

# Reptilian Pheromones

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## I. INTRODUCTION

### A. Background

Reptiles may arguably be described as primarily visually oriented creatures. It is by now well known that they exhibit a wide variety of visual signals or behaviors that are important in all aspects of their life cycle (see Carpenter and Ferguson, 1977). Only relatively recently has chemical communication been recognized as an important aspect of reptilian biology. Baumann and Noble conducted the first experimental investigations on the importance of chemical communication in reptiles in the 1920s and 1930s. Baumann (1927, 1929) investigated the courtship behavior of *Vipera aspis*, whereas Noble (1937) investigated courtship, trailing, and aggregation in *Thamnophis* and *Storeria*. It is now clear that the daily problems reptiles face in survival, such as prey detection, predator avoidance, and mate recognition, in many cases require the ability to perceive chemical cues from the environment.

The study of chemical cues, semiochemicals (natural products with signal function), and/or pheromones is now recognized as an integral part of research on reptilian social behavior. For the purposes of this review I will use the original definition of a pheromone, which states that a pheromone is a chemical or semiochemical produced by one individual that effects a change in the physiology or behavior of conspecifics (Karlson and Luscher, 1959). Behavior mediated by chemical cues was observed well into the last century. However, until recently, few experimental studies have sought to document the intricate and complex processes involved in the production and perception of pheromones in reptiles. Accounts of behaviors elicited by pheromones are prevalent in the literature, as are excellent reviews (see Evans, 1961; Carpenter and Ferguson, 1977; Madison, 1977; Burghardt, 1970, 1980; Simon, 1983). The purpose of this review is to doc-

ument the many behavioral accounts of pheromonal communication in the various reptilian taxa. For each order I have attempted to categorize the behaviors in terms of responses elicited in signal recipients such as sex attraction, aggregation, and the like. In places, I have also included a brief description of those glands and other structures that have been described as producing semiochemicals. More complete descriptions of the histology and histochemistry of these glands may be obtained from the original references. Finally, I have attempted to review critically the literature dealing with the chemical nature of the pheromones themselves. This field of study has only recently received the attention of chemical ecologists; however, even the limited number of available studies has demonstrated dramatically the great potential of reptilian models for investigation of the chemical senses among the vertebrates. Because more work has been done on snakes than any other reptiles, this chapter reverses the usual order of groups and starts with these.

### B. Evolution of Semiochemicals in Reptiles

Reptiles possess a remarkable diversity of glands and glandular secretions (Quay, 1972). Indeed, interest in squamate glands began well over a hundred years ago and even included studies by Darwin (1874). But most of these early reports were superficial with little or no investigation of morphology or histology. Gabe and Saint Girons (1965) conducted an extensive study of the cloacal anatomy of 23 families of lepidosaurs. However, the most thorough study of squamate glands is the doctoral dissertation of Anne Whiting (1969), which comprises an excellent survey of the morphology and histology of all the known cloacal glands in squamates. Because of the vast number of synonymous terms for cloacal glands in squamates I will follow Whiting's (1969) terminology.

Gadow (1887) divided the cloaca into three regions: the coprodaeum, the urodaeum, and the proctodaeum. The coprodaeum is really an extension of the large intestine and comprises the largest and most anterior section of the cloaca. The urodaeum receives both the urinary and genital ducts. The most posterior portion, or proctodaeum, is continuous with the urodaeum and opens to the environment through the cloacal vent.

Chemical cues are very efficient energetically in that they are cheap to produce, they relay a message long after the producer is gone, and they work in the dark and over very great distances. In his study of the evolution of social behavior and communication in mammal-like reptiles, Duvall (1986) proposes a mechanism for the evolution of semiochemical communication. It is widely accepted that virtually any exudate can serve as a chemical signal. Duvall states that chemical

exudates such as feces or urine, skin lipids, or other metabolic by-products are inexpensive in the sense that they are continually available for use as chemical signals. That these exudates may have been coopted or exapted to serve a semiochemical function has been suggested (Graves et al., 1986; Maderson, 1986) and specifically investigated in reptiles (Duvall et al., 1987). Duvall discusses two ways used by both early and present-day reptiles to mark the substrate. An individual may "passively mark" or deposit secretions as it moves through the habitat. For example, the animal leaves cloacal cues as it rests or drags the cloaca across the ground while walking. These behaviors are distinct from "active marking," in which the animal performs a behavior specifically to leave a chemical cue on the substrate by means such as chin wiping or cloacal rubbing. Finally, specialized exocrine glands are known to elaborate behaviorally active semiochemicals; examples are chin glands in tortoises and cloacal scent glands in snakes.

## II. SERPENTES

### A. Glands

Reptiles possess a remarkable diversity of glands and glandular secretions (Quay, 1972). In snakes, by far the best-known glands are the paired cloacal scent glands or anal sacs (Fig. 4.1). Interest in these glands began at least several hundred years ago, when Tyson (1683) described the glands as appearing in both sexes of rattlesnakes. These glands appear to be uniquely ophidian and are located in the tail, dorsal to the hemipenes in males and in the corresponding position in females (Whiting, 1969). A duct from the anterior end of each gland

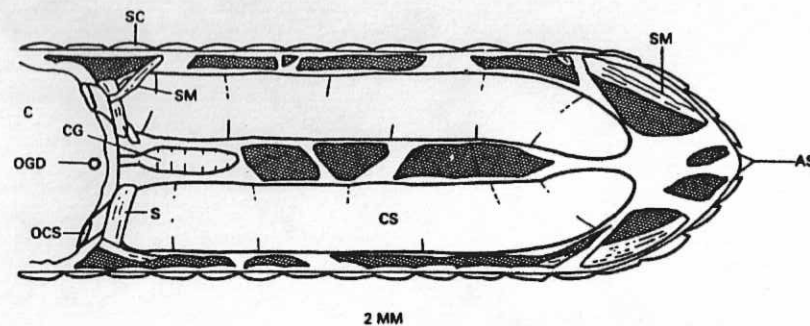


Fig. 4.1 *Leptotyphlops dulcis* ventral view (full section) of the tail region illustrating the large cloacal sacs and median, unpaired cloacal gland. AS, Apical spine; C, cloaca; CG, cloacal gland; CS, cloacal sac; OCS, opening of cloacal sac duct; OGD, opening of cloacal gland duct; S, voluntary muscle sphincter; SC, scale; SM, skeletal muscle. (From Kroll and Reno, 1971.)

*Sternotherus odoratus* are called stinkpots because they eject malodorous secretions from their anterior musk glands when disturbed. The secretion is highly pungent and aversive to humans and presumably other mammals. It consists primarily of four  $\omega$ -phenylalkanoic acids (Eisner et al., 1977). These are phenylacetic, 3-phenylpropionic, 5-phenylpentanoic, and 7-phenylheptanoic acid, the last two being newly described natural products. As the turtles appear to eject the fluid only in response to provocation, a defensive role has always been assumed for these chemicals. Mealworms coated with the  $\omega$ -phenylalkanoic acids are rejected by swordtails; however, the dose required for rejection is at the limit of the capacity of the gland. Presumably, any piscine predator of *Sternotherus* would be considerably larger than swordtails. In addition, turtles have many other predators, including mammals, that might provide a better test. Perhaps the chemicals act as a kind of aposematic signal that warns predators of the distastefulness of the turtle. The musk of the Australian *Chelodina longicollis* also has been tested for its capacity to deter a wide variety of potential predators, including mammals, birds, and reptiles (Kool, 1981). However, musk applied to food, into the nares, or just present in the vicinity of the predators does not elicit behaviors differing significantly from controls, so that the inguinal musk of the long-

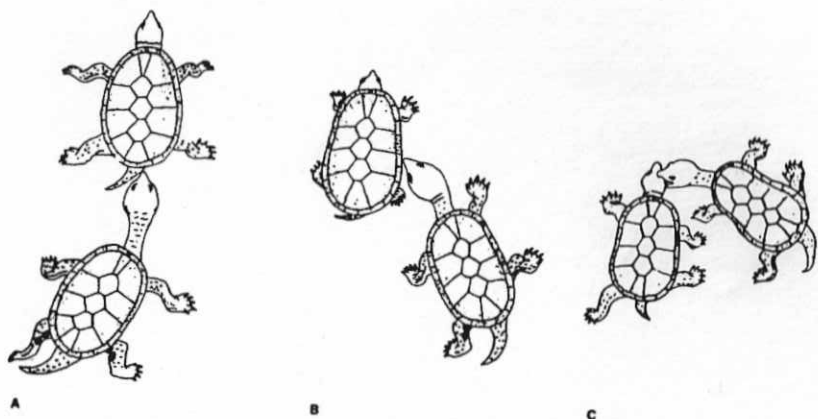


Fig. 4.22 Initial tactile courtship behavior in kinosternid turtles. (A) The approach; (B) nudging at the bridge near the musk gland; (C) biting at the head. (From Mahmoud, 1967.)

necked turtle does not act as a predator deterrent, although it may be a sex attractant (Kool, 1981). Secretions of two adult females test positively for proteins; however, there is no evidence of the presence of carbohydrates or glycerides (Eisner et al., 1978). GC/MS analysis reveals no highly volatile, low-molecular-weight compounds. However, when treated with diazomethane, fatty acids are detected as their corresponding methyl esters, specifically oleic, linoleic, palmitoleic, palmitic, stearic, and citronellic acid. These fatty acids could impart the "stink" for which the tortoise is well known. Ironically, the secretion also contains  $\beta$ -ionone, which is known as lavender oil, the odor of violets.

Secretions from the axillary glands of *Sternotherus* may serve a dual function. They are involved in antipredator mechanisms, whereas during the breeding season, the glandular contents may serve as sex recognition cues by which courting males discriminate females (Eisner et al., 1977). Apparently the musk of a female stinkpot turtle, although repulsive to mammals, is perceived quite differently by courting male *Sternotherus*.

## VI. CROCODILIA

### A. Glandular Morphology

Crocodylians of both sexes have three types of integumentary glands. The first set is a series of minute glands of unknown function found in two longitudinal rows under the dorsal scales near the midline (Voeltzkow, 1899; Reese, 1921; Wright and Moffat, 1985). Reese (1921) states that the secretions lack odor and suggests that their small size and wide distribution over the dorsal surface might indicate that they are of use in keeping the scales in good condition.

The other two are musk glands that have been investigated sporadically over the last century (Gerhardt, 1933, and references therein). These glands lie in the cloaca and on the underside of the throat (Voeltzkow, 1899; Gadow, 1901; Reese, 1920; 1921; Wright and Moffat, 1985; Weldon and Sampson, 1987; 1988). The cloacal glands are paired, lie within the lips of the cloaca (Gadow, 1901), and develop from the lower layer of the epidermis (Reese, 1921). Their morphology and development were extensively studied in juvenile *Alligator mississippiensis* (Reese, 1921). Other investigators have provided extensive histological studies of posthatchling crocodylians (Disselhorst, 1904; Petit and Geay, 1904; Voeltzkow, 1899). Recent studies using modern histological and histochemical techniques addressed the cloacal glands of adult *A. mississippiensis* (Weldon and Sampson, 1987) and the chin and cloacal glands of juvenile *Crocodylus porosus* (Wright and Moffat, 1985).

In adult *Alligator mississippiensis*, the cloacal or paracloacal glands are large, oval, and encapsulated with a single duct (Weldon and Sampson, 1987) (Fig. 4.23). The capsule is surrounded by a layer of smooth muscle. The glands are holocrine, and the secretion consists of lipids but no mucopolysaccharides. The smooth muscle surrounding the capsule has been observed to evert the gland.

The chin glands of *Crocodylus porosus* open as two narrow fissures or slits toward the posterior end of the underside of the lower jaw (Wright and Moffat, 1985) (Fig. 4.24). They are unique to the order Crocodylia (Weldon and Sampson, 1988). The small, ovoid glands are eversible; the inner portion of the slit and part of the gland then protrudes as a conspicuous black rosette. Surrounding each gland is a region of dense collagenous connective tissue covered by a cup-shaped layer of striated muscle. At the ultrastructural level, chin and cloacal glands are indistinguishable (Wright and Moffat, 1985). Lipids occur in the holocrine secretions of the cloacal glands but not in those of the chin glands (Weldon and Sampson, 1988). The oval chin glands of male *Alligator mississippiensis* are surrounded by striated muscle and lack a distinct lumen or secretory duct (Weldon and Sampson, 1988).

### B. Pheromonal Functions

Secretions from the chin and cloacal glands may serve as sex attractant pheromones, territorial markers, interspecific allomones, or defensive secretions. Wright and Moffat (1985) suggest that in these animals the secretions may play a dual role, as do the secretions of *Sternotherus odoratus* (see Section V.E). The secretory products may serve as defensive secretions in juveniles and may be involved in reproductive and territorial behavior of adults. Although neither of these hypotheses has been tested, there are numerous anecdotal reports of behaviors elicited in response to these secretions. For example, addition of the secretion of the chin gland of a juvenile *Caiman crocodylus* into water in which other juveniles have aggregated is reported to cause them to thrash about (Gorzula, 1985). However, repetition of the experiment produced no discernible reaction. It would be interesting to see whether the composition of these secretions changes with age or differs between the sexes.

The secretion of the chin glands has been described as a smeary, pale brownish substance, a concentrated essence of musk (Gadow, 1901). The secretion is most active during the rutting time, at which time the glands are partly everted. Young crocodiles and alligators often evert these glands when handled. The cloacal glands are referred to as strongly scented organs that occur in both sexes and have

thrash about a release response



Fig. 4.23 *Alligator mississippiensis*. Cloaca of alligator showing region from which paracloacal glands were excised. (Photo by P. J. Weldon.)

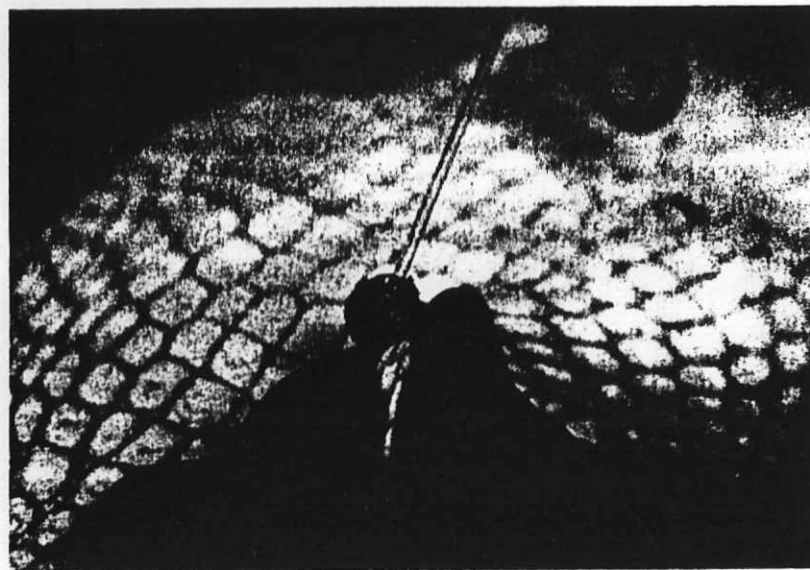


Fig. 4.24 *Alligator mississippiensis*. A gular gland is everted and a capillary tube containing secretions is withdrawn. (Photo by P. J. Weldon.)

an "obviously" hedonic function (Gadow, 1901). It is suggested that the sexes are probably able to follow and find each other thanks to the plume of scented water each individual leaves behind. The glands are supposedly most active during the breeding season, thus implying a reproductive function (Reese, 1920); this assumption is supported further by observations of marking actions (Ditmars, 1910). Male American alligators are stated to attract their mates by roaring and by releasing musky secretions from the glands in the throat and cloaca (Bellairs, 1957). All such reports assume that the secretions are carried on the surface of the water. McIlhenny (1935), who spent his entire life observing the American alligator in his native Louisiana, reports that when the bull alligator roars, it raises its head above the water and throws off a considerable quantity of sweet, pungent-smelling musk. This musk scents not only the air, but the surface of the water as well and lingers in the vicinity for some hours. He suggests that females do not use the chin glands but do produce considerable quantities of musk from their cloacal glands. Male alligators frequently evert the musk glands during the mating season, thus releasing a pungent perfume that is carried by the wind for considerable distances (Evans, 1961). The scent is claimed to attract the female to the male's pool.

Other reports are less clear. Neill (1971) states that it is not known how the sexes of *Alligator mississippiensis* locate each other and suggests that cloacal glands lay a detectable trail. Although it is unknown whether the throat glands play any role in courtship, he claims that the scent of the musk is not intensified during courtship, copulation, bellowing, or fighting. He observes that no detectable scent is given off during bellowing, but LeBuff (1957) suggests just the opposite. Silverstone (1972) never observed fluid being ejected from the throat glands, as reported by McIlhenny (1935). Musk is claimed to be in the air during most bellowing choruses, although eversion of the mandibular glands is rare (Vliet, 1986). However, an oily sheen on the surface of the water often appears near the cloaca (Vliet, 1989). Perhaps alligator musk is mainly transported on the surface of the water and not through the air.

Another report indicates that during the breeding season, the pair of *Alligator mississippiensis* swims about and the male rubs his throat (and presumably the chin glands) across the snout of the female (Evans, 1961; Burrage, 1965). The male has been seen to evert the chin glands and subsequently to rub them over the nares of the female, perhaps introducing a courtship pheromone (Garrick, 1978). Interestingly, most reptiles rely on the vomeronasal organ for the detection of semiochemicals, whereas crocodilians lack this organ.

### C. Chemical Studies

Investigation of the chemical nature of crocodilian scent gland secretions began over 50 years ago. A dimethylheptenol was isolated and originally named *yacarovol*—the Spanish term for alligator (Fester and Bertuzzi, 1934). Later it was reported that *yacarovol* is actually citronellol, whereas cholesterol was verified in the secreted musk (Fester et al., 1937).

Gular gland secretions from seven adult male and one female *Alligator mississippiensis* have been collected outside the breeding season (during September) and extracted in chloroform (Weldon and Sampson, 1988). Both glands of females then contain significantly more secretion than those of the males (Weldon et al., 1990).

Fractionation of lipids on a silica column, to separate polar from nonpolar lipids, discloses far more nonpolar than polar material in both the male and female secretions. Thin-layer chromatography (TLC) of the polar secretions from the gular and paracloacal glands shows bands that comigrate with sterols, free fatty acids, triglycerides, and steryl esters (Weldon and Sampson, 1988; Weldon et al., 1990). <sup>13</sup>C-NMR data exhibit absorptions that suggest free and esterified fatty acids. Other peaks suggest the presence of other esters and the glycerol moiety of triglycerides. Cholesterol, free fatty acids, acetate esters (C<sub>12</sub>-C<sub>18</sub>), higher-molecular-weight esters and butyl esters, as well as α-tocopherol, have been identified by GC-MS in the paracloacal glands of *A. mississippiensis* (Weldon et al., 1988). A similar set of butanoates, long-chain esters, fatty acids, saturated and mono-unsaturated alcohols (C<sub>11</sub>-C<sub>18</sub>), and citronellol have also been identified by GC-MS in the paracloacal glands of *Paleosuchus palpebrosus* and *P. trigonatus* (Shafagati et al., 1989). The gular gland secretions of the American alligator contain cholesterol, fatty acids, squalene and possibly other hydrocarbons, and α-tocopherol (Weldon et al., 1987). Saturated and unsaturated fatty acids, as well as 10-octadecanolide, occur in glandular secretions from *Crocodylus acutus* and *C. rhombifer* (Polo et al., 1988a, b).

### D. Behavioral Studies

Two studies have directly measured the behavioral response to glandular secretions in a crocodilian. The olfactory bulbs of *Caiman crocodylus* respond to chemical stimulation (Huggins et al., 1968). Specifically, the muscles adjacent to the nares show electromyographic responses, and the olfactory bulbs show EEG responses. Only a few sniffs occur in response to artificial stimuli such as oil of cloves or ethyl alcohol, but sniffing behavior lasts for long periods whenever caimans are exposed to musk from the glands of another caiman. In

the second study, yearling *A. mississippiensis* respond to airborne odorants in an olfactometer (Johnsen and Wellington, 1982). Gular pumping has been used as a measure of sniffing activity in response to seven stimuli: cloacal gland secretions (from two alligators), mandibular gland (chin gland) secretions (from one alligator), citronellol, androstenol, amyl acetate, and a blank. Alligators respond most strongly to the cloacal gland secretions of an adult male. Responses to the cloacal gland secretions and the chin gland secretions differ significantly from those to the synthetic compounds.

### VIII. CONCLUSIONS

This review presents a wide variety of data that share a common feature, that of demonstrating in some way the production or perception of pheromones by reptiles. However, this is the extent of the commonality. Even a brief perusal causes one to note the discrepancies in the relative quantity of information on pheromones for each of the reptilian orders. There has been considerable work on snakes and lizards, some work on turtles and crocodilians, but rhynchocephalians have received little attention and amphisbaenians have not been studied at all.

Even among the snakes and lizards, only few groups have been investigated. For example, we know a great deal about trailing pheromones and courtship pheromones in snakes, but most of the information derives from a few species of *Thamnophis*. What of the many other genera of snakes? It seems likely that many, if not all, of the major groups of snakes respond to integumentary lipid pheromones, for example, in courtship. Demonstration of courtship pheromones in widely divergent groups of snakes would indicate that these pheromones may be an ancient character rather than recently derived. These pheromones are species-specific in most insect species, yet despite some interesting studies on trailing pheromones, this possibility has not been adequately tested in snakes.

For lizards, much information exists on pheromonal communication in one small group of closely related skinks. The unequivocal demonstrations of their behavioral responses to pheromones indicate the feasibility of similar studies in other lizards, especially autarchoglossans. All of the skink studies were conducted in aquaria. The behaviors analyzed, such as tongue-flicking, are robust, easy to quantify, and sometimes repeatable through many trials. This is the case for few other vertebrate models. Brooding behavior is another topic that could yield some interesting data. Several studies suggest that skin lipid as well as cloacal cues may be important in species and sex recognition. As new types of glands elaborating behaviorally active compounds are still being described, exciting avenues remain open

for future studies. Finally, the interesting data on the lipid and proteinaceous components of femoral gland secretions hold great promise for clarifying species and individual recognition and territorial marking; they even provide tools for constructing phylogenies.

In terms of phylogenetics, *Sphenodon* is perhaps the most important, yet least studied, taxon in regard to potential pheromones. If *Sphenodon* were to have pheromones, it would certainly argue for an ancient rather than derived history for these compounds and the behaviors elicited by them. These issues remain completely unexplored.

The cloacal and gular glands of crocodilians have been a source of controversy over the years. They produce a lipid and proteinaceous secretion; however, the purpose of these secretions and the behaviors elicited in response to them remain unknown. As crocodilian behavior has been well described, these animals would be good candidates for studies in chemical ecology. Several investigators have identified interesting compounds in crocodilian glands; these compounds have yet to be tested in bioassays.

Turtles also produce and respond to chemical cues. For instance, the mental glands of tortoises elicit social responses. In addition, a source of pheromones in the cloaca of several species of aquatic turtle seem to identify breeding females to males. No one has investigated the behaviors or the source of these putative sex pheromones in the cloaca of any turtle.

The chemical ecology of reptiles, however, shows a clear dichotomy. The many fine studies of reptilian ecology are not paralleled by many chemical studies of the compounds involved. Of course, this trend is prevalent for most, if not all, vertebrates. In striking contrast, studies of pheromonal communication in insects have been successful in isolating and identifying literally thousands of pheromones, as well as in documenting the behaviors they elicit. Indeed, studies involving insect models have proven successful in identifying mechanisms of chemoreception at the molecular level. In contrast, investigators of vertebrate pheromones have had limited success in their investigations of pheromone chemistry. This reflects the association of many mammalian pheromones with urine or feces, thus complicating the isolation procedure. In addition, the behaviors elicited by these pheromones are complex, difficult to reproduce, and frequently nonspecific (such as sniffing).

Studies of reptilian pheromones clearly hold great promise. A number of discrete glands produce semiochemicals that elicit behaviors quantified in laboratory and field studies. Although interpretation of these behaviors is by no means easy, it appears that reptilian behaviors are more stereotyped than their mammalian counterparts. The literature describing the sources of semiochemicals in reptiles

also allows a few generalizations. The chemical compounds serving as pheromones seem to be limited to lipids (at least as of this writing)—specifically lipids of high molecular weight and relative non-volatility. This suggests a dependence on vomeronasal rather than olfactory detection. A concerted effort by zoologists pursuing reptilian natural history and behavior and by natural products chemists holds great promise for understanding the complex aspects of those reptilian behaviors governed by chemical signals.

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## Endogenous Rhythms

HERBERT UNDERWOOD

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### I. INTRODUCTION

#### A. Endogenous Rhythms

It is now widely recognized that all organisms, whether unicellular or vertebrate, can exhibit daily rhythms in a veritable host of behavioral, physiological, and biochemical parameters. The origin of this rhythmicity is obscure; however, it has been speculated that the selective