same biological function in each case.

If this suggestion is correct, motion sickness is an adaptive response evoked by an inappropriate stimulus. It will be elicited by any situation which generates repeated challenges to the highly skilled and continuous information-processing activity responsible for maintaining the alignment between two closely coupled spatial reference systems.

A number of features of motion sickness support this hypothesis. The importance of the coordination between vestibular and proprioceptive sensation is attested by the finding that the movements of the head relative to the body caused by vehicular motion are larger in more susceptible subjects (*1*). If the head is held fast the amount of sickness falls. With few exceptions (for example, conditioned sickness) vestibular stimulation is necessary for motion sickness to occur. The disorder is not found when the vestibular system has been destroyed or the eighth nerves cut.

There is also evidence for the importance of the eye-head system. Movement of all or a large part of the field of vision without movement of the body can cause sickness. The ineffectiveness of movement of a small part of the field indicates that it is shift in the visual framework relative to that provided by other sensory systems that is the important factor. Movement of the visual field does not induce sickness when the labyrinths are defective, a disturbance of correlation between visual and proprioceptive inputs being ineffective alone. It is probable that proprioceptive and visual systems are at best only loosely coupled in the absence of vestibular information, and disparities do not lead to readjustive efforts or, if they do, since these might normally occur via recalibration in relation to the vestibular input in each case, they do not function as early warning signs of toxic effects.

Infants and young puppies appear not to be susceptible. This is consistent with the explanation offered since young mammals are fed on milk or preselected food which is unlikely to be toxic, and are often subject to random and unpredictable movements when they are carried. It may also be predicted that the condition should be rare in species with highly specialized or limited diets, or which are very tolerant of the toxins which may occur in their diets.

Vomiting, and the defecation and salivation which may also occur, are consistent with a reaction designed to eliminate toxins. But why do nausea and malaise occur? The answer may be that when an animal encounters a toxic substance it should not only eliminate it, it should also avoid it in future. There is now considerable evidence that gastrointestinal disturbance occurring some hours after ingesting a food and produced in various ways can cause a conditioned aversion to the tastes and smells experienced (*6*). This suggests that the subjectively unpleasant aspects of motion sickness, the nausea and malaise, may occur because they contribute to this process of aversive conditioning. A common symptom of motion sickness is unusual sensitivity to repulsive sights or odors, suggesting sensitization of previous aversive conditioning. The marked depression sometimes experienced may be part of the same phenomenon, but it might also be a precautionary adaptation, in view of the excitatory effects sometimes produced by ingested toxins.

Finally, one may note that other types of anomalous vomiting, such as that consequent on a head injury, raised intraocular pressure, or severe pain, may have analogous explanations: these conditions may activate the same or other toxin early warning systems.

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Refractoriness in Female Lizard Reproduction: A Probable Circannual Clock

Abstract. *Postreproductive* Cnemidophorus uniparens *maintained under free-running conditions of constant darkness for 7 months became reproductive at the same time as controls exposed to a long photoperiod. This lizard exhibits a pause in reproductive activity (refractory period) commencing in late summer in nature and terminating in mid-December in captivity. Both groups terminated refractoriness and started reproducing simultaneously in December despite maintenance of the experimental group in darkness since September. These results confirm the hypothesis that the refractory period in this lizard is under endogenous control.*

A distinctive feature of certain temperate lizards is an interval, like that shown by birds (*1*), following termination of breeding in nature, during which gonadal development cannot be stimulated experimentally by photothermal manipulation. Such a refractory period was first noted in lizards by Mayhew (*2*) and has subsequently been confirmed for several other species (*3–7*). Refractoriness commences more or less in late summer and terminates spontaneously in the laboratory approximately during November and December, after which warm temperature stimulates gonadal development regardless of photoperiod. Although light was previously considered the principal cue for lizard reproduction (*2, 8*), Tinkle and Irwin (*3*) revealed that in the lizard *Uta stansburiana*, photoperiod is not essential for timing the female reproductive cycle. Results with other temperate species (*4–7*) have confirmed Tinkle and Irwin's findings. In at least one of these species (*Cnemidophorus uniparens*), refractoriness is not at the level of the gonad but apparently at the hypothalamo-hypophysial level (*9*); the refractory period in this species is apparently under endogenous control (*10*). Although photothermal alterations do not seem to change timing of the reproductive cycle in these species, it is not clear what effect extended free-running conditions (all light or all dark and constant temperature) may have on the duration of the refractory period. Here we test the effects of prolonged darkness and warmth on reproductively refractive parthenogenetic lizards *C. uniparens* to further elucidate probable control of the refractory period.

Animals were collected between 6 and 10 June 1973 in Sierra County, New Mexico. They were housed in groups of three in 56-liter terraria and exposed to a photothermal regime of 14 hours of light and 10 of darkness (LD 14 : 10). Heat and light were provided by a 125-watt reflector lamp (General Electric) located 35

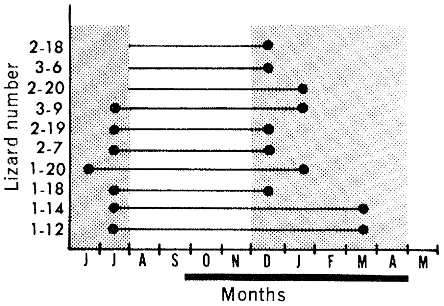

Fig. 1. The reproductive cycle of captive female *C. uniparens* maintained in darkness from the latter part of September 1973 to the latter part of April 1974 (indicated by dark horizontal bar below months).

cm above the floor of each terrarium. Animals selected a temperature of 33° to 36°C during the illumination phase and were maintained at 20°C during the dark period. Beginning on 25 September 1973, a group of 12 were placed in incubators (Lab-Line) (three animals per terrarium and two terraria per incubator) and maintained for 7 months in near total darkness (15 minutes of fluorescent light approximately three times per week for feeding, watering, and cleaning) and a constant temperature of 35°C. The experiment was terminated on 24 April 1974. Animals were palpated at frequent intervals to determine reproductive condition. A reproduction was scored on the basis of detection of oocytes that were larger than 4 to 5 mm but were not ovulated (four animals) or an ovulation or clutch laid (24 animals) [refer to Cuellar (*6*) for the time interval between the onset of vitellogenesis and ovulation or oviposition]. Ten of the 12 experimental lizards survived the 7-month darkness period. Of these, five reproduced during December 1973, three during January, and two during March 1974 (Fig. 1) corresponding to the time refractoriness terminates in this species under conditions of light (*6*, *10*). Similarly, of the controls, two reproduced during December 1973, two during February, nine during March, and five during April 1974 (Fig. 2). The fact that both groups broke refractoriness more or less simultaneously and reproduced for approximately the same length of time (4 months) suggests a high degree of synchrony unrelated to exogenous cues. We do not know the number of clutches that *C. uniparens* lays in the field, but judging from the present and previous results (*6*, *9*, *10*), they probably develop more than one clutch per season since those that laid during July in captivity may also have laid another during late May or early June before being captured.

Although both groups stopped reproducing simultaneously in July, the majority (80 percent) of those maintained in darkness reproduced in December and January (Fig. 1), whereas 73 percent of the controls reproduced during March and April (Fig. 2). One possible explanation is that darkness accelerates termination of refractoriness (Fig. 1) and another is that light retards it (Fig. 2). Temperature may also be important, since those maintained in darkness were exposed to constant warmth, whereas temperature for the controls fluctuated daily. Nevertheless, we suspect that none of these possibilities may be relevant. For instance, in separate studies in which *C. uniparens* were maintained either on short (LD 10 : 14) or long (LD 14 : 10) day length regimes (*6*, *10*), most reproduced during December and January, corresponding to the same time as the experimental group maintained in darkness. Conversely, 11 of 14 of a sample collected during August 1975 and maintained on an LD 12 : 12 photoperiod reproduced during February and March 1976 (*11*), which corresponds to the same time as the controls in this experiment. Whatever the reason may be for the earlier breeding observed in the experimental animals, it does not appear to be due to conditions induced by the free-running regime. This experiment confirms an earlier hypothesis (*10*) that the refractory period in this lizard is governed by a circannual oscillator which does not depend on either thermoperiod (preferred temperature) or photoperiod. For example, *C. uniparens* maintained on either long or short photoperiods exhibited three reproductive cycles of egg-laying period followed by refractory period during 2 years of captivity. Similar obligatory egg-laying cycles have been suggested in certain snakes (*12*) and circumstantial evidence exists for other lizards (*3*, *4*).

In male birds, however, the refractory period can be experimentally dissipated by short day lengths and protracted by long ones (*13*). Similar facultative control is known in certain male lizards in which low temperatures accelerate the termination of refractoriness (*5*). Facultative control of reproduction is also characteristic of certain mammals in which both photoperiod and diet can alter length of the nonbreeding period. A diet of green plants, for instance, can induce an estrous response during the winter in the field vole *Microtus montanus* (*14*). Nonreproductive innate cycles have also been reported in other reptiles. Hernandez and Coulson (*15*) found evidence of endogenous rhythmicity in the physiology of hibernation in alligators. Hutton (*16*) suggested an "internally controlled" seasonal cycle of metabolism in the red-eared turtle, and Stebbins (*17*) suggested an "innate seasonal rhythm" of activity in the lizard *Sceloporus virgatus*. Fisher (*18*) has also suggested circannual periodicity ("circannual periodik") in the lizard *Lacerta sicula*. To the best of our knowledge our report constitutes the first demonstration of circannual periodicity in the reproductive cycle of a female vertebrate under free-running conditions of darkness.

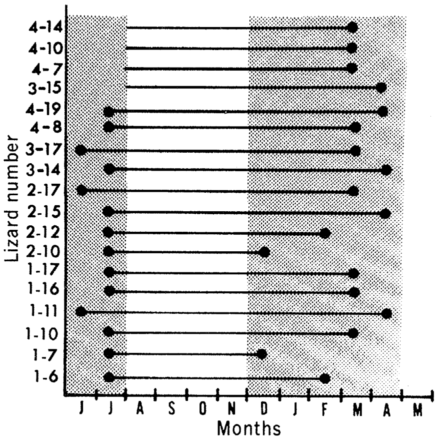

Fig. 2. The reproductive cycle of captive female *C. uniparens* exposed to an LD 14 : 10 photothermal regime starting in June 1973. Dark circles connected by a line represent lizards that underwent one or more ovulations. Stippled areas represent the time this species is known to be reproductive in the laboratory when exposed continuously to various alternating photothermal conditions after capture in June (*6*, *10*). Interval between stippled areas represents duration of the refractory period.

Apparently the initial reproductive cycle starting in the spring, and its subsequent refractory period constituted a programmed chain of events, which was triggered by an environmental cue (onset of spring), and then continues to completion (*19*). This is supported by the fact that these events occurred again under constant conditions, that is, without a second exposure to the original environmental cue that triggered the first cycle (*10*), which demonstrates that the length of both the refractory and reproductive periods are under genetic control. Once refractoriness ends during hibernation (brumation), low temperatures prevent breeding until spring and thus synchronize individuals with each other (*7*), enabling the population to be "physiologically prepared" (that is, in a nonrefractory state) at the time of emergence. This would permit the rhythm to be set (phased) once a year upon emergence and would allow for variation from year to year in optimal breeding time.

It is now well known that endogenous

factors initiate and control the duration and pattern of many annual processes and that such endogenous annual rhythms have significant adaptive value allowing animals to precisely anticipate yearly events such as winter (*19–21*). In temperate lizards, the refractory period commences when temperatures in nature are still sufficiently warm to permit further reproduction. However, the majority of such lizards are oviparous, and their eggs require long underground incubation (on an average of 40 to 50 days). In latitudes having pronounced winters, clutches laid after July and August would produce young when conditions for growth and storage of energy reserves for winter hibernation are less than optimal (*4, 22*). Hence, the frequency of individuals characterized by early breeding and fewer clutches would tend to increase in such populations, eventually adjusting each to coincide with maximum survivorship at any given latitude.

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Chemical Basis for Feeding Adaptation of Pine Sawflies *Neodiprion rugifrons* and *Neodiprion swainei*

Abstract. *Larvae of two pine sawflies,* Neodiprion rugifrons *Midd. and* Neodiprion swainei *Midd., consume only old foliage of jack pine,* Pinus banksiana *Lamb., and leave juvenile foliage intact early in the growing season. The chemical basis for this unique adaptation is a feeding deterrent chemical, 13-keto-8(14)-podocarpen-18-oic acid, which was isolated from juvenile foliage. The content of this deterrent chemical decreases as the foliage begins to mature until needles become acceptable to* Neodiprion swainei *larvae by August (60-day-old foliage) and to second-generation* Neodiprion rugifrons *by September (90-day-old foliage). The precise timing of larval acceptance of juvenile foliage indicates a highly specific relationship between these insects and their host tree based on the composition of chemicals in the foliage.*

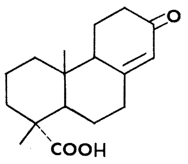
Diprionid sawflies are a well-defined group of nonsocial hymenopterous insects that are closely associated with coniferous forests. They are known by the presence of varieties of distinct races, physiological strains, and species that are well adapted to specific host plants and their physiological conditions (*1*). Such group characteristics make them particularly suitable for studies on the mechanisms of speciation through insect–host plant interactions.

Neodiprion rugifrons Midd. and *Neodiprion swainei* Midd. are species that feed exclusively on jack pine, *Pinus banksiana* Lamb. The most characteristic aspect of their feeding behavior is that in the spring the larvae consume only mature foliage and reject juvenile (current season) foliage. This feeding behavior generally ensures the survival of the host. The surviving foliage then is used for oviposition by the female sawflies and for larval feeding by the next generation late in the growing season.

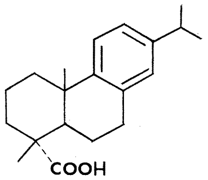
The purpose of this study was twofold: (i) to reveal the mechanism responsible for differentiation of juvenile foliage from mature foliage by feeding larvae and (ii) to investigate how this mechanism is related to the mode of life of the insects and the host plants.

Preliminary investigations (*2*) indicated that the basis for the sawflies' preferential feeding lies in a feeding deterrent or deterrents present in the juvenile foliage. To test deterrence, a colony of sawfly larvae was transferred to a twig of mature foliage treated on one end with an extract of juvenile foliage and their feeding activities were observed (*3*). Whenever the test extract contained a biologically active deterrent, the larvae did not feed on the treated foliage; instead, they moved away and settled on the portion of the twig that was not treated with the extract.

To isolate and identify the deterrent chemicals, juvenile foliage less than 1 cm long was extracted with *n*-hexane and then with ethyl acetate. The extracts were condensed and the deterrents were separated and isolated by successive chromatography (*4*). Two major deterrent chemicals obtained in pure form were designated compounds A and B.



A



B

Judging by the quantities present in the original juvenile foliage and their specific potencies, these compounds account for 64 and 25 percent of the total deterrence, respectively.

The chemical structure of the major feeding deterrent, compound A, was established by rigorous spectroscopic analyses (*5*). To our knowledge, this novel resin acid has not been reported previously. In addition, we synthesized compound A by partial ozonolysis, using neoabietic acid as the starting material (*6*). In laboratory tests, the synthetic compound produced the same degree of deterrence as the natural product. We also demonstrated the effectiveness of compound A in the field. Two isolated young trees were selected in the natural jack pine stands of Arena, Wisconsin. Four or five colonies of second- to third-instar *N. swainei*, consisting of 16 to 43 larvae per colony, were established randomly on old foliage in July 1975. After 24 hours, a 30-ml portion of a solution of compound A (2 mg/ml in 5 ml of ethanol and 25 ml of water) was sprayed over one entire tree. The other tree was sprayed with the same amount of the solvent and water for control. All colonies in the tree treated with compound A were disrupted for at least 3 hours. No larvae commenced feeding for at least 6 hours. After 24 hours approximately half of the larvae were found on the juvenile foliage, an unnatural place for them to settle, and none were observed to feed on this foliage. By contrast, the larvae on