to be rare in Australian snakes. This provides a strong contrast with many species of snakes studied previously in North America and Europe.

Reproductive Activities

In most venomous snakes for which data are available, adult females reproduce every second year, or less often (Klauber, 1956; Saint Girons, 1957, 1972; Tinkle, 1957). In Australian elapids, however, most adult females reproduce every year (Shine, 1977*b*). This apparent difference in reproductive rates stimulated an investigation of the effects of reproduction on seasonal activity patterns of adult females of the two most common species, *Notechis scutatus* and *Pseudechis porphyriacus*. Below, I document effects of gravidity on activity patterns.

Basking.—Snakes were classified as "basking" if they were lying out in the open, loosely coiled with the body fully exposed to the sun. This definition excludes snakes which were thermoregulating by lying stretched out, because such animals were often difficult to distinguish from foraging individuals. Table 3 shows that the proportion of snakes in the "basking" position when first sighted was higher in gravid than nongravid females (at the same time of year), in both *P. porphyriacus* and *N. scutatus*.

This high frequency of basking is consistent with observations that gravid snakes maintain high body temperatures (Hirth and King, 1969; Stewart, 1965) or a narrow range of body temperatures (Osgood, 1970). Interestingly, some gravid heterothermic mammals (e.g., bats, sloths) do the same (Wimsatt, 1969).

Feeding.—Gravid *N. scutatus* and *P. porphyriacus* reduce their food intake, especially in the latter part of gestation. In both species, the proportion of snakes containing food at the time of capture was significantly lower in gravid snakes than in nongravid adult females collected at the same time of year (Table 3).

A similar reduction in feeding during gestation occurs in lizards (e.g., Fitch, 1954; Mount, 1963), other snakes (Duguy, 1972; Fitch and Shirer, 1971; Gregory and Stewart, 1975; Keenlyne, 1972; Keenlyne and Beer, 1973; Klauber, 1956; Prestt, 1971; and Stewart, 1975), and fish (Springer, 1960). Possible reasons include: (1) the developing embryos may occupy so much

TABLE 4.—Frequency of feeding in elapid snakes in relation to ecdysis. Values in table are numbers of snakes, and percentages of each sample, feeding and not feeding. Significance levels based on chi-square with one degree of freedom. Null hypothesis is that individuals about to undergo ecdysis feed no less frequently than other individuals.

	Specimens about to undergo ecdysis		Specimens not about to undergo ecdysis			
Species	Food in stomach	Stomach empty	Food in stomach	Stomach empty	χ^2	*P*
Austrelaps superbus	1 (11%)	8 (89%)	22 (46%)	26 (54%)	2.49	< .1
Notechis scutatus	0 (0%)	24 (100%)	47 (46%)	55 (54%)	10.27	< .001
Pseudechis porphyriacus	6 (26%)	17 (74%)	105 (64%)	60 (36%)	15.72	< .001

of the body cavity that there is limited space for food in the digestive tract (Mount, 1963); (2) the large volume of the clutch may prevent the female from foraging efficiently; (3) reduced mobility of the gravid female may render her more vulnerable to predators, and she can reduce this risk by ceasing to move about and hence, ceasing to feed; and (4) it may be difficult to maintain optimum temperatures for embryonic development while foraging.

In the elapid species studied, the rate of feeding during gestation is also reduced by the common occurrence of ecdysis during the gestation period (Shine, unpublished). Food intake decreases prior to ecdysis (Table 4).

Movements.—The sedentary nature of gravid elapids (see below) may be due to their vulnerability to predators. Similar behavior has been described in gravid colubrids (Clausen, 1936), crotalids (Fitch and Glading, 1947; Fitch and Shirer, 1971), and viperids (Naulleau, 1968; Prestt, 1971).

Distance from water.—Gravid females of all species were invariably found within 150 m of water, and usually much closer (*A. superbus*, $n = 20$, $\bar{x} = 45$ m for gravid, 188 m for nongravid; *N. scutatus*, $n = 34$, $\bar{x} = 71$ m for gravid, 185 m for nongravid; *P. porphyriacus*, $n = 57$, $\bar{x} = 17$ m for gravid, 130 m for nongravid). Gravid *P. porphyriacus* averaged significantly closer to water than nongravid females (extension of the median test; $n = 20, 37$; $\chi^2 = 3.86$; $P < .05$). This trend may reflect either proximity to shelter, which is more abundant near the water, or the need for water intake during embryonic development (Shine, 1977*b*).

Aggregations.—Elapids almost always were encountered singly in the field. The only consistent exceptions were gravid *Pseudechis porphyriacus* (Table 5). Single records of aggregation in *Unechis gouldii* and *Austrelaps superbus* were also obtained (Table 5). However, aggregation was not recorded in gravid *Notechis scutatus* ($n = 20$). Published data indicate that aggregations of gravid females occur in a taxonomically diverse array of snake species (Table 6).

These records indicate that there is some positive selective advantage in aggregative behavior. Gregory's (1975) explanation, that aggregations result from a scarcity of sites suitable for thermoregulation or avoidance of predators, is probably true in some instances, but is unlikely to be a complete answer. Suitable cover does not appear to be a limiting factor in the aggregations of *Pseudechis porphyriacus*. The reduction of feeding by gravid snakes removes the most obvious disadvantage of aggregation, that is, competition for food. One possible advantage of aggregation is that a group may be more effective at detecting and deterring predators than is a single individual. However, a group might be more likely to be found by a

TABLE 5.—Records of aggregation in gravid Australian elapid snakes. Gravid condition of all specimens confirmed by dissection.

Species	Date	Time	Locality	Snakes (n)
Pseudechis porphyriacus	17 Dec 1973	1030	Wollomombi Ck., 30 km E Armidale: basking 2 m from stream	3 gravid ♀♀, 1 non-gravid ♀
	29 Jan 1974	1030	Tom's Gully, 15 km W Armidale: basking 6 m from stream	3 gravid ♀♀
	12 Feb 1974	0900	Wollomombi Ck., 31 km E Armidale: basking 2 m from stream	2 gravid ♀♀
	Dec 1973	no data	Nowra, N.S.W.: basking by brushpile	3 gravid ♀♀
	25 Jan 1970	late afternoon	Seal Ck., 5 km S Malacoota Airport, East Gippsland, Victoria	4 gravid ♀♀
Austrelaps superbus	3 Jan 1975	1345	Mother of Ducks Lagoon, 30 km N Armidale: basking by brushpile	2 gravid ♀♀
Unechis gouldii	24 Feb 1974	0900	Chiswick, 10 km S Armidale: under rock	3 gravid ♀♀ 1 adult ♂

predator. This phenomenon deserves further attention.

Overall, these data show that reproduction greatly modifies activity patterns in adult female elapids. The most likely explanation for annual reproduction in these species is the short length of the gestation period relative to the summer activity period (about 14 weeks out of 9 months; Shine, 1977*b*). This leaves the females enough time to gather energy for reproduction in the following year. In "biennial" species, gestation often occupies most of the active season (Saint Girons, 1957).

Daily Activity Cycles

Large colubrids, crotalids, and viperids are usually nocturnal or crepuscular (Klauber, 1956; Mayhew, 1968), possibly because these are the times when the major prey items of the snakes (small mammals) are most active. Small mammals are rare in Australia, and the elapids studied feed mainly on lizards and frogs (Shine, 1977*c*). In keeping with these types of prey, the elapids are generalized "searching" foragers rather than nocturnal "ambush" predators (Shine, 1977*c*).

Most elapids studied were found to be diurnal, with some crepuscular activity. Active *Austrelaps superbus* ($n = 53$) were collected from 0900 to 1600 h, with a single specimen at 1900 h. Active *Notechis scutatus* ($n = 64$) were found from 0800 to 1700 h, with two individuals at 2100 h. Most *Hemiaspis signata* ($n = 53$) were collected under cover; of 4 active snakes, 3 were found during the day and 1 at 2100 h. Active individuals of the two largest species, *Pseudechis porphyriacus* ($n = 164$) and *Pseudonaja textilis* ($n = 20$), were only collected during daylight hours (0800–1700 h). However, nocturnal activity was recorded in two *Pseudechis porphyriacus* in another study area, in a much warmer climatic region (Shine, 1978). In contrast to the other species, only 2 of 129 *Unechis gouldii* were found away from cover. Captive individuals ($n = 12$) were secretive and entirely nocturnal.

These activity records are consistent with observations of Kellaway and Eades (1929), Ormsby (1950), McPhee (1959), Worrell (1963), Rawlinson (1965), and Cogger (1971, 1975). The higher frequency of diurnal activity in the New England elapids than in most other large snakes may be due to differences in type of prey and in foraging strategy.

TABLE 6.—Summary of published records of aggregations of gravid snakes.

Family	Species	Locality	Authority
Colubridae	*Storeria occipitomaculata*	Manitoba, Canada	Gregory, 1975
	Thamnophis sirtalis	Manitoba, Canada	Gregory, 1975
Crotalidae	*Agkistrodon contortrix*	Massachusetts, USA	Allen, 1868
	Agkistrodon contortrix	Kansas, USA	Gloyd, 1933
	Agkistrodon contortrix	Kansas, USA	Fitch, 1960
	Agkistrodon contortrix	Kansas, USA	Fitch and Shirer, 1971
	Agkistrodon contortrix	Connecticut, USA	Finneran, 1953
	Agkistrodon piscivorus	Florida, USA	Wharton, 1966
	Crotalus viridis	South Dakota, USA	Klauber, 1956
Elapidae	*Pseudechis porphyriacus*	New South Wales and Victoria, Australia	Present study
Viperidae	*Atheris superciliaris*	Malawi, Africa	Stevens, 1973

One could expect the diurnal activity of the elapids to correlate with high preferred body temperatures, and all three species attained body temperatures of 30–35°C (Table 7). Preferred temperatures of these species in laboratory thermal gradients fell within the same range (Witten, 1969). Heatwole (1976) found that the mean cloacal temperature of active *N. scutatus* was 29.3°C, and of *P. porphyriacus* was 30.3°C. Webb (1973) found a preferred temperature of about 35°C for an adult *P. textilis* in an outdoor enclosure. Thus, the four large New England elapids have similar preferred temperatures, close to those reported for other diurnal terrestrial snakes and higher than expected for snakes in general (Brattstrom, 1965). Interspecific differences in temperature tolerances among these elapids are also small (Heatwole, 1976; Spellerberg, 1972). Minor interspecific differences are difficult to interpret, since the "preferred" thermal level of a species is affected by a multitude of variables (e.g., acclimation [Goodman, 1972], feeding [Cogger, 1974; Goodman, 1972; Regal, 1966], sloughing or injury [Kitchell, 1969], season [Goodman, 1972; Hirth and

TABLE 7.—Telemetry records for body temperatures of elapid snakes in the New England area.

Species	Sex	Snout–vent length (cm)	Locality	Date of release	Date of recapture/ last record	*n*	Range of recorded body temp. (°C)
Notechis scutatus	♂	81.6	Uralla Lagoon, 15 km S Armidale	22 Sep 74	8 Nov 74	48	11.2–29.0
	♂	74.0	Uralla Lagoon, 15 km S Armidale	15 Jan 75	6 Feb 75	38	18.7–35.0
	♀	75.8	Uralla Lagoon, 15 km S Armidale	2 Feb 75	27 Feb 75	33	23.0–34.2
Pseudechis porphyriacus	♂	112.9	Power's Ck., 20 km E Armidale	28 Oct 74	12 Dec 74	27	20.5–33.0
	♀	108.0	Power's Ck., 20 km E Armidale	12 Nov 74	13 Nov 74	10	30.2–32.0
Austrelaps superbus	♀	72.0	Mother of Ducks Lagoon, 30 km N Armidale	5 Dec 74	3 Jan 75	13	30.8–33.5

King, 1969], and reproductive condition [Hirth and King, 1969; Osgood, 1970; Stewart, 1965]).

Activity Ranges

Most previous studies of movements of snakes have revealed distinct "activity ranges," that is, small areas within which individuals remain for long periods of time. Sizes of activity ranges are usually calculated by the convex polygon method of Jennrich and Turner (1969); published data indicate that activity ranges in nonmigratory snakes vary in extent from 0.002 ha for *Carphophis vermis* (Clark, 1970) to 0.3 ha for *Vipera aspis* (Naulleau, 1966). Fitch's (1949) data indicate an even larger activity range for *Crotalus viridis*, but he used a different (and not directly comparable) technique to assess size of the activity range. Results of my own study, using implanted radiotelemeters, are summarized below and in Table 7.

Notechis scutatus.—Two adult male tigersnakes were found to have roughly rectangular activity ranges comprising 0.75 and 0.77 ha (calculated by the method of Jennrich and Turner, 1969), after monitoring for 6 wk and 3 wk, respectively. One of two gravid females studied was located only once, 2 d after release. She had moved 120 m in this time. The other gravid female moved 80 m from her release point to a rock crevice within 2 d, but was then virtually sedentary (movements restricted to a circle of about 3 m diameter) for the next 14 d (26 location records). When next checked 10 d later, she had given birth and returned to the point of initial capture.

Pseudechis porphyriacus.—An adult male blacksnake remained within 5 m of the capture point for at least 3 d after release. Twelve days later he was located 200 m away, lying in the entrance to a rabbit burrow. He remained within 10 m of this site for a further 21 d, when an unsuccessful recapture attempt was made. Eight days later he was found 400 m away from his previous location (550 m from initial release point). These data do not permit home range to be estimated, but the capacity for rapid movements over a long distance indicates a large activity range in this species.

The male blacksnake remained within 30 m of a stream throughout the tracking period, but individuals of this species often move further away from water. Collecting data show that adult male blacksnakes were sighted, on average, 420 m from water ($n = 87$, range 0–1000 m), and females 132 m from water ($n = 57$, range 0–1000 m). This difference between the sexes is significant (extension of the median test, $\chi^2 = 13.28$, $P < .001$). Transmitter malfunction precluded gathering many data on the second blacksnake, a preovulatory female. Her initial post-release movement of 400 m in 24 h again indicates rather high mobility of this species.

Austrelaps superbus.—A preovulatory female copperhead moved 100 m to a large brushpile at the edge of a swamp within 5 d of her release. She ovulated at about this time (based on subsequent dissection), and remained in or near the brushpile for a further 21 d. She then returned to a similar brushpile a few meters from the point of release.

These results suggest that gravid females (in both *A. superbus* and *N. scutatus*) are very sedentary. However, the male elapids move about more extensively than do most other snake species so far studied. This is consistent with the large body size of the elapids used in the present work: larger reptiles have larger activity ranges (Turner et al., 1969).

Conclusions

This study suggests several differences in activity patterns between Australian elapids and North American and European snakes studied previously. (1) Communal hibernation and long-distance spring and autumn dispersal are virtually absent in the elapids. These behavioral patterns clearly depend on environmental temperature regimes (Vitanen, 1967), and the present study suggests that no part of mainland Australia is cold enough to induce communal hibernation. (2) The elapids studied are primarily diurnal foragers, and have high thermal preferenda. These characteristics may reflect the "searching" foraging strategy adopted by most Australian elapid species (Shine, 1977*c*). (3) Two elapid species (*N. scutatus* and *P. porphyriacus*) have unusually large activity ranges. This result may be due to the large body sizes of the species studied, rather than intrinsic differences between snakes of different families.

In most other respects, the elapids resemble snakes of other continents. A paucity of information on snake ecology makes any general comparisons tenuous at present.

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