- Problems must first be identified by people with an intimate knowledge of the local environment.
- Certain categories of problems (such as agricultural) can only be solved in the local environment.
- There must be a new and more effective system for rapid sharing of information about planned and executed research and development results.

These difficulties strongly suggest the desirability of establishing joint programs between U.S. scientists and technologists and their counterparts in developing countries as well as of stimulating LDC scientists, engineers, and their institutions to cooperate among themselves.

Possible U.S. Actions

At present there are no international organizations, U.S. agencies, or private institutions which have the full capability of handling a substantial program of R & D assistance along the lines indicated above. In view of this, the U.S. government might well take the following actions:

1) Within the foreign policy apparatus, it could develop a capacity to cooperate fully with and provide adequate U.S. technical manpower to international organizations that can strengthen scientific and technological competences in developing countries. Neither the Department of State nor AID currently has this capacity.

2) It could develop a new institutional capacity to work bilaterally and cooperatively with all developing nations which wish to do so on joint programs aimed at the following:

- The establishment of LDC research institutions designed to solve specific development programs;
- The training of LDC technical people capable of helping solve problems of development;
- The establishment of quick response links among information dissemination centers for science and technology in developing and developed nations;
- The establishment of mutually attractive arrangements between institutions in developing countries and U.S. industrial, governmental, and academic institutions, the object of which is jointly desired activity, whether it be profit-making or intellectually rewarding; and
- The establishment of joint bilateral and multilateral commissions that would have broad mandates to examine development problems in which science and technology have a significant role and that also have bilateral or multilateral funding to enable them to support the search for solutions.*

3) It could create a new institutional entity for the purpose of facilitating the access of developing countries to "overdeveloped" world scientific and technological activities in universities, research institutes, government laboratories, and the private sector—a clearinghouse of sorts whose principal resource would be a knowledge of what is going on where in the United States and elsewhere and a capacity to translate the sometimes inchoate yearnings of our and LDC academics, entrepreneurs, and government leaders into cooperative relationships for the definition of achievable goals.

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* The establishment of bilateral commissions in the last year without either planning for their content or providing funds for their operation comes close to being scandalous.

Psychobiology of Reptilian Reproduction

Environment, hormones, and behavior interact to regulate different phases of the lizard reproductive cycle.

David Crews

The interaction of behavioral, endocrinological, and environmental factors regulating vertebrate reproduction has been the subject of intensive investigation in recent years. Psychobiological research, most notably on the ringdove and canary, indicates that environmentally induced endocrine-dependent male courtship behavior, acting along with climatic and physical aspects of the environment, stimulates pituitary gonadotropin secretion and, consequently, ovarian development, steroidogenesis, and reproductive behavior in the conspecific female (*1*). The adaptive significance of the integration of internal and external stimuli controlling reproduction, however, has been obscured because experimenters have traditionally used inbred laboratory species living under entirely artificial conditions. Although present-day reptiles cannot be considered to be more primitive than extant birds and mammals, their common ancestry and similarities make reptiles an important vertebrate class with which to investigate the social and environmental control of reproduction. Of the reptiles, lizards are particularly well suited for psychobiological research. Many lizards are small, readily available, and easily cared for in the laboratory. In addition, many species retain their complete behavioral repertoire and complex social systems in captivity. More important from a psychobiological point of view, however, is that there already exists good basic information regarding the behavior, physiology, and general ecology of a number of species of two lizard genera, *Anolis* and *Sceloporus*.

Here I will describe laboratory experiments, conducted under seminatural conditions, on the interaction of internal and external factors in the regulation of the reproductive cycle of the American chameleon, *Anolis carolinensis*. The natural history of this lizard has been extensively studied (*2*) and the behavior reported here is typical of free-living populations. The results provide insights into the generality and adaptive value of these interactions which may prove to be of general application to other vertebrate species.

Anolis carolinensis is a small temperate-zone lizard found throughout the south-

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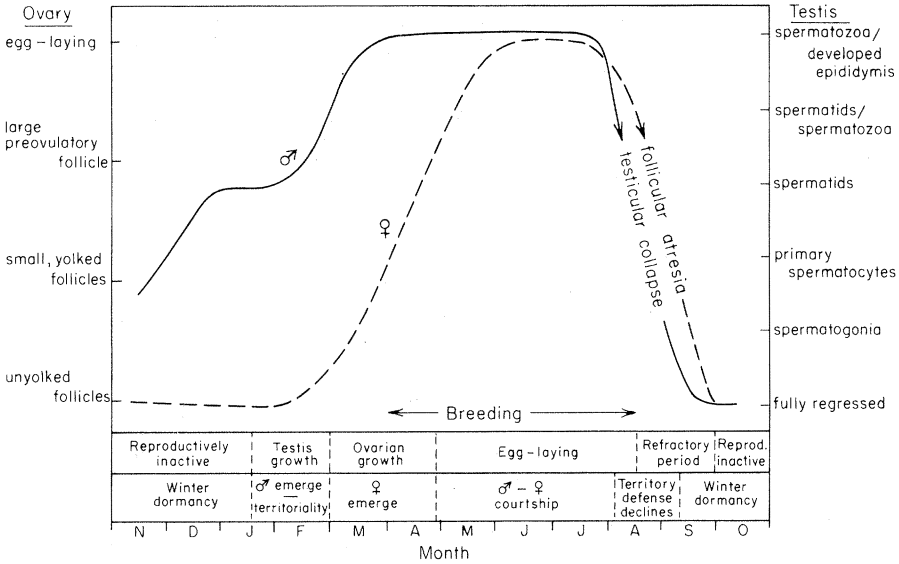


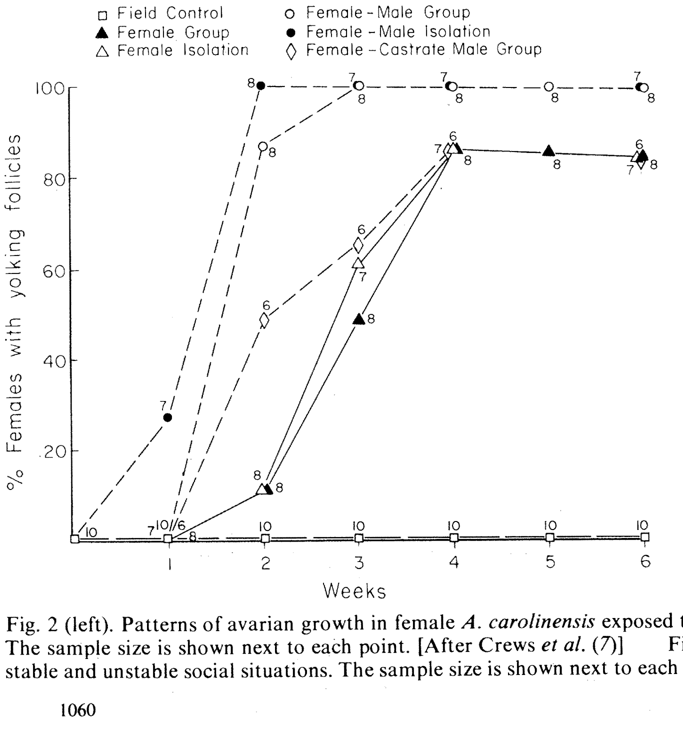
Fig. 1. Sequence of behavioral and physiological events in the annual reproductive cycle of the lizard *A. carolinensis*.

eastern United States (*2*). From late September to late January both males and females are reproductively inactive (see Fig. 1) and cluster in groups beneath the bark of dead trees and under fallen logs and rocks. Beginning in late January the males emerge from this period of winter dormancy and establish breeding territories. Approximately 1 month later the females become active, and by May they are laying one shelled egg every 10 to 14 days. After the breeding season both males and females enter a brief refractory period during which they are insensitive to environmental factors that are responsible for stimulating gonadal recrudescence in the spring.

The environmental factors controlling testicular activity in *A. carolinensis* have been extensively studied (*3*). Temperature and photoperiod act to cue different phases of the annual testis cycle; temperature controls primarily the regenerative phase of spermatogenesis between late fall and spring and photoperiod controls testicular maintenance and eventual regression in late summer.

The annual ovarian cycle of *A. carolinensis* may be divided into three distinct periods. (i) Previtellogenesis, lasting from November to February, is characterized by inactive ovaries containing only uniformly small translucent, unyolked follicles and atrophic oviducts. (ii) Vitellogenesis (yolk deposition) begins in March; at this time a single follicle begins to accumulate yolk and enlarges rapidly until it is ovulated at a diameter of about 8 mm by the end of 2 weeks. During the ensuing breeding season, a single follicle matures and is ovulated alternately between ovaries every 10 to 14 days. Vitellogenesis ceases in late August and the yolking follicles already present in the ovary begin to degenerate rapidly. (iii) Regression, follicular atresia in which follicles undergoing atresia differ from normal follicles and from corpora lutea in that they are highly vascularized, discolored (orange-yellow), flaccid, and mottled in appearance. These corpora atretica are gradually absorbed and disappear completely from the ovary during October. Thus, although the phases of the annual ovarian cycle have been described, the respective roles of temperature, photoperiod, and humidity in the regulation of the cycle are less well known (*4, 5*).

The interaction of environmental, behavioral, and physiological events governing reproduction in *A. carolinensis* was systematically examined in three series of experiments. In the first series, the roles of various stimulus factors associated with the male in the initiation of seasonal ovarian activity in winter dormant females were determined. In the second, some of the internal and external stimuli to which the females are exposed during the normal breeding season were identified and the manner in which they interact to control female sexual receptivity elucidated. In the third, the physiological control of the sexual refractory period following the breeding season was investigated.



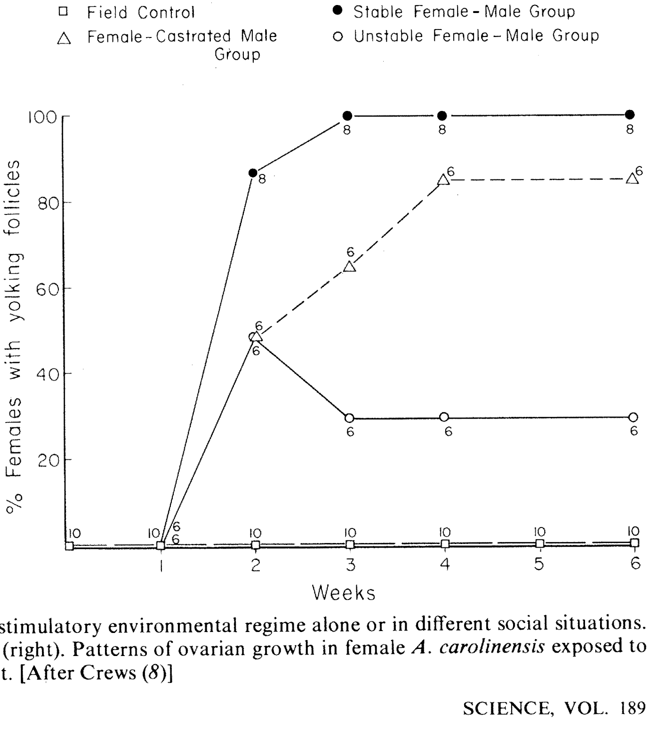


Fig. 2 (left). Patterns of avarian growth in female *A. carolinensis* exposed to a stimulatory environmental regime alone or in different social situations. The sample size is shown next to each point. [After Crews *et al.* (*7*)] Fig. 3 (right). Patterns of ovarian growth in female *A. carolinensis* exposed to stable and unstable social situations. The sample size is shown next to each point. [After Crews (*8*)]

Control of Seasonal Ovarian Recrudescence

All of the experiments on the role of the male in the control of seasonal ovarian recrudescence (OR) were conducted with newly captured reproductively inactive, winter dormant females, thereby providing an unchanging baseline measure of ovarian activity against which the effects of the various experimental manipulations were assessed (*6*).

The purpose of the first experiment (*7*) was to determine (i) whether an unseasonal environment would stimulate OR in winter dormant females, (ii) whether the presence of conspecifics affected the rate of environmentally induced OR, and (iii) whether the sex and physiological state of these conspecifics were also important in stimulating OR. To answer these questions, winter dormant females were exposed to the unseasonal environmental regimen (*6*) either alone (female isolation), or in all-female groups (female group), isolated female-male pairs (female-male isolation), female-male groups (female-male group), or female-castrated male groups (female-castrate male group).

Although the unseasonal environmental regimen stimulated vitellogenesis in winter dormant females, the presence of other females did not appear to be any more stimulatory than the environmental regimen alone (see Fig. 2). The presence of intact males, however, significantly increased the rate of environmentally induced OR. The presence of castrated males did not significantly increase the rate of OR in females.

Only females housed with intact males laid shelled eggs. Females in all other groups laid unshelled eggs, an indication of subnormal gonadotropin secretion (*4, 5*).

In an attempt to stimulate OR maximally, a second experiment (*8*) was conducted in which males that had been previously "environmentally induced" and thus were already sexually active were placed in a cage with winter dormant females (see Fig. 3). Contrary to expectations, however, fewer than half of the females were reproductively active at any one time. In addition, daily observations indicated striking differences between the groups in the degree of social stability and the predominant male behavior pattern (see below).

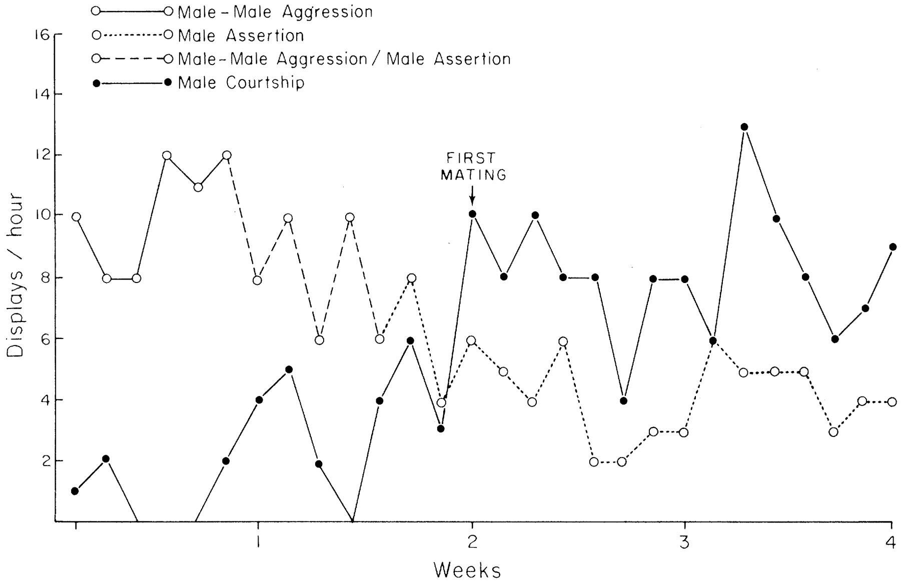


Fig. 4. Transition from male-male aggression to male assertion displays and male courtship by the dominant male among environmentally induced lizards. [After Crews (*8*)]

When winter dormant males and females were exposed to a stimulatory environmental regimen in the laboratory, there was an initial high level of aggressive behavior between males and little or no courtship (see Fig. 4). By the end of the first week, however, there was a gradual change in both the nature and frequency of the predominant male behavior pattern; this change coincided with a single male becoming dominant in the group. This transition was marked first by a shift from male-male aggression to assertion displays by the emerging dominant male. A general decline in the frequency of these displays and a simultaneous increase in male-female courtship behavior followed (only the dominant male courts); the first mating usually occurred by the end of the second week.

When females were exposed to sexually active males (see Fig. 3), there was a constant high level of male-male aggression for the entire 6 weeks. In addition, no male became dominant and no copulations occurred. In the few instances in which courtship did occur, the courting pair was always interrupted by aggressive males. In the castrated male group, neither male-male aggression nor courtship was ever observed.

It was thus not clear from the results of this experiment whether the facilitation and inhibition of environmentally induced OR were due to the males' performance of a particular behavior pattern or attributable to a more general complex of male-related stimuli. However, observations indicated that male courtship might facilitate the environmental induction of ovarian activity while aggression between males might inhibit environmentally induced OR.

In a third experiment (*8*), winter dormant females were exposed to (i) male-male aggression for 6 weeks, (ii) male courtship for the first 3 weeks and then male-male aggression for another 3 weeks, or (iii) male-male aggression for 3 weeks and then male courtship for the remaining 3 weeks. Since the pattern of ovarian activity among females exposed predominantly to 4 to 5 weeks of courtship had already been established (see Fig. 3), this group was not included.

As predicted, there was a low, unchanging level of ovarian development among females exposed to male-male aggression for the entire 6-week period (see Fig. 5). Females exposed to male-male aggression for the first 3 weeks showed a comparable low level of ovarian activity, but when the social stimulus was changed to male courtship there was a very rapid increase in ovarian development. Finally, females initially exposed to male courtship exhibited an immediate and marked facilitation of OR, but upon reversal of the social stimulus ovarian activity declined.

These experiments suggest that male courtship insures normal gonadotropin secretion, the absence of male courtship results in subnormal gonadotropin secretion (as indicated by the laying of unshelled eggs), and the presence of male-male aggression inhibits or greatly reduces environmentally induced gonadotropin secretion (*9*).

Further experiments in which females exposed to high and low amounts of male courtship exhibited significantly different rates of OR suggest that gonadotropin secretion is graded in accordance with the amount of male courtship to which the female is exposed (*8*).

Other experiments indicate that castration abolishes male courtship behavior and consequently prevents male courtship facilitation of environmentally induced OR (*10*). Androgen replacement therapy reinstates not only male courtship activity to preexisting levels but also courtship facilitation of OR.

Ritualized behavior patterns such as male courtship displays are integrated sequences of complex motor patterns or acts. Thus, it was also of interest to determine whether it was necessary for the female to perceive the entire display of the male in order for courtship to have its effect. To investigate this, experiments were conducted to determine the relative effectiveness of different components of male courtship in facilitating environmentally induced **OR** and in mate selection (*11*).

The courtship display of *A. carolinensis* consists of a rhythmical up and down bobbing movement of the body coordinated with the exposure of the dewlap, a bright red flap of skin beneath the chin (*12*). By surgically removing the hyoid cartilage that extends the dewlap, males could be obtained that performed all of the behavior patterns associated with courtship except the physical extension of the dewlap. In other males, the color of the dewlap was changed from red to blue by local injections of India ink.

The rate of environmentally induced ovarian activity among females housed with blue-dewlapped males was not significantly different from that among females housed with normal red-dewlapped males. Females housed with hyoidectomized males exhibited a significantly lower rate of OR, which was comparable to that of females exposed to castrated males. In mate selection tests, receptive females did not respond sexually to the courtship of hyoidectomized males but did respond to the courtship of blue-dewlapped males. These experiments suggest that the critical factor in both courtship facilitation of environmentally induced OR and in mate selection in *A. carolinensis* is the ability of the male to extend the dewlap.

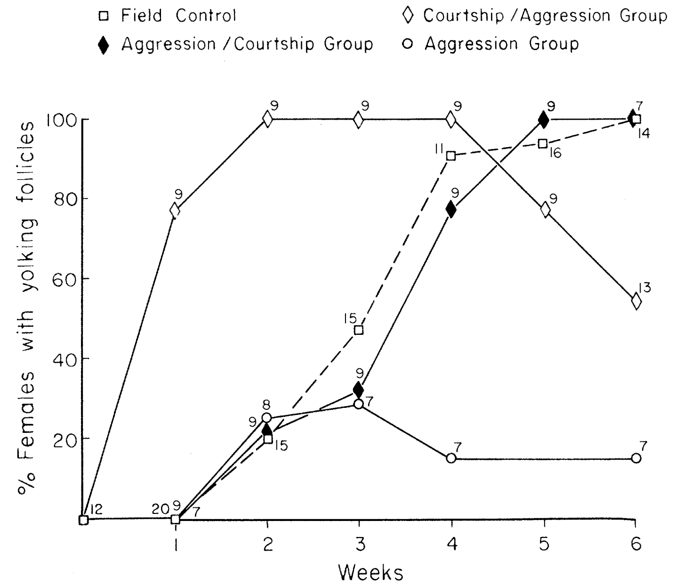


Fig. 5. Patterns of ovarian growth in female *A. carolinensis* exposed to different male behavior patterns. The sample size is shown next to each point. [After Crews (*8*)]

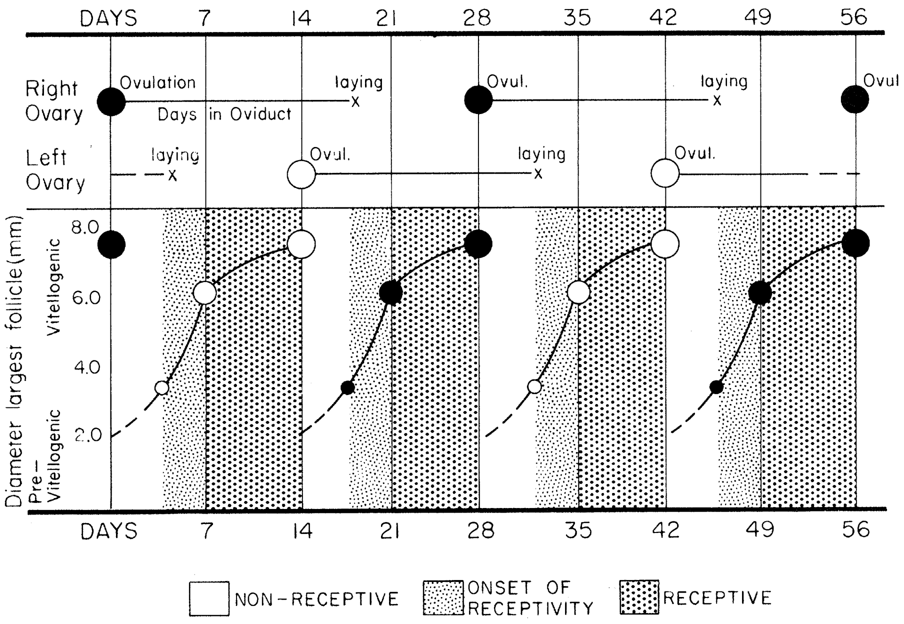


Fig. 6. Relationship between maturation and ovulation of the ovarian follicle and sexual receptivity during the breeding season in *A. carolinensis*. [After Crews (*18*)]

Several investigators have suggested that dewlap color serves as a species-isolating mechanism among sympatric anoles (*13*). Although the results discussed here would appear to contradict this, it should be emphasized that *A. carolinensis* is allopatric in the United States, except in southern Florida where it is sympatric with *A. distichus*, a small anole of similar body size, microhabitat, and breeding season (*2*). It is not known whether *A. carolinensis* evolved a red dewlap as a consequence of interspecific interaction with other anoles in the West Indies, the origin of radiation of *Anolis* (*14*). It would certainly be of interest to study the physiological and behavioral effects of components of male courtship in *A. carolinensis* in its area of sympatry in Florida and the West Indies.

In many species of seasonally breeding temperate vertebrates, the males emerge from winter hibernacula or overwintering grounds, establish territories, and are in breeding condition before the females arrive (*15*). The results presented here suggest an evolutionary explanation of this phenomenon. Assuming that in temperate animals these sex differences in spring emergence act to insure the presence of reproductively active, territory-holding males at a time when the females are emerging, it is clearly adaptive for females to remain dormant while there is this high incidence of aggressive behavior among males which are establishing territories. Male-male aggression declines as males come to recognize territorial boundaries. When the females emerge, therefore, the territorial male's shift to courtship behavior would act in concert with environmental stimuli to facilitate recrudescence. In addition, females would not be unnecessarily exposed to predation; that is, they would be able to offset their increased vulnerability by rapidly reaching breeding condition. Were males and females to emerge at the same time, however, females would be exposed to the high frequency of male-male aggression necessary for the establishment of territories which, as these experiments indicate, would inhibit ovarian development. Another possible function of courtship-facilitation and aggression-inhibition of environmentally induced ovarian activity is to insure breeding synchrony in the population.

Thus, it is possible that while emergence from hibernation may be cued by environmental or endogenous factors, or both, the rate at which females respond to these environmental cues may have evolved to coincide with territory establishment and the subsequent waning of male-male aggression. The experiments described here suggest a function for differential emergence in temperate zone vertebrates which can be tested by field experimentation.

Control of Female Sexual Receptivity

When a female *A. carolinensis* is introduced into a cage containing a sexually active male, the male immediately challenges (*12*). If the female does not attempt to flee or hide, the male will begin to court by slowly advancing toward her, interrupting his approach to perform a series of courtship displays typical of the species. A female that remains standing for the advancing male will invariably arch her neck, enabling him to take a neck grip. The male then straddles the female, pushes his tail beneath hers so as to oppose their cloacal regions, and intromits one of two hemipenes; the copulating pair remains immobile in this posture until separation.

Noble and Greenberg (*16*) suggested that *A. carolinensis* was similar to birds and mammals (*17*) in that there exists a causal relationship between maturation of the ovarian follicle and sexual receptivity. However, their approach of ovariectomizing females and later implanting crystalline hormones and noting changes in genital morphology and sexual behavior demonstrated only that sexual receptivity was dependent on the presence of the ovaries. To investigate this question more directly, female sexual receptivity in a standard mating test was correlated with both the size of the largest ovarian follicle and the follicular cycle (*18*). Using this procedure, neither the reproductive condition nor the sexual receptivity of the female was known before testing. In three different groups of females tested in this manner, females environmentally stimulated in either all-female or male-female groups and freshly captured breeding females, the same correlation was found (see Fig. 6). None of the females later found to be reproductively inactive was receptive to the courtship of the test male. Similarly, none of the females later found to be in their first follicular cycle but with small (< 3.5 mm) yolking follicles was receptive. In contrast, all females with large preovulatory follicles (> 6.0 mm), regardless of their follicular cycle, stood for the courting males.

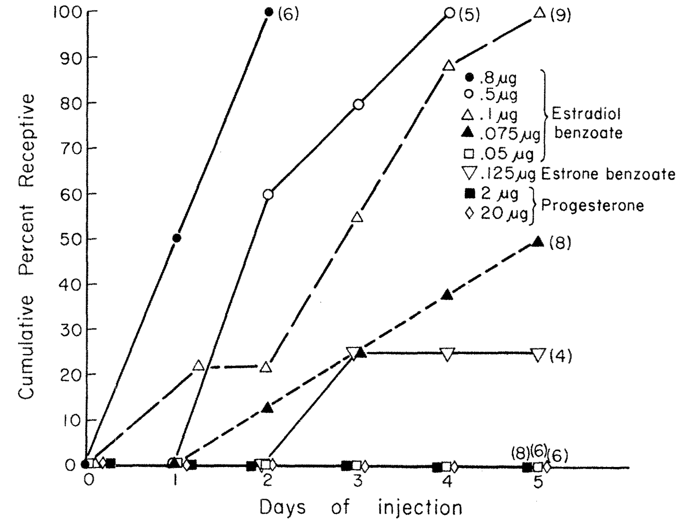


Fig. 7. Cumulative percentage of ovariectomized *A. carolinensis* sexually receptive to male courtship following daily injections of either estradiol benzoate, estrone benzoate, or progesterone. The number of animals is shown next to each point.

In every group not all of the females later found to have follicles of between 3.5 and 6.0 mm in diameter were receptive to the test male. This suggests that the transition between nonreceptivity and receptivity occurs during this phase of follicular development. The exact point of the transition, however, varies from female to female, which may suggest individual differences in neural sensitivity to follicular secretions, different quantities of secretion, or different time courses in steroid uptake by neural tissues. It is likely that estradiol is the major ovarian hormone involved in female sexual receptivity. Oviduct development in both ovariectomized and reproductively inactive lizards is stimulated by injection of estradiol (*19*) and is closely correlated with follicular maturation during recrudescence (*5*). Further, ovariectomized *A. carolinensis* receiving daily injections of varying amounts of estradiol benzoate, estrone benzoate, or progesterone dissolved in sesame oil were more responsive to the estradiol benzoate [see Fig. 7; see also (*20*)]. Finally, experiments on the uptake of tritiated estradiol-17β by brain and peripheral tissue of ovariectomized female *A. carolinensis* suggest that brain, oviduct, and fat body are sites of maximum estrogen uptake (see Table 1). Dissection of the brain into forebrain, midbrain, and hindbrain regions indicates that the midbrain does not concentrate estradiol relative to

Table 1. Concentration of ethyl acetate soluble radioactivity (counts per minute in tissue) relative to blood plasma (T/P) and gastrocnemius muscle (T/M) in right fat body, oviducts, and brain tissues of ovariectomized *A. carolinensis* at five time intervals following intraperitoneal injection of 1 µci of high specific activity [1,2,6,7-^{3}H]estradiol-17β in absolute alcohol vehicle (*34*). Abbreviations: *N*, number of animals; $\bar{x}$, mean; S.E., standard error.

Tissue	Ratio	Relative concentration									
		30 minutes (N = 6)		60 minutes (N = 6)		90 minutes (N = 6)		120 minutes (N = 7)		240 minutes (N = 5)	
		$\bar{x}$	S.E.	$\bar{x}$	S.E.	$\bar{x}$	S.E.	$\bar{x}$	S.E.	$\bar{x}$	S.E.
Right fat body	T/P	1.22	0.93	0.28	0.04	0.72	0.15	0.55	0.17	0.47	0.09
	T/M	16.54	7.95	13.74	4.17	14.72	4.03	6.75	1.11	5.31	1.33
Oviduct	T/P	0.51	0.18	0.76	0.31	0.93	0.22	1.79	0.68	2.84	0.65
	T/M	4.57	1.86	30.47	9.96	15.76	2.13	20.45	4.28	34.00	12.06
Brain (whole)	T/P	0.12	0.06	0.08	0.02	0.15	0.03	0.15	0.04	0.12	0.02
	T/M	1.72	0.47	3.45	1.02	2.75	0.64	2.06	0.48	1.27	0.37
Forebrain	T/P	0.12	0.07	0.06	0.01	0.18	0.04	0.11	0.04	0.10	0.02
	T/M	1.82	0.49	2.66	0.72	3.38	0.82	1.81	0.65	1.19	0.43
Midbrain	T/P	0.12	0.06	0.12	0.06	0.13	0.02	0.17	0.03	0.12	0.02
	T/M	1.75	0.48	4.27	1.39	2.48	0.54	2.25	0.50	1.30	0.38
Hindbrain	T/P	0.11	0.06	0.07	0.01	0.13	0.03	0.16	0.05	0.13	0.04
	T/M	1.60	0.45	3.42	0.95	2.39	0.55	2.01	0.30	1.31	0.30
Muscle	M/P	0.05	0.01	0.03	0.01	0.06	0.02	0.09	0.03	0.08	0.02
Plasma	P/M	25.98	6.61	51.56	15.76	20.37	2.95	16.85	3.59	13.51	3.99

other brain areas; these results, however, do not necessarily mean a lack of localized uptake by specific hypothalamic nuclei.

These findings provide interesting implications for our understanding of the breeding biology of *A. carolinensis*. Female *A. carolinensis* display the typical anoline pattern of reproduction (*21*). In contrast to most temperate lizards, which lay one or more clutches per season, *A. carolinensis* lay a single egg every 10 to 14 days for the duration of the breeding season. This pattern of ovarian activity is generated by the development and ovulation of a single ovarian follicle alternately between ovaries. The close correlation between sexual receptivity and stage of follicular maturation suggests that sexual receptivity is dependent on cyclic changes in the secretion patterns of gonadotropic and ovarian hormones during normal follicular development and is thus rhythmical in nature (see Fig. 6). Support for this hypothesis has been provided by several field investigators who report that autopsies of copulating female anoles always reveal large, preovulatory follicles (*22*).

Females allowed to mate are no longer receptive to male courtship 24 hours after copulation, but are receptive several weeks later; this suggests that mating might serve to inhibit further sexual receptivity within each follicular cycle, but not later sexual receptivity during subsequent follicular cycles.

Mating inhibition of female sexual receptivity is apparently a widespread phenomenon: it occurs in insects, birds, and mammals (*23*). Although it has not been demonstrated experimentally in reptiles, Greenberg and Noble (*24*, pp. 401–402) observed that one female "mated on April 13 but ran twice from the male during the same day and did not mate again until April 27." Similarly, in his field study of *Anolis garmani*, Trivers (*25*) found that females which copulated undisturbed did not copulate again for at least a month. When copulation was experimentally interrupted, the female continued to be receptive until she achieved complete copulation. Hunsaker (*26*) suggested that stimuli arising from intromission terminate receptivity in lizards. He noted that reproductively inactive female *Sceloporus* (*torquatus* group) continued to be sexually receptive if the cloaca was covered with tape, thereby preventing intromission by the male.

To investigate this phenomenon in reptiles, an experiment (*27*) was conducted to determine (i) whether mating inhibited further sexual receptivity within each follicular cycle, (ii) how rapidly the transition from sexual receptivity to nonreceptivity occurred after successful copulation, and (iii) the critical stimuli that are responsible for this inhibition.

Sexually receptive female *A. carolinensis* were retested for sexual receptivity 24 hours, 6 hours, 3 to 5 minutes, or less than 1 minute after an uninterrupted mating or after normal courtship and mounting without copulation. A third group of females was exposed to hemipenectomized males, which could court and assume the normal copulation posture but were unable to intromit.

While all the females that were just courted and mounted by the males remained receptive to male courtship, none of the females paired with intact males that completed copulation was sexually receptive when retested 24 hours, 6 hours, or 3 to 5 minutes later. Of the 12 females retested within 1 minute after separation from the male, 3 were still sexually receptive; in these three instances copulation was incomplete. All seven females tested with hemipenectomized males were sexually receptive 3 to 5 minutes later.

Hemipenectomized males courted normally but the duration of copulation was significantly longer than for unoperated males. Furthermore, many often failed to maintain cloacal contact throughout mating despite their proper copulation posture, and they never initiated separation from the female. This suggests that sensory feedback from the hemipenis during intromission or ejaculation plays a role in the maintenance and termination of copulation in the male lizard.

Coition-induced inhibition of female sexual receptivity has a clear adaptive value. Female *A. carolinensis* tend to mate with the male in whose territory they have their home ranges (*28*). In the natural habitat, mating usually occurs in exposed areas, such as on tree trunks, fences, and walls. The copulating pair is therefore particularly vulnerable to predators, since they can be approached and touched without immediately separating. This is presumably due to the male's inability to disengage himself rapidly from the female once intromission is achieved. In addition, copulation in this species is prolonged. During the breeding season, female *A. carolinensis* undergo approximate 7-day periods of sexual receptivity which are correlated with their cyclic pattern of ovarian activity (see Fig. 6). Inhibition of further sexual receptivity during each follicular cycle by mating could serve to minimize predation and increase the female's reproductive potential. Furthermore, the specialized sperm storage ducts in the female (*29*) allow her to continue to lay fertile eggs for the entire breeding season even if the territorial male is no longer present.

Control of the Refractory Period

Female *A. carolinensis* are sexually refractory during the early portion of the regressive phase of the annual ovarian cycle. Environmental (social and climatic) stimuli that promote rapid ovarian growth in winter and spring are generally ineffective in stimulating females in August and September (*30*). Furthermore, females respond less rapidly to exogenous gonadotropins during the fall than in winter and spring; refractoriness therefore may be due to changes in sensitivity to hormones. This close temporal relationship between the presence of the corpora atretica (CA) and the period of reduced sexual responsiveness suggested that the CA play an important role in maintaining refractoriness. To test this, Licht and I (*31*) examined the correlation between the disappearance of the atretic follicles and the termination of refractoriness to environmental stimulation. Further endocrine studies, in which the CA or a normal follicle was removed and the female's resulting sensitivity to exogenous gonadotropins was noted, showed that the onset of sexual refractoriness in female *A. carolinensis* arises spontaneously, independent of external factors, and that the CA produces a substance which markedly reduces ovarian sensitivity to environmentally induced gonadotropin secretion.

Female *A. carolinensis* depend on lipid stores to compensate for the scarcity of food in late winter and early spring as well as for the biosynthesis of vitellogenic protein by the liver in the spring (*32*). During the breeding season, females may produce as much as twice their own body weight in eggs (*33*); hence the prolongation of egg production or initiation of a second reproductive cycle in the fall by aberrant environmental factors (such as Indian summer) would be disadvantageous. This suggests, then, that the inhibitory effect of the CA on ovarian sensitivity to hormones may serve as an adaptive mechanism by which the female's refractoriness to otherwise stimulatory influences would be insured.

Conclusions

These experiments indicate that although climatic factors stimulate seasonal ovarian recrudescence in winter dormant females, androgen-dependent male courtship behavior strongly facilitates the stimulatory effects of the environment, while aggression between males inhibits the initiation of ovarian activity; this modulation is a result of differential effects of the male's behavior patterns on gonadotropin secretion in the female. Furthermore, the cue responsible for both the long-term physiological effects and short-term behavioral effects of male courtship is the extension of the dewlap. During the breeding season, female sexual receptivity is restricted to a time immediately preceding the ovulation of each follicle and is dependent on cyclic hormonal conditions normally arising during follicular maturation. If the female mates during this period, further sexual receptivity within that follicular cycle is inhibited. Finally, there is evidence that the atretic follicle plays an important role in maintaining the female's refractoriness to both internal and external factors that would otherwise stimulate inappropriate ovarian growth during the fall. This is the first demonstration of the possible physiological basis of sexual refractoriness.

This investigation of the interaction of environmental, behavior, and hormonal factors controlling various phases of the reproductive cycle in the lizard *A. carolinensis* demonstrates that principles originally discovered in the laboratory with highly inbred species can be generalized to animals in the field and shown to have clear adaptive value in the animal's natural history. Thus, while the utilization of inbred species contributes greatly to our understanding of the factors affecting reproduction, the integration of these factors can only be appreciated fully in an ecological context where the adaptive significance of such interactions becomes apparent.

References and Notes

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6. The same procedure was used in all of the experiments in this series. Animals were shipped to the laboratory within a day of capture. Four days after their arrival, they were divided into groups and placed in environmental chambers. The chambers were Sherer-Gillet 48-LTP and programmed to provide an unseasonal environmental regimen consisting of a photic cycle of 14 hours light and 10 hours darkness; a daily thermal cycle of 32°C during the photoperiod and 23°C during the dark phase, and constant relative humidity of 70 to 80 percent. During each experiment weekly samples of representative females were taken from the various experimental groups, and their reproductive condition was determined. The reproductive condition of animals in the field (field control) was also monitored with weekly shipments of freshly captured anoles. Four different measures of female reproductive condition were utilized in these experiments; the least sensitive index of ovarian state, percentage of females with yolking follicles, is used here to illustrate the effects of the various experimental manipulations. Since ovarian weight decreases markedly with the ovulation of each follicle, intergroup comparison of ovarian weight was not an adequate measure of ovarian development once ovulation occurred. Therefore, within each sample, nongravid females (those without oviducal eggs) were ranked according to ovarian weight, while postovulatory females were ranked using the following categories: (i) one oviducal egg and one corpus luteum (CL) present, and (ii) one or more oviducal eggs and two or more CL present. Ranked differences between groups were then compared using nonparametric statistical procedures. In addition, the ovarian condition of each female was rated at autopsy by placing her in one of the following categories: (i) ovarian follicles undeveloped (previtellogenic); (ii) ovarian follicles beginning to yolk but the largest follicle equal to or less than 3.5 mm in diameter; (iii) yolked ovarian follicles with the largest follicle greater than 3.5 mm in diameter but as yet unovulated; (iv) one oviducal egg and one CL present; and (v) one or more oviducal eggs and two or more CL present. Median ovarian condition for each group each week was then computed. Finally, a reproductive index was computed for each female by dividing the total weight of ovaries, oviducts, and (if present) oviducal eggs by the female's total body weight minus her fat body weight. To compare females with a greater number of CL than oviducal eggs to other females, a constant, representing the mean weight of a fully shelled oviducal egg, was added to the numerator for these females. Parametric statistics were then performed using the derived reproductive index.
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9. There are several reasons why the lack (or decrease) in ovarian development among females exposed to male-male aggression can be considered an instance of true inhibition and not a case of nonactivation or due to the absence of male courtship. First, the ovarian follicles of an increasing number of females exposed to male-male aggression during the latter half of the experiment became atretic and no new follicular cycle was initiated. Second, the recent demonstration of an endogenous circannual ovarian cycle in *A. carolinensis* combined with the observation that freshly captured females were undergoing recrudescence at a time when the majority of females exposed to constant male-male aggression had inactive ovaries would further argue for an active inhibition of ovarian development. If the inhibition effect was due to a third factor such as crowding and not to aggression, females exposed to different male behavior patterns but housed under otherwise identical experimental conditions would not be expected to exhibit such strikingly different patterns of ovarian activity. Finally, to counter the argument that it was perhaps the absence of courtship and not the presence of male-male aggression that inhibited OR, it should be remembered that in the first two experiments, females exposed to castrated males, who showed neither courtship nor male-male aggression, exhibited significant ovarian development while the pattern of ovarian activity among females exposed to male-male aggression was low and unchanging (or decreasing).
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