anion isethionate (2-hydroxyethanesulfonate) did not decrease the hyperpolarizing action of either isoproterenol or dibutyryl cyclic AMP. Therefore, at least in smooth muscle, beta-adrenergic hyperpolarization is not due to inward chloride movement.

Our findings raise the possibility that changes in membrane potential produced by cyclic AMP may interact with, and possibly modulate, metabolic processes in the liver.

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Artibeus jamaicensis: Delayed Embryonic Development in a Neotropical Bat

Abstract. *In Panama the phyllostomid bat* Artibeus jamaicensis *is seasonally polyestrous, and young are born in March or April and July or August. Blastocysts conceived after the second birth implant in the uterus but are dormant from September to mid-November, when normal development again resumes.*

A recent investigation of the breeding patterns of Central American bats (*1*) indicated that the frugivorous bat *Artibeus jamaicensis* (family Phyllostomidae) is polyestrous and that, in Panama at least, it has birth peaks in March through April and in July through August, near the end of the dry season (January through April) and in the first half of the rainy season. Although polyestry is probably not uncommon in tropical bats (*1*, *2*), the reproductive cycle of *A. jamaicensis*, and perhaps other species of *Artibeus*, is unique in that a 2.5-month period of delayed embryonic development occurs during the height of the rainy season (September through November). I report here details of the early embryology and the phenomenon of delayed embryonic development in the Jamaican fruit bat.

The annual reproductive cycle of *A. jamaicensis* in Panama, as determined by the dissection of 450 females and microscopic examination (*3*) of 167 of those specimens collected throughout the year in the Panama Canal Zone, is as follows. Most adult females carry single embryos in January and February and give birth in March or April. A postpartum estrus then occurs, as indicated by several lactating specimens caught in March. (The uteri of these specimens were still enlarged and filled with debris but they contained sperm, and each specimen had a newly forming corpus luteum in one ovary.) Females may be simultaneously pregnant and lactating in March, April, or May. After a gestation period of no more than 4 months, the second young is born in July or August. A postpartum estrus may also occur after this birth, although direct evidence for this is provided by only two sectioned specimens. Blastocysts from this fertilization apparently implant in the uterus in late August or early September but do not begin continuous development until mid-November. These embryos become macroscopically visible in December and are born in March or April.

Several features of implantation and early embryology in *A. jamaicensis* are similar to those of the neotropical bats *Glossophaga soricina* (family Phyllostomidae) and *Desmodus rotundus* (family Desmodontidae) (*4*, *5*). These include

Table 1. Size of corpus luteum and lutein cells in pregnant individuals of *A. jamaicensis*. Mean lengths of lutein cells were obtained by measuring four lutein cells per corpus luteum wherever possible. In the lutein cell column *N* indicates the actual number of cells measured; S.E., standard error.

Type of female	Corpus luteum			Lutein cells		
	N	Mean diameter (μm)	S.E.	*N*	Mean length (μm)	S.E.
With delayed blastocyst	19	1803.16	68.02	96	33.53	0.972
With nondelayed blastocyst	5	1918.00		26	29.81	0.980
With macroscopically visible embryo	12	2284.58	86.62	44	38.47	1.268

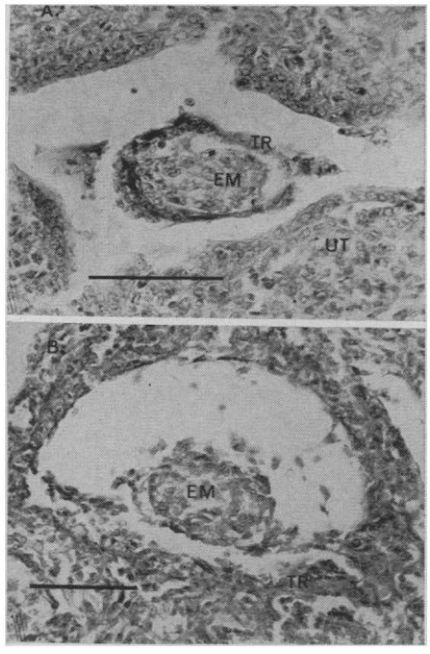

Fig. 1. Photomicrographs of embryos of the bat *Artibeus jamaicensis*. (A) Unimplanted uterine blastocyst. (B) Newly implanted blastocyst of a specimen caught in September. Scale is 100 μm. Abbreviations: *EM*, embryonic mass; *TR*, trophoblast; and *UT*, uterus.

(i) precocious development of the blastocyst, which, by the time it reaches the uterus, has differentiated into a trophoblast thickened at the embryonic pole and an embryonic cell mass (Fig. 1A); and (ii) implantation that is interstitial and cytolytic. A blastocyst that had just completed implantation in a specimen caught in September consisted of an embryonic cell mass measuring 110 μm in greatest width and an entodermal yolk sac closely appressed to the inner surface of the trophoblast which was still in the process of invading the endometrium (Fig. 1B).

Embryos that implant in August or September apparently undergo a period of retarded development lasting about 2.5 months. Although no macroscopically visible embryos were noted in females captured in September through November, microscopic examination indicated that most (21 of 32) specimens were carrying implanted blastocysts. Those specimens not in this condition were probably the young of the year, as judged by the immature condition of their ovaries. The fact that six of eight females caught in September and having blastocysts were lactating or had recently lactated, again suggests that the blastocysts are products of a postpartum estrus. Since few of the specimens caught in October and none of those caught in November were lactating, the embryonic diapause is probably not caused by lactation.

The diapausing blastocysts, which are morphologically similar in all specimens examined, consist of an oblong, spheroidal embryonic mass 200 to 380 μm in greatest diameter, a unilaminar yolk sac, and a trophoblast that is generally thickened along the embryonic pole (Fig. 2, A and B). In appearance the diapausing blastocyst resembles the early implanted blastocyst of *Glossophaga soricina* as described by Hamlett (*4*). The trophoblast develops into a chorioallantoic placenta (*6*) between September and November (Fig. 2, A and B).

Although no noticeable morphological changes occur in the embryonic mass between September and early November, the mass does grow in size. At implantation, the cell mass measures about 110 μm in width. Four September cell masses average 241 μm in width (range, 212 to 300 μm), whereas four from October average 276 μm (range, 200 to 380 μm), and two from November average 320 μm (290 to 350 μm). Thus, development does not completely cease during diapause, but cell division apparently slows to a fraction of its normal rate.

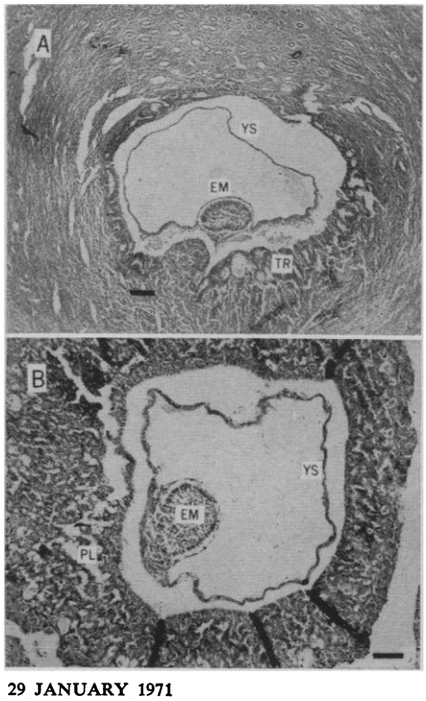

Fig. 2. (A) Diapausing blastocyst from a specimen caught in September. Note the relatively undifferentiated condition of the trophoblast. (B) Diapausing blastocyst of a specimen caught in November. Note the well-differentiated placenta. Scale is 100 μm. Abbreviations: *EM*, embryonic mass; *TR*, trophoblast; *UT*, uterus; *YS*, yolk sac; and *PL*, placenta.

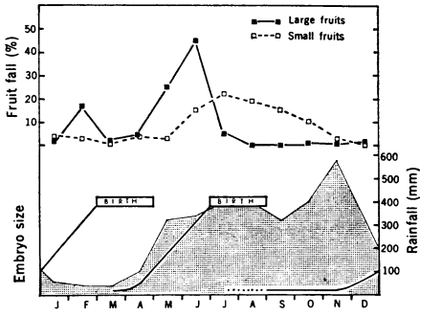

Fig. 3. The relationship between rainfall, fruit availability, and the natality periods of *Artibeus jamaicensis* in Panama. Data on rainfall are for Cristobal, on the Atlantic coast of the Canal Zone. Data on fruit are from Smythe (*12*). Embryos are postulated as being conceived in July or August, but more data are needed to confirm this.

Normal development probably begins in mid- to late November. One specimen collected on 19 November had a blastocyst with an amniotic cavity, a feature not seen in examples collected before this. By December, embryos are macroscopically visible, and the young are born in March or April, after a gestation period of about 7 months compared with a gestation period of about 4 months for embryos that are not delayed.

The mechanism responsible for embryonic diapause is unknown, but the histological condition of the ovaries and uteri of affected females offers some clue to its possible causes. The sizes of the corpus luteum of pregnancy of females with delayed blastocysts and those of females with microscopic but normally developing blastocysts taken in March and April were not different. In both sets of females, the corpus averages about 1830 μm in diameter compared with 2280 μm in females with macroscopically visible embryos; lutein cells in the smaller corpora are significantly smaller ($P < .01$) than those in corpora of maximum size (Table 1). An indication that the corpus luteum may be functional during the period of delay is the fact that females with diapausing embryos have a progestational uterus characterized by a hypertrophied endometrium and enlarged uterine glands which often contain secretory material. However, since the corpus does not grow appreciably during the period of diapause, low amounts of luteotrophic hormone may be operating

indirectly to slow embryonic development by preventing lutein cells from functioning maximally. A similar mechanism has been postulated as the cause of embryonic diapause in the tammar wallaby *Macropus eugenii* (*7*). Alternatively, diapause may be caused by the temporary lack of some factor in the uterine environment, such as a uterine protein that governs blastocyst growth (*8*).

Although not a common reproductive pattern in bats, delayed implantation or development is known to occur in several other species of Chiroptera. Only one nonhibernating species, *Eidolon helvum* (family Pteropidae) from Uganda (0°), is known to undergo delayed implantation (*9*). Females of this frugivorous species are fertilized in April or May, but implantation does not occur until October or November; a single young is born in February or March. The time of both implantation and birth coincide with peaks in rainfall. In the "quasi-hibernating," temperate-dwelling phyllostomid *Macrotus waterhousii*, fertilization occurs between September and November, and embryonic development proceeds slowly during the winter; the young are born in June (*10*). Wimsatt (*11*) inferred from Bradshaw's incomplete account that this may represent another case of delayed implantation, but definite proof of this is lacking. As a final example, *Miniopterus schreibersii* (family Vespertilionidae), a true hibernator, displays delayed implantation during its period of winter dormancy (*11*). In this species, fertilization occurs before the bats enter hibernation, but implantation does not occur until after spring arousal so that the young are born in the early summer.

Although the ecological settings of the different bats which display delayed implantation or development are varied, the timing of events is such as to allow young to be born at energetically favorable times of the year. This seems to be the case in *A. jamaicensis*. Blastocysts conceived in Panama in July through September and developing directly would result in births occurring in November through January. This means that females would be pregnant or lactating and young would be weaned at times when the availability of fruit is relatively low. Therefore, delayed development allows the young to be born, and the females to be most active at a time when fruit is most plentiful (*12*) (Fig. 3). Although the adaptive value of delayed development in *A. jamaicensis* seems relatively clear, the proximate factors behind this adaptation are unknown and suggest an obvious area for further study.

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Synergy of Ethanol and a Natural Soporific—Gamma Hydroxybutyrate

Abstract. *γ-Hydroxybutyrate and ethanol, as well as γ-butyrolactone and ethanol, are potentiative with respect to duration of loss of the righting reflex (sleep time). The concentration of ethanol in the liver decreases from 30 to 90 minutes after rats are injected with ethanol, but there is no change when ethanol is injected with γ-butyrolactone. In view of the fact that γ-hydroxybutyrate is a natural intermediate in brain, the effects of ethanol on the central nervous system may be mediated through its interaction with γ-butyrolactone.*

Synergistic effects (*1*) on duration of action have been observed between ethanol and cortisone, epinephrine, the phenathiazine derivatives, and the barbiturates (*2*). With cortisone, prior treatment with ethanol causes sleeping time to be merely "prolonged" (*3*); with the other agents mentioned the action seems to be potentiative. γ-Butyrolactone (GBL) has been re-

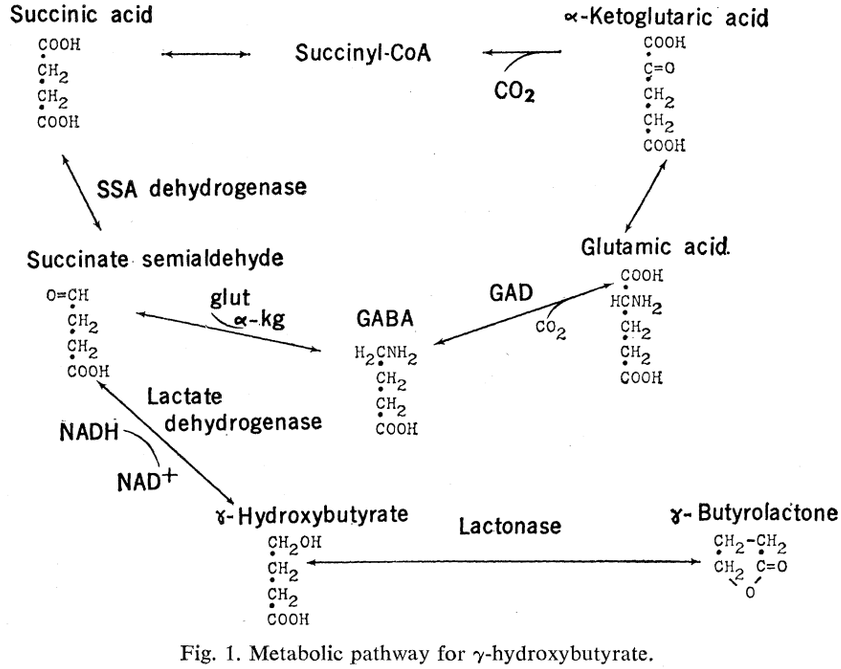

Fig. 1. Metabolic pathway for γ-hydroxybutyrate.