tion. By 42 days (experiment 1) a multilobed "organ" had formed beneath the kidney capsule, consisting mostly of adipose tissue. Histologic sections revealed scattered foci consisting of islets of Langerhans of varying size and shape and variable numbers of ducts in a thin fibrous stroma with a rich vascular supply. No exocrine elements were apparent. Electron micrographs reveal normal-appearing beta and alpha cells; typical secretory granules are present in the beta cells, and the many empty envelopes suggest active insulin secretion (*7*). At the present time we cannot estimate the extent of growth in size or number of islets of Langerhans in situ after transplantation.

Our rate of success continues to increase in current experiments as various factors of the transplantation protocol are altered. These parameters include precise location and arrangement of the transplants on the kidney, insulin regimen around the time of transplantation, handling of the donor tissue, and so forth. The kidney has proved to be an ideal locus in terms of ease of accessibility for the initial placement of the fetal pancreases and subsequent evaluation, and in terms of attracting an early and vigorous vascularization.

JOSIAH BROWN
I. GABRIELLA MOLNAR
Department of Medicine, University of California, Los Angeles 90024

WILLIAM CLARK
YOKO MULLEN
Department of Biology and *Department of Microbiology and Immunology, University of California, Los Angeles 90024*

References and Notes

1. R. C. Lillehei, R. L. Simmons, J. S. Najarian, C. M. Kjellstrand, F. C. Goetz, *Transplant. Proc.* **3**, 318 (1971); ACS/NIH Organ Transplant Registry, "First scientific report," *J. Am. Med. Assoc.* **217**, 1520 (1971).
2. W. F. Ballinger and P. E. Lacy, *Surgery* **72**, 175 (1972).
3. C. B. Kemp, M. J. Knight, D. W. Scharp, P. W. Lacy, W. F Ballinger, *Nature (Lond.)* **244**, 447 (1973).
4. R. J. Leonard, A. Lazarow, O. D. Hegre, *Diabetes* **22**, 413 (1973).
5. H. Browning and P. Resnick, *Yale J. Biol. Med.* **24**, 141 (1951–52); E. L. House, M. S. Jacobs, B. Pansky, *Transplant. Bull.* **28**, 435 (1961); A. E. Gonet and A. E. Renold, *Diabetologia* **1**, 91 (1965); O. E. Hegre, L. J. Wells, A. Lazarow, *Diabetes* **19**, 906 (1970).
6. R. E. Coupland, *J. Endocrinol.* **20**, 69 (1960).
7. Details are in preparation.
8. Supported by grants from the Kroc Foundation and the Diabetes Association of Southern California. We thank Celia Brown and Jim Dee for valuable technical assistance and Dr. William H. Carnes for assistance with histologic study. Dr. W. E. Dulin of the Upjohn Company, Kalamazoo, Michigan, kindly supplied streptozotocin.

11 February 1974

Geckos: Adaptive Significance and Energetics of Tail Autotomy

Abstract. Coleonyx variegatus *is adapted to readily sacrifice its tail to predators. This adaptation is associated with characteristic tail behavior and rapid tail regeneration. There is no facultative metabolic increase associated with tail regeneration, and energy normally allocated to body growth and maintenance is diverted to tail regeneration. This supports the contention that tail behavior, autotomy, and rapid regeneration evolved as mechanisms promoting survival in terms of predator escape.*

Tail autotomy in geckos and a number of other lizard species is considered a mechanism for reducing mortality from predation, although little quantitative experimental data have been presented in support of this hypothesis (*1*). The eublepharid geckos are remarkable in that a regenerated tail may be larger than the original (*2*). Moreover, the tail display of these lizards may be used to distract a predator's attention away from the head or body. It has been suggested that *Coleonyx* tails serve as fat stores contributing to increased survival over periods of fasting due to unpredictable environmental conditions (*3*). This effect appears secondary when the high incidence of regenerated tails (up to 74 percent in natural populations) is considered (*4*). These data and those reported here suggest that *Coleonyx* tails are adapted primarily for use in predator escape.

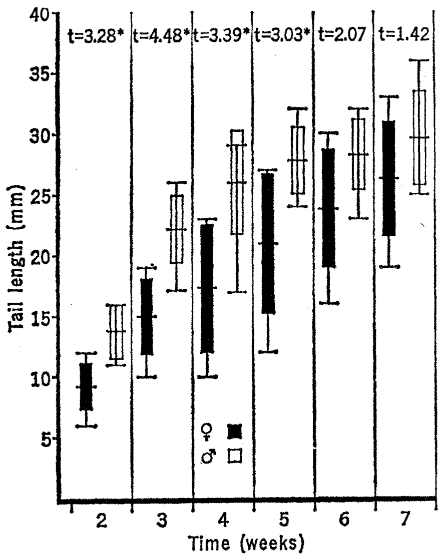
Behavioral experiments with a natural *Coleonyx* predator, the spotted night snake (*Hypsiglena ochrorhyncha*) (*5*), were designed to determine the advantage associated with having an autotomous tail. Predator-prey encounters took place in a 1.0 by 1.8 m arena with sand substrate interrupted by rocks and brush to simulate natural conditions. Red light was used for initial observations (*6*), but white light was subsequently used because it had no apparent effect on predator or prey behavior. We first tested for differences in predator attack frequency or prey behavior related to the presence or absence of tails on geckos [see (*7*)] and found none ($\chi^2 = 0.288$, $P > .05$).

Second, we determined the advantage associated with possessing an autotomous tail. Eight tailed geckos were introduced into the arena and allowed 15 minutes to adjust. Then a night snake was introduced. Geckos responded to the night snake by carrying the tail high above the body and waving it back and forth. Occasionally, geckos seemed attracted to undulatory movements of the snake and approached it with the tail-waving display. The geckos responded to any sudden movement of the predator by rapid retreat. When a gecko was within striking range, the snake would orient to the thickest part of the prey or the waving tail. Attacks were scored as either capture or escape. In 30 such trials, 11 (37 percent) of the geckos escaped while losing portions of the tail, and 19 (63 percent) were captured by night snakes. In our tests (*7*), no tailless geckos escaped from snake attack.

Rapid regeneration of the lost tail would be expected in *Coleonyx* because of the adaptation of the tail for predator escape. Regeneration rates were monitored on 14 geckos after tails were removed at the base (*8*). In the first 5 weeks, tail growth of males ($N=7$) averaged 0.80 mm per day and that of females ($N=7$) averaged 0.60 mm per day (Fig. 1), as compared to an average of 0.82 mm per day in the field (both sexes) (*4*). More rapid regeneration in males suggests different selection pressures between sexes and can be attributed to several

Table 1. Mean caloric values and ash and water contents of *Coleonyx variegatus* tails and bodies.

Part	Caloric content: Per milligram of dry weight	Caloric content: Per milligram of ash-free dry weight	Ash (% of dry weight)	Water (% of wet weight)
Original tails ($N = 3$)	5.79	6.31	9.01	75.50
Regenerated tails ($N = 19$)	6.24	6.68	7.06	75.66
Bodies ($N = 22$)	5.06	5.90	16.70	73.74



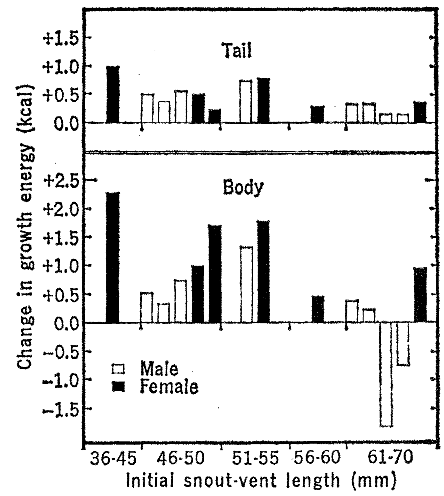


Fig. 1 (left). Sexual dimorphism in tail regeneration rates in adult male and female geckos (*Coleonyx variegatus*). Tails of seven females and seven males were broken at the base (*8*); geckos had free access to food during the trial. Vertical bars indicate 1 standard deviation, outermost horizontal lines represent range, and asterisks denote significant differences ($P < .05$). Fig. 2 (right). Relationship of calories invested in tail regeneration and calories invested in body growth in *Coleonyx variegatus.* Changes in caloric content are calculated from ash-free dry weights. The proportion of energy invested in regeneration increases with size, which reflects relative age (*4*). Two males that apparently rejected most food lost body weight but still regenerated a portion of the tail.

not mutually exclusive factors such as differential predation as the result of behavioral dimorphism, intrasexual aggressive differences (*9*), or mating behavior dimorphism (*10*).

Inasmuch as regeneration requires substantial amounts of energy, metabolic comparisons of tailed and untailed geckos were made with a Gilson differential respirometer to determine if facultative metabolic increases were associated with rapid regeneration. There was no significant difference ($t = 0.253$, $P > .05$) between tailed geckos (0.398 cm^3 of O_2 per gram of body weight per hour; $N = 29$) and geckos regenerating tails (0.407 cm^3 of O_2 per gram per hour; $N = 20$).

After 7 weeks, when tail regeneration was nearly completed, the geckos were killed. The regenerated portion of the tail was removed from geckos in the experimental group (*11*) and the whole tail from those in the control group. Bodies and tails were weighed and then freeze-dried, weighed again, ground, ashed, and burned by using a Phillipson microbomb calorimeter. Caloric values per milligram were higher for *Coleonyx* tails (Table 1) than for bodies and even higher than for most eggs (the life history stage with greatest caloric content per milligram) of other lizard species studied (*12*).

Growth data indicated age-specific differences in the ratio of tail growth to body growth. Because of the difference in caloric content per milligram of bodies and tails, growth data were converted to calories (Fig. 2). Older geckos did not use as much energy for body growth as did younger ones and allocated a larger proportion of energy to tail regeneration. Male geckos allocated a larger proportion of energy to tail regeneration than did females (Fig. 2). In addition, males have smaller bodies than females (*4*), which further enhances this proportional sexual dimorphism in the ratio of tail energy to body energy. In view of the differences in selective pressures between sexes discussed above, allocation of less energy for tail regeneration in females may reflect adaptive compromise between competing energy allocations for tail regeneration and processes such as reproduction.

The autotomy mechanisms, tail behavior, and rapid regeneration of the tail at the expense of growth and maintenance energy in *Coleonyx* are highly significant as predator defense mechanisms. The gecko's capacity to convert food into fat at a rapid rate (*3*), in addition to the fact that a majority of the fat stores are not in the tail (*3*), further supports this contention; nontail fat stores may be as important for tail regeneration as they are for use during fasting periods. It is difficult to propose evolutionary explanations of adaptive compromise for a fat storage tail that is highly autotomous unless the lizard losing the tail regains the lost energy by returning and ingesting it (*1*). This assumes, first, that the tail sometimes escapes from the predator and, second, that the lizard returns and ingests it. In our experiments there were no instances in which predators lost the tail. In ten trials in which geckos were left with their broken tails overnight, none ingested them.

A different adaptive compromise is suggested for *Coleonyx* in which the primary mechanism is allocation of fat deposition to the tail. This system permits rapid regeneration of a large tail and increases the effectiveness of tail display for predator escape. Also, in the event that the tail is not lost, an emergency energy store (*3*) is available. The adaptive compromise in *Coleonyx* is also unique in that, once the tail is lost, selective pressure for rapid tail regeneration for either predator escape or fat storage would be the same.

J. D. CONGDON
L. J. VITT
W. W. KING

Department of Zoology,
Arizona State University,
Tempe 58281

References and Notes

1. D. R. Clark, *J. Exp. Zool.* **176**, 295 (1971).
2. A. C. L. G. Gunther, *The Reptiles of British India* (Ray Society, London, 1864).
3. H. R. Bustard, *Science* **158**, 1197 (1967).
4. W. S. Parker, *Am. Midl. Nat.* **88**, 209 (1972).
5. R. C. Stebbins, *Reptiles and Amphibians of Western North America* (McGraw-Hill, New York, 1954).
6. Since both predator and prey are nocturnal, all trials were made at night, and red light was used initially to evaluate the effect of lighting.
7. Four tailed and four untailed geckos were introduced into the arena and allowed a 15-minute adjustment period. Then a night snake was introduced. This was repeated 30 times.
8. Tails were removed by holding the tail near the base and allowing the geckos to autotomize the tail.
9. Y. L. Werner, *Vie Milieu Ser. C Biol. Terr.* **19**, 199 (1968).
10. J. A. Oliver, *North American Amphibians and Reptiles* (Van Nostrand Reinhold, Princeton, N.J., 1955).
11. The tail was removed by cutting at the point where regeneration had initiated.
12. R. E. Ballinger and D. R. Clark, Jr., *J. Herpetol.* **7**, 129 (1973); D. W. Tinkle and N. F. Hadley, *Copeia* (1973), p. 272.
13. We thank N. F. Hadley for use of equipment and technical assistance and N. Dickson for calculation of caloric determinations. Partially supported by NSF grant GB 39852 to J.D.C.

12 November 1973; revised 13 February 1974