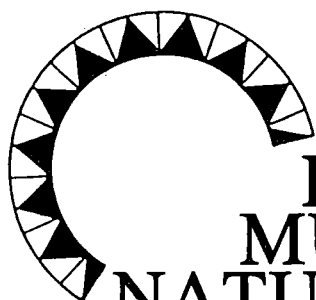# BULLETIN

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**REPRODUCTIVE STRATEGIES
OF FEMALE *DIDELPHIS***

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ABSTRACT

A two-year experimental field study was conducted simultaneously in Venezuela and Florida to test the hypothesis that in polygynous mammals offspring sex ratio is affected by maternal capacity for reproductive investment. Female common opossums (*Didelphis marsupialis*) and Virginia opossums (*D. virginiana*) were used as model animals. At each study site three groups of adult virgin females (10/group/year) were trapped prior to the breeding season, weighed, radiocollared and released. Females were randomly assigned to Control, Provisioned, or Delayed Reproductive groups. Provisioned females were located at daytime rest sites and provisioned with about a 125 gm mixture of sardines and cat food at 2-day intervals from at least three weeks prior to conception until the end of the breeding season. Delayed Reproductives were those whose embryonic young were removed repeatedly from the pouch to assess the potential reproductive cost to females who conceived but lactated for only a brief time. All females were recaptured at monthly intervals for weighing and to record the sex and size of pouch young or, in the case of Delayed Reproductives, to remove any new pouch young.

In both Florida and Venezuela, reproduction was highly seasonal and most (> 90%) females in the population produced two litters per year. The mean litter size (mode=7) for both sites did not differ significantly between the first and second litters, nor was there any effect of treatment on litter size. The interval between the birth of the first and second litters was of similar duration for Provisioned and Control females. Length of lactation was also similar for Provisioned and Control females, although the length of lactation for the second litter was 1-2 weeks longer in both Florida and Venezuela. There was no differential investment in male or female offspring during the teat-attachment phase, but Provisioned females exhibited greater parental investment. The weight at weaning of young from Provisioned females was significantly higher than young of Control females. Provisioned females invested disproportionately in males by producing male-biased sex ratios and by producing a higher percentage of litters that were male biased. Females, whether provisioned or not, that were in good condition tended to produce more male-biased litters. A drought in Florida in 1985

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disrupted the feeding program, consequently few females received their dietary supplement and a small percentage of litters were male biased. In Venezuela, male offspring of Provisioned females were recaptured post-weaning significantly more often than males of Control females, although the comparison was not significant for the Florida data. Females who were denied the stress of lactation tended to survive longer, the difference in survivorship approached significance in Venezuela. The extended survivorship of Delayed Reproductives was not biologically significant as few lived more than two years, and mean longevity for all groups was less than two years. Opossums of both species appear to be geared to perform a maximum reproductive effort in the year following their birth.

RESUMEN

Con el objeto de someter a prueba la hipótesis de que en mamíferos poligínicos la proporción de sexos es influenciada por la capacidad de inversión reproductiva de la madre, se realizó durante dos años un estudio de campo experimental en Venezuela y Florida. Se utilizaron como animales modelo hembras de rabipelado (*Didelphis marsupialis*) y hembras de Virginia opossum (*D. virginiana*). En ambos sitios de estudio y previo al comienzo de la temporada reproductiva, se capturaron tres grupos de hembras vírgenes (10/grupo/año), con el objeto de pesarlas y colocarles radiocollares. Las hembras fueron asignadas al azar en tres grupos: Control, Abastecidas y de Reproducción Retrasada. Las hembras Abastecidas fueron localizadas en sus lugares de descanso diurno, ofreciéndoseles 125g de una mezcla de sardinas y alimento para gatos cada dos días, desde al menos tres semanas antes de la concepción y hasta el fin de la temporada reproductiva. Las hembras de Reproducción atrasada sufrieron la remoción repetida de las crías alojadas en el marsupio, con el objeto de evaluar el costo reproductivo potencial en hembras que, aún cuando concivieron, sólo lactaron por un corto período. Todas las hembras fueron mensualmente pesadas y determinados el tamaño y sexo de las crías en el marsupio, removiendo además las crías de las hembras de Reproducción atrasada.

Tanto en Florida como en Venezuela la reproducción fue altamente estacional y la mayoría de las hembras (>90%) produjeron dos camadas al año. Para ambos sitios de estudio, el tamaño medio de camada (moda=7) no difirió significativamente entre la primera y segunda camada ni entre diferentes tratamientos. El intervalo entre el nacimiento de la primera y segunda camada fue similar para hembras Abastecidas y Control. Aunque la lactancia de la segunda camada fue una a dos semanas más larga que la lactancia de la primera camada en Florida y Venezuela, ésta fue similar entre hembras Abastecidas y Control. Crías machos o hembras no recivieron una inversión diferente durante la fase de adherencia al pezón, aunque las hembras Abastecidas mostraron mayor inversión materna, siendo sus crías más pesadas al destete que crías de hembras Control. Las hembras Abastecidas invirtieron más en crías machos al producir camadas con una proporción de sexos sesgada hacia los machos, y al producir una mayor proporción de camadas con este sesgo. La tendencia de producir más camadas sesgadas hacia crías macho fue observada en hembras en buena condición tanto Abastecidas como Control. En Florida, una sequía causó la interrupción de el programa de abastecimiento en 1985 y sólo algunas hembras recibieron su suplemento dietario, disminuyendo el porcentaje de camadas sesgadas hacia crías macho. Después del destete, una mayor proporción de machos hijos de madres Abastecidas fueron recapturados en comparación con machos hijos de madres Control. Esta diferencia fue significativa en Venezuela, pero no en Florida. Las hembras en las que se suprimió el estrés de la lactancia tendieron a vivir más y esta diferencia fue casi significativa en Venezuela. La mayor sobrevivencia de hembras de Reproducción Retrasada no fue biologicamente significativa ya que pocas vivieron más de dos años, y la longevidad media para todos los grupos fue menor que dos años. Las hembras de ambas especies parecen estar predispuestas a desarrollar un esfuerzo reproductivo máximo durante el año que sigue a su nacimiento.

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INTRODUCTION

In the last several decades, the evolution of life histories has been a major theoretical focus (reviewed by Stearns 1976, 1977, 1992). Despite the proliferation of theory in recent years, life history evolution remains poorly understood, chiefly because field data bearing on theory, or even on the sampling assumptions of the theory, are scarce. A crucial variable in many life history models considers how reproductive energy should be allotted between the sexes, and how this allocation should change with age and physical condition (Fisher 1930; Williams 1979; Trivers and Willard 1973; Charnov 1982).

Assuming there is a specific amount of reproductive effort available, how should it be allocated among male and female offspring? Darwin (1871) briefly considered this question, but the first real analysis was by Fisher (1930). He concluded that, because the total reproductive value of males equaled the total reproductive value of females in diploid organisms, parental expenditure should be equally divided between the sexes. Fisher was vague about what parental expenditure was, but it could be restated that total reproductive effort should be equally divided between males and females. Fisher's conclusions have since been more formally defined (Shaw and Mohler 1953; MacArthur 1965; Charnov 1975; Maynard Smith 1978).

It should be emphasized that Fisher's (1930) conclusions do not predict a one-to-one adult population sex ratio. If the reproductive effort to produce a single male differs from the reproductive effort to a produce a female, then the overall sex ratio at birth will be inversely related to their relative cost, preserving equal sexual expenditure. Furthermore, Fisher's conclusions do not make predictions about what individual parents would do (Williams 1979). It is a population prediction which might be fulfilled equally well if half the population

invested only in males and the other half only in females, or if each parent invested equally in males and females (Crow and Kimura 1970; Williams 1979).

A particularly interesting extension of Fisher's (1930) conclusions considers the effects of maternal condition (Trivers and Willard 1973; Reiter et al. 1978; Williams 1979) on sexual investment. Trivers and Willard (1973), using a polygynous mammal as their model animal, argued that if amount of parental investment affected the expected reproductive success of individual offspring, then females in good condition should tend to have sons whereas those in poor condition would tend to have daughters. Their reasoning was that because variance in male reproductive success is higher than female variance in polygynous species, the reproductive gain to a parent able to invest more than average would be greater if the offspring were male; while a parent able to invest less than average would maximize its benefits if its offspring were female. Alternatively, offspring sex ratios at birth could be equal but with greater investment in males than females (Reiter et al. 1978), or parental investment may be managed by altering litter size itself (Myers 1978). Even so, Williams (1979) demonstrated graphically that selection should favor mothers in poor condition who produce female-biased litters and females in good condition who produce male-biased litters.

In spite of abundant evidence supporting adaptive adjustment of sex ratios in invertebrates (Hamilton 1967; Charnov et al. 1981; Green et al. 1982), data are scant, inconclusive, and often contradictory for mammals. There is ample evidence that investment is greater in sons in many (Short 1970; Nordan et al. 1970; Glucksman 1974; Reiter et al. 1978; Clutton-Brock et al. 1981; Gosling 1986; Rutberg 1986; McFarland Symington 1987; van Schaik et al. 1989) but not all (Altmann 1980; Silk et al. 1981; Simpson and Simpson 1982; Silk 1983; van Schaik and Hrdy 1991) polygynous mammals. However, few mammalian species have shown significant deviation from either an adult sex ratio of parity, or litter sex ratios statistically distinguishable from a binomial distribution (Williams 1979; Charnov 1982; Clutton-Brock and Albon 1982). Williams (1979) found no support for any theory of adaptive sex ratio and concluded sex ratio was just another Mendelian character. However, most adaptive sex ratio theory says nothing about adult population-wide sex ratios. Furthermore, sex ratio at birth is immaterial to most theories, as sex ratio at independence is the important datum, especially in mammals where there is usually considerable parental care. More importantly, at least some mammals do seem to modify their sex ratios in response to changes in physical state or age. Maternal age and nutritional state have been correlated with both increasing and decreasing sex ratios in a variety of mammals (reviewed in Clutton-Brock and Iason 1986). In coypu (*Myocastor coypu*), for example, young females in superior body condition abort small, female-biased litters, whereas large litters and small, predominantly male litters are retained (Gosling 1986). Maternal stress has produced female biases in birth sex ratios in laboratory rats (Lane and Hyde 1973), mice (Geiringer 1961; Rivers and Crawford 1974), and golden hamsters (Labov et al. 1986). McClure (1981)

demonstrated that female wood rats, when food-stressed, discriminated against male offspring, thereby producing female-biased litters at weaning. In cervids, however, Verme (1969) reported male-biased sex ratios among fawns born to nutritionally deprived white-tailed deer (*Odocioleus virginianus*), whereas well-fed does produced more female fawns (Verme 1983). McGinley (1984) interpreted Verme's (1969) results to be consistent with the hypothesis of Trivers and Willard (1973), because small litter size increases a female's ability to invest more per individual offspring (but see Caley and Nudds 1987). In semidomesticated reindeer, females that were heavier at conception produced more sons (Kojola and Eloranta 1989). There are also several avian examples that support the theory of facultative manipulation of sex ratios (reviewed by Gowaty 1991).

While many recent papers report a tendency toward adjustments of offspring sex rations, no one has to our knowledge performed food supplementation experiments on free-ranging mammals to specifically examine sexual investment theory. While doing research on other mammalian species in Venezuela and Florida, we noted that "old-looking" female opossums tended to produce female-biased litters. We thus set out to analyze the effects of maternal age and resource availability on the distribution of sexual investment from birth until independence in the common (*Didelphis marsupialis*) and Virginian (*D. virginiana*) opossum. The initial results from Venezuela supported the theory (Austad and Sunquist 1986), but there were many details of the Venezuelan study, and none of the findings from the parallel study in Florida, that were published.

ACKNOWLEDGEMENTS

THE SPECIES SETTING

While the New World Didelphidae may be broken into three major extant lineages (Reig et al. 1987), we are concerned with the Didelphini, and in particular the species of the genus *Didelphis*, specifically the reproductive strategies of just two species, *D. virginiana* and *D. marsupialis*. When relevant, we will discuss data from studies of *D. albiventris*. Reviews of marsupial reproduction may be found in Collins (1973), Hunsaker (1977), Lee and Cockburn (1985), Tyndale-Biscoe and Renfree (1987), and Eisenberg (1988). Russell (1982) has reviewed the patterns of parental investment in marsupials. Reviews on the biology of *D. virginiana* are included in Gardner (1982) and Seidensticker et al. (1987).

Didelphis virginiana is distributed from upper New York State to central Costa Rica. *D. marsupialis* ranges from eastern Mexico to northeastern Argentina. *D. albiventris* has a fragmented distribution in northern South America, being generally found in premontane habitats but becoming the numerically dominant species in the more xeric areas of Brazil, and finally the sole species in southern Argentina to about 40° south latitude.

All three species have a similar morphology. They are the size of a domestic cat, but are rat-like in body form. The tail is very sparsely haired and prehensile. The ears are naked and show varying degrees of depigmentation. The female possesses a well-developed pouch or marsupium. After approximately five months of age, males are noticeably larger than females. Male weights in *D. virginiana* can reach 4.6 kg while females rarely attain 3.0 kg. The underfur of *D. albiventris* and *D. virginiana* can be well developed but *D. marsupialis*, with its lowland, tropical distribution, usually lacks a well-developed underfur. Basically all three species occupy similar ecological niches. The separation of *D. marsupialis* from *D. virginiana*, based on morphology and cytogenetic evidence, has been ably documented by Gardner (1973). Varejao and Valle (1982) present a similar analysis for distinguishing *D. albiventris* from *D. marsupialis*.

D. virginiana is probably the most recently derived of the three species. Subsequent research may indicate that *"albiventris"* is a composite of at least two species. It may be fairly stated that the tropical, lowland, mesic habitat adapted form, *D. marsupialis*, most nearly resembles the ancestor of all three recognized species.

THE ENVIRONMENTAL SETTING

Our research was carried out at two primary localities: (1) The Katharine Ordway Preserve-Carl S. Swisher Memorial Sanctuary, a 9,300 acre tract (37.6 km^2) administered jointly by the Florida Museum of Natural History and the

School of Forest Resources and Conservation (University of Florida), is located in northwestern Putnam County approximately 25 miles (40 km) east of Gainesville, Florida. The preserve consists of a habitat mosaic including a dark-water riverine system connecting with the St. Johns' River and sandhills containing depression ponds and lakes. The sandhills are dominated by longleaf pine (*Pinus palustris*) and turkey oak (*Quercus laevis*), while the dark-water system exhibits mesic adapted trees and shrubs typical of north Florida (*Quercus virginiana, Magnolia grandiflora, Nyssa sylvatica, Carya glabra,* and *Vaccinium* sp.). Descriptions of these habitats are included in Laesle (1942), Humphrey et al. (1985), and Franz and Hall (1990). Rainfall and correlated primary productivity are markedly seasonal; however, there is considerable between-year variability in the timing and extent of the rains. In an average year heavy rains should occur in December-January and again from May to September. Mean annual rainfall is 135 cm (National Oceanic and Atmospheric Administration 1960-1990), and about 60 percent of that falls between May and September. Temperature variation is marked with cool months achieving freezing temperatures (<32°F or 0°C) on some days from December to March.

(2) Hato Masaguaral, a working cattle ranch owned by Sr. Tomas Blohm in the state of Guarico, Venezuela. This location is also a habitat mosaic located at 8°34'N and 67°35'W. The protected area consists of approximately 3,000 ha and includes tree islands (matas), low lying wet areas (esteros), and sandhills (medanos). Open grasslands with scattered palms and low stature forests are the dominant habitats. The vegetation and related drainage patterns have been described by Troth (1979). The area is characterized by a strongly seasonal climate divided generally into six dry months (Nov.-Apr.) and six wet months (May-Oct.). Annual precipitation averages 1478 ± 66 mm (August 1984) and low lying areas are commonly flooded during the wet season. Temperature varies only slightly during the year; the average monthly maximum and minimum temperature is 35.2°C and 21.2°C, respectively (Troth 1979). Although the temperature variation is not as profound as that found in north Florida there is a distinct seasonal variation in primary productivity. Rainfall is pronounced from May to October but a drought occurs from December to April. As Robinson (1986) has documented, rainfall synchronizes the primary productivity of this tropical ecosystem. The original works on *D. marsupialis* in Venezuela are summarized in O'Connell (1979) and August (1984).

In summary, we studied two species of didelphids in two strongly seasonal environments. While one species, *D. virginiana*, is adapted to withstand rather cool temperatures, both species have been able to adapt with respect to pulsed primary productivity and to strongly seasonal environments.

EXPERIMENTAL DESIGN AND METHODS

Field work was initiated at both locations in 1982 and efforts in 1983 focused on marking as many pouch young as possible, thus ensuring that those female opossums used in the experiment in 1984 were of known age as was their reproductive status. In Florida, study animals were captured in Tomahawk live traps set at approximately 0.4 km intervals along a major flow-through creek system on the property. Both sides of the creek system were trapped and the total number of trap sites was 50. In Venezuela, a total of 62 Tomahawk live traps was set within an area measuring about four square kilometers; traps were set at intervals of 0.25 km along six trap lines radiating from the ranch compound. At both locations, trapping was conducted for five to seven consecutive days each month. Most study animals were captured and recaptured during these routine sessions, although for a few individuals it was sometimes necessary to set traps just outside their den in order to recapture them; multiple traps were typically set around dens at the time the young were to be weaned.

In order to study the reproductive strategies of *D. marsupialis* and *D. virginiana* we developed the following experimental protocol (see also Austad and Sunquist 1986). At each study site three groups of adult virgin females (10 each) were trapped prior to the breeding season, weighed, measured, and fitted with a radio collar. Radio telemetry enabled us to precisely locate females, retrap them, and provision them at set intervals. An examination of the female's pouch at monthly intervals enabled us to evaluate her reproductive condition, to age and sex the young, and to toe clip and monitor the growth of pouch young. The three groups of females were designated as follows: (1) Controls [C] were those that were monitored only to gather data on the sex, growth, and survivorship of their offspring and their physical condition; (2) Provisioned [p] were those from whom the same data were collected but whose diet was supplemented with 125 gms of catfood and fish at 2-day intervals. Provisioning was initiated from at least three to four weeks prior to conception (based on the seasonality previously established) and continued until the end of the breeding season; Delayed Reproductives [DR] were those whose embryonic young were removed repeatedly from the pouch. Females reenter estrus within two to eight days following loss of young (Gardner 1982). Adding the gestation period of 13 days to the time of return to estrus indicates a female could potentially have a new litter every two to three weeks. By trapping monthly we were able to remove the next set of pouch young when they were less than two weeks old. The delayed reproductive treatment was included to yield information on the potential reproductive cost to females who conceived, but lactated for only a brief interval.

Definitions and Criteria

Date of birth.-- The ontogeny of pouch young has been well documented in *D. virginiana* and the timing of developmental stages appears to be reasonably fixed so that from the appearance of certain morphological characteristics young can be aged to within three days for their first month in the pouch (Reynolds 1952; Gardner 1982). The date of birth was then set by backdating from the estimated age of the young. This method was also used to age young of *D. marsupialis*. In addition, the birth date of many litters was known to have occurred within a 1- to 3-day period based on repeated examination of individual females at short intervals.

Length of lactation.-- The length of lactation was measured as the number of days from the birth date of a litter until lactation had ceased. The latter was judged to have occurred when milk could no longer be expressed from the teat. A reduction in mammary development (teat and tissue) usually preceded the cessation of milk production. Repeated captures of females at the estimated time of weaning facilitated regular examinations. Weaning of young was thought to occur just prior to the end of lactation.

Longevity.-- Longevity was measured as the number of days from birth to death only for those individuals whose birth and death dates were reliably known.

Survivorship.-- Annual survivorship was measured as the proportion of females who were known to have survived into their second year of reproduction. This method essentially represents the minimum number known alive as those few individuals who disappeared or whose fate was not known were excluded from the analysis.

Home range.-- Home range sizes of females were computed using the minimum convex polygon method (Mohr 1947). Range sizes were calculated for individuals who were monitored for three months or longer. Animals were occasionally located at night, but most locations represent daytime rest sites, thus range sizes are likely to underrepresent actual area used. Provisioned females were located at two-day intervals for at least eight months per year, or two to three times more often than females in the Control and Delayed Reproductive groups.

Growth rate.-- Growth rates of pouch young were determined from animals who were removed from females in the Delayed Reproductive treatment, and from young who became temporarily detached from the teat during marking or examination of the female. The weight (mass) of young in the pouch was reliably predicted from tail length for opossums in Venezuela and Florida.

Lifetime reproductive output.-- Lifetime reproductive output of females was measured as the total number of litters an individual was known to have had and that she subsequently reared to at least 70 days of age. The 70 days represents the youngest age at which an opossum was found to have survived on its own, although most young of this age would probably not survive. Control and

Provisioned females were lumped since there was no significant differences in their longevity or reproductive parameters.

Recapture rate of young.-- Recapture rate of offspring was determined only for young who were marked in the pouch and subsequently captured when independent.   The age of independence was set at 100-110 days, which also coincides with the length of lactation.

Some Natural History Data for *Didelphis*

The natural history of *Didelphis* has received several recent reviews (Hunsaker 1977; Gardner 1982; Seidensticker et al. 1987).   The young of *Didelphis* are born after a 13- to 14-day gestation period, and upon emerging from the birth canal climb unassisted to the pouch whereupon they attach to a teat. During their development we can distinguish two phases prior to weaning. A phase of obligate teat attachment where the young remain with the nipple constantly in the mouth until approximately 60 days of age. Then follows the so-called nest phase where the young are left in a nest while the female often forages alone and returns each day to suckle the young.   The nest phase begins to terminate with weaning when the young commence to forage either by accompanying the mother or as a single individual.   Weaning occurs at approximately 100 days of age. Since there is an obligate teat attachment phase the maximum number of young is fixed at 13 in *Didelphis*, since this is the average teat number. Shortly after obtaining independence the young gradually disperse. The dispersal phase may be brief or extended, whereupon they establish a more or less permanent home range.   Wright (1989) noted that surviving female offspring may remain within their mother's home range for months while male siblings begin to expand their range within a month or so of independence (see also Gillette 1980). Although some workers report *Didelphis* to be nomadic, in our experience the study populations in Florida and Venezuela showed rather stable home ranges as adults unless there was some environmental change (e.g., drought) that forced them to switch their foraging localities (Sunquist et al. 1987).

Upon attaining sexual maturity in the year after their birth the males range widely during the breeding season, apparently seeking out females with which to mate (Ryser 1992). A male will guard and copulate with a female during her estrous period.   Males are known to fight severely among themselves contesting over a female. The female requires a secluded denning site for rearing her young, and a suitable foraging area.   Once a female becomes established she tends to remain, utilizing the same home range and denning sites throughout her entire period of reproduction. In both species, females tend to produce on the average two litters in the year following their birth. Rarely, does a female attempt reproduction in the third year. There is reason to believe that the females, even under optimal conditions, become reproductively senescent when past 28 months

of age (see Jurgelski 1974). If a female should lose her litter before weaning she will come into estrus within 2 to 8 days, and upon conception attempt another reproductive effort. Normally it takes a female slightly over 100 days to raise a litter, and thus only two litters are possible in a seasonal environment during the year following her attainment of sexual maturity. It is possible then to distinguish two age classes of young animals which we term "first-litter animals" and "second-litter animals." Given the two birth peaks (Fig. 1), it will be noted that the litters from the two birth pulses may have different survival advantages. It will be appreciated that those young deriving from the second litter will attain sexual maturity in the following year at a smaller body size than their half-siblings who were born following the first conception of a reproductive year. This is an important consideration in the analysis of our data. In the following presentation we explore several issues. Since a female has 13 teats, we ask the question, why does the mean litter size average around seven young? We wondered what effect provisioning their mother would have on the development of young. Furthermore, we investigated the consequences of preventing a female from undertaking a long lactation. Would such a female attempt to increase her litter size on subsequent reproductive attempts? Would such a female have an increased lifespan? Finally, we tried to assess what effect maternal condition had on litter size and the weaned weight of young.

Our research on the Florida species was more difficult than was the case in Venezuela. This derives from several factors. First, the population in Florida existed at a lower density, and trapability of entire litters at the time of dispersal was more difficult than in Venezuela. A drought in the spring of 1985 caused most of our Florida females to shift to areas of permanent water. In some cases, females were inaccessible to us in swamps. This disrupted the feeding program and did not allow us to replicate the 1984 manipulations. Thus, in the presentation of results sometimes we refer only to Venezuela where all of the experimental procedures were replicated in the second year.

RESULTS

For both study areas the maximum longevity of females was about 1,000 days but mean longevity was less than two years. The earliest recorded age at first reproduction for females was about 245 days in Florida and 172 days in Venezuela. The seasonal onset of reproduction in Florida is much sharper than in Venezuela (see Figure 1).

The study site in Venezuela has a pulsed productivity, but during the rainy season has a higher productivity compared to the sandhills of north-central Florida. As a result, densities of *Didelphis* were consistently higher in Venezuela and home ranges smaller than was the case in Florida (O'Connell 1979, August 1984, Sunquist et al. 1987, Ryser 1992).

REPRODUCTIVE SEASONALITY--FLORIDA
(1983-1988, N = 304)

NUMBER OF LITTERS BORN

REPRODUCTIVE SEASONALITY--VENEZUELA
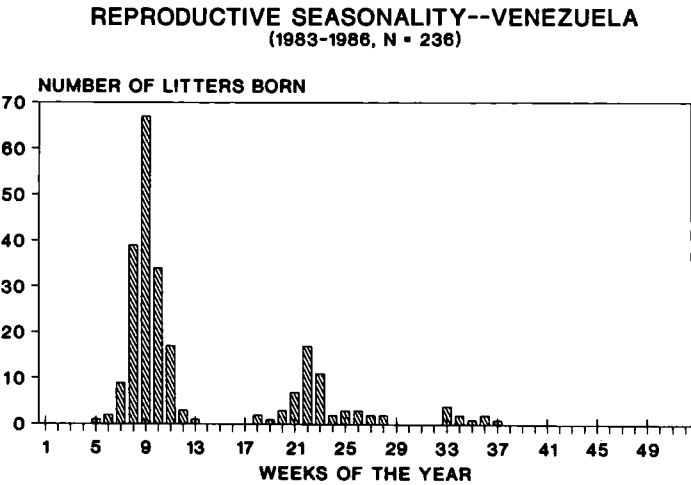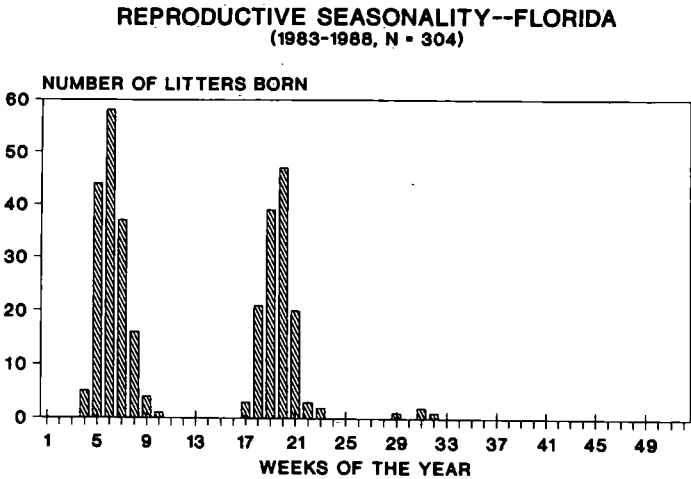### (1983-1986, N = 236)

NUMBER OF LITTERS BORN

Figure 1. Reproductive seasonality of opossums in Florida and Venezuela.

Mortality sources differed between Venezuela and Florida. In Florida, adult females were killed by bobcats (*Felis rufus*, n=4); great horned owls (*Bubo virginianus*, n=3); alligators (*Alligator mississippiensis*, n=2); foxes (*Urocyon cinereoargenteus*, n=2); and humans (n=3). In Venezuela confirmed predation included the ocelot (*Felis pardalis*); boa (*Constrictor constrictor*); caiman (*Caiman crocodylus*), but above all the screw worm (*Callitroga* sp.) inflicted an unrelenting morality in the llanos (Wright 1989, Sunquist unpubl.).

First, let us place the reproductive performance of the two species in perspective. Here we include additional data from Venezuela and Florida, since we had several parallel studies going on over the years and accumulated a great deal of data for non-manipulated females. In Florida, most females produced only two litters and the mean litter size was seven (Table 1). At the onset of the first reproductive period, 96.8% of adult females had young in the pouch (n=185). Of those females that did not produce, four were very old and did not attempt reproduction in their third year. At least 91.1% of the females in the population gave birth to a second litter (n=156). Of the 14 that did not reproduce, 8 were old individuals. Some females attempted a third litter (7.4%; n=68). Only one female successfully reared three litters in a given calendar year. In Florida, none of the females attempted to have young in the same year as their birth. The age of first reproduction by a female in Florida varied from 245 to 345 days depending on whether she was a first- or second- litter female.

In Venezuela, at the onset of the first reproductive period, 93% of the females (n=200 of 215) had pouch young. Of the 15 without young in the pouch, nine were females weighing less than 1 kg (very young) and four were judged to be old. In the second attempt at reproduction, 97% of the females had young in the pouch (n=59). The two females without young were judged to be old. As in Florida, 7.4% of the females in Venezuela attempted to raise a third litter (n=136). Furthermore, in Venezuela, 7% of the females (n=84) had young in the same year as their birth. Age at first reproduction in Venezuela varied from 172 to 345 days. As in Florida, only one female in Venezuela successfully reared three litters in a single calendar year. The proportion of females in the population which were breeding are the minimum estimates since some females may have had a litter but were not recaptured to confirm.

In both habitats, reproduction is highly seasonal. Figure 1 summarizes the time of birth for the first and second litters in Florida and Venezuela. In Florida, the birth peaks occur in the second week of February and the last week of May. In Venezuela, the birth peaks are about three weeks later than in Florida. The figure indicates also that a minority of females will attempt to rear a third litter.

Our two treatment groups did not differ in home range size from the controls; this result held for both Florida and Venezuela (Table 2). The extent of the home range does not, however, reflect activity, and we did not monitor movements on an hourly basis during the night. Hence, the control groups may well have ranged more within their home range than the treatment groups. It

Table 1. Litter size (± SE) of non-manipulated female *Didelphis*.

Location	1st Litter	2nd Litter	t-test
FLORIDA (1983-88)	6.68 ± 0.10 (n = 145)[a]	6.57 ± 0.20 (n = 120)[a]	$p = 0.607$
VENEZUELA (1983-86)	7.38 ± 0.16 (n = 87)	7.95 ± 0.46 (n = 40)	$p = 0.252$

[a]Includes data collected by D. Wright in 1987-88.

Table 2. Home range size analysis of female *Didelphis*.

Location	Treatments			Test
	C	p	DR	
Home range size (ha ± SE)				
VENEZUELA	34.0 ± 5.1 (n = 14)	29.3 ± 4.9 (n = 15)	38.1 ± 5.5 (n = 12)	ANOVA $p > 0.05$
FLORIDA	58.7 ± 9.6 (n = 18)	84.7 ± 9.9 (n = 17)	73.1 ± 6.7 (n = 6)	t-test, C vs. p $p = 0.056$
Months monitored				
VENEZUELA	9.0 (range 6-18)	8.5 (5-16)	12.1 (5-18)	
FLORIDA	9.2 (3-18)	9.6 (3-23)	11.8 (8-16)	

should be noted that the Venezuela population showed consistently smaller home ranges, reflecting the higher productivity of the Venezuelan habitat when compared with the sandhills of Florida.

The temporal patterning of reproduction is summarized in Table 3. The interval between the birth of the first and second litters was of similar duration for provisional and control females. The difference in interbirth interval was not significant for Venezuela but approaches it for Florida. The duration of lactation for the first and second litters were approximately the same for the provisioned and the control females at both locations. However, the length of lactation for the second litter was 1-2 weeks longer. A comparison of the duration of lactation for the first litter and the interval between the birth of first and second litters indicates that females were lactating and pregnant at the same time.

There was a significant difference in the weight of a female at first breeding, depending on whether she was born in the first or second litter of the previous year. This difference was most pronounced in the Venezuelan population. First-litter females weighed on average 1.63 kg at first conception, while second- litter females weighed 1.17 kg (see Table 4). In Venezuela second-litter females lactated for a longer period of time during the rearing of their first litter than did the older cohort (see Table 5). When we examined the effort of provisioning it was clear that the smaller second-litter females could rear a litter more quickly than comparable aged controls. Thus, provisioning had a positive effect (see Table 6).

During the teat-attachment phase there was an occasional loss of young. The number of young lost from a litter varied from one to four (mode=1) and there was no apparent differential by sex. All losses occurred when the young were from 17 to 50 days of age. There were twice as many reductions in provisioned versus control litters in both Venezuela and Florida but the differences were not significant (Table 7).

The mean litter size for both Florida and Venezuela did not differ significantly between the first and second litters born (Table 1), nor was there any effect of treatment on litter size when provisioned animals were compared with controls (see Table 8). When, for individual females, we examined successive litters, that is change in litter size from first to second as a function of treatment, those females that were provisioned tended to increase their litter size slightly in both Venezuela and Florida (Table 9). There was also a suggestion in the Venezuelan population that the experimental females that were not allowed to reproduce (DR's) attempted larger litter sizes on successive conceptions until the end of the reproductive season when litter size declined.

Figures 2 and 3 summarize the growth data for pouch young during the teat-attachment phase. There appears to be no differential investment in male or female offspring during the first 60 days of lactation. Regression analysis indicated no significant difference between males and females in slope (Venezuela: $t=0.963$, 1 d.f., $p=0.3359$; Florida: $t=-0.985$, 1 d.f., $p=0.3260$). It will be appreciated that tail length is a very good predictor of body weight for young in

Table 3. Temporal pattern of reproduction.

Location	Treatments		
	C	p	t-test
Interval (days ± SD) between birth of 1st and 2nd litter			
VENEZUELA	97.7 ± 8.4 (n = 28)	95.0 ± 4.7 (n = 14)	$p > 0.20$
FLORIDA	97.3 ± 5.0 (n = 64)[a]	94.2 ± 7.1 (n = 12)	$p > 0.05 < 0.10$
Length of lactation (days ± SD) for 1st litter			
VENEZUELA	93.2 ± 5.5 (n = 18)	93.1 ± 2.8 (n = 14)	$p > 0.90$
FLORIDA	94.1 ± 5.0 (n = 15)	92.0 ± 4.1 (n = 6)	$p > 0.70$
Length of lactation (days ± SD) for 2nd litter			
VENEZUELA	105.2 ± 6.5 (n = 9)	107.3 ± 6.5 (n = 7)	$p > 0.50$
FLORIDA	102.5 ± 9.8 (n = 17)[a]	99.3 ± 7.8 (n = 7)	$p > 0.40$

[a] Includes data collected by D. Wright in 1987-88.

Table 4. Weight (kg ± SD) of control females at first breeding as a function of age.

Location	1st Litter	2nd Litter	t-test
VENEZUELA	1.63 ± 0.16 (n = 23)	1.17 ± 0.18 (n = 17)	$p < 0.005$
FLORIDA	1.87 ± 0.17 (n = 18)	1.26 ± 0.46 (n = 16)	$p < 0.05$

Table 5. Length of lactation (days $\pm$ SD) by 1st and 2nd litter control females for 1st litter of year.

Location	1st Litter Females	2nd Litter Females	t-test
VENEZUELA	92.5 $\pm$ 5.6 (n = 11)	97.3 $\pm$ 5.0 (n = 4)	$p > 0.05 < 0.1$

Table 6. Length of lactation (days $\pm$ SD) by 2nd litter females for 1st litter of year.

Location	Treatments		t-test
	C	p	
VENEZUELA	97.3 $\pm$ 5.0 (n = 4)	93.7 $\pm$ 1.4 (n = 6)	$p > 0.05 < 0.1$

Table 7. Number of litters in which a size reduction occurred as a function of treatment.

Location	Treatments		Fisher's exact test
	C	p	
VENEZUELA	5/30	10/30	$p = 0.116$
FLORIDA	1/15	3/13	$p = 0.356$

Table 8. Litter size and sex ratio analysis.

	VENEZUELA Treatment		FLORIDA Treatment	
	C	p	C	p
Litter size (± SD) at start of lactation	7.50 ± 2.02 (n = 36)	7.75 ± 2.01 (n = 36)	6.80 ± 1.53 (n = 26)	7.31 ± 1.81 (n = 29)
Litter size at weaning	7.14 ± 2.15 (n = 22)	7.14 ± 1.70 (n = 21)	6.56 ± 1.81 (n = 9)	7.17 ± 2.16 (n = 6)
Sex ratio (M:F) at start	132:138 (n = 36)	158:121[a] (n = 36)	81:70 (n = 23)	103:81[a] (n = 25)
Sex ratio at weaning	75:82 (n = 22)	85:65[b] (n = 21)	28:31 (n = 9)	25:18 (n = 6)
Number of male biased litters	18/31	20/32	13/23	12/19
Number of litters with equal sex ratios	5	4	0	6

[a] $p < 0.05$, binomial test
[b] $p > 0.05 < 0.1$

the pouch. On the other hand, during the nest phase the young males begin to increase in size relative to their sibling females, and at weaning young males average about 3 to 10 gm heavier than females. When we examined the control versus experimental litters for both Venezuela and Florida, the weight at weaning of young from provisioned females was significantly higher (see Table 10).

As reported by Austad and Sunquist (1986), one effect of provisioning is to bias a female's litter towards a larger percentage of males (Table 8). This is in part a function of the condition of the female not only at the time of conception but also at the end of lactation, which would affect the second litter. Thus it is not unlikely that females producing their first litter will on average be in better condition than when they produce the second litter so we would expect a higher percentage of first litters to be male biased. In general, there were more litters that were male biased for provisioned females compared to controls. For example, in Florida in 1984, 11 of 13 litters were male biased ($p < 0.05$), whereas in 1985, the year of the drought, only one of six litters was male biased

Table 9. Successive litter size.

	Treatments		
Location	C	*p*	DR
VENEZUELA	(n = 13)	(n = 14)	(n = 14)
Litter size increased			
from 1st to 2nd	5/13	11/14	11/14
Decreased	6/13	2/14	0/14
No change	2/13	1/14	3/14
FLORIDA	(n = 9)	(n = 10)	(n = 7)
Litter size increased			
from 1st to 2nd	2/9	5/10	4/7
Decreased	2/9	4/10	2/7
No change	5/9	1/10	1/7

Fisher's exact test, comparing the association of litter size change by treatment.
Venezuela: C versus *p*, *p* = 0.055; Florida: C versus *p*, *p* = 0.657.

Table 10. Weight (g ± SD) of young *Didelphis* at weaning.

	Treatments		
Location	C	*p*	*t*-test
First litter			
VENEZUELA	91.7 ± 17.9	151.3 ± 33.0	$p < 0.0005$
	(n = 29)	(n = 15)	
FLORIDA	102.9 ± 1.8	153.0 ± 12.4	$p < 0.0004$
	(n = 5)	(n = 5)	
Second litter			
VENEZUELA	81.8 ± 21.3	128.2 ± 33.7	$p < 0.0005$
	(n = 14)	(n = 24)	

OPOSSUM GROWTH DATA
FEMALES (VENEZUELA)

$\log Y = 1.5719 \log X - 3.4795$

$r^2 = .9938$

$N = 281$

LOG BODY WEIGHT (g)

LOG TAIL LENGTH (mm)

OPOSSUM GROWTH DATA
MALES (VENEZUELA)

$\log Y = 1.5822 \log X - 3.4949$

$r^2 = .9931$

$N = 302$

LOG BODY WEIGHT (g)

LOG TAIL LENGTH (mm)
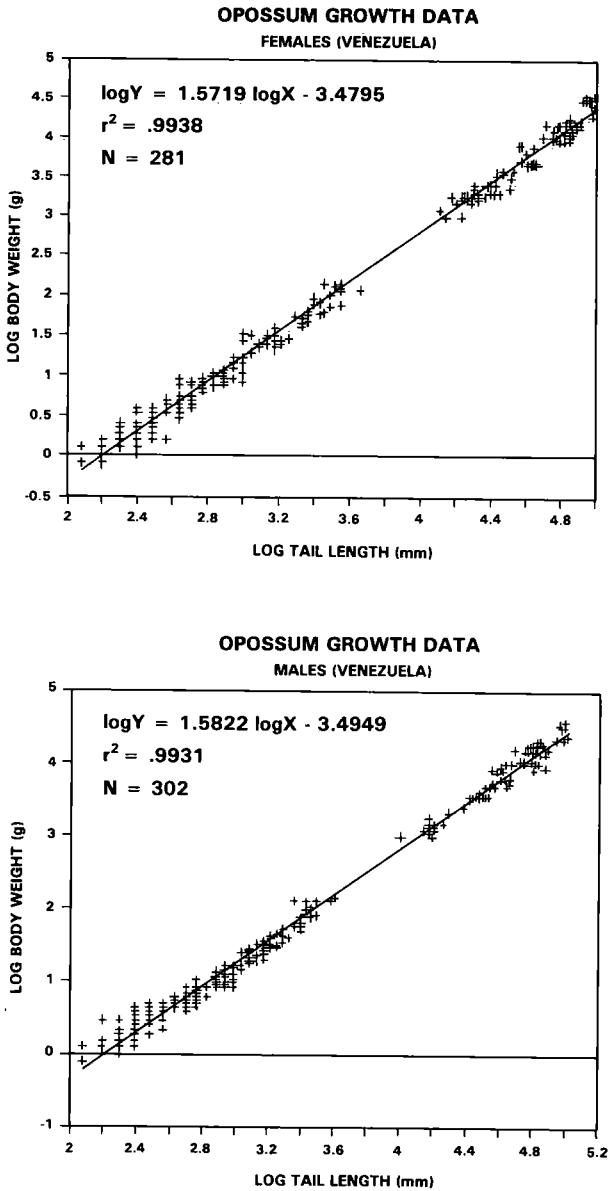
Figure 2. Body weight (mass) of female and male opossum young in the pouch as predicted by tail length (Venezuela).

OPOSSUM GROWTH DATA

FEMALES (FLORIDA)

logY = 1.4817 logX - 2.4648
r^2 = .9935
N = 86

LOG BODY WEIGHT (g)

LOG TAIL LENGTH (mm)

OPOSSUM GROWTH DATA

MALES (FLORIDA)

logY = 1.4615 logX - 2.3815
r^2 = .9918
N = 71
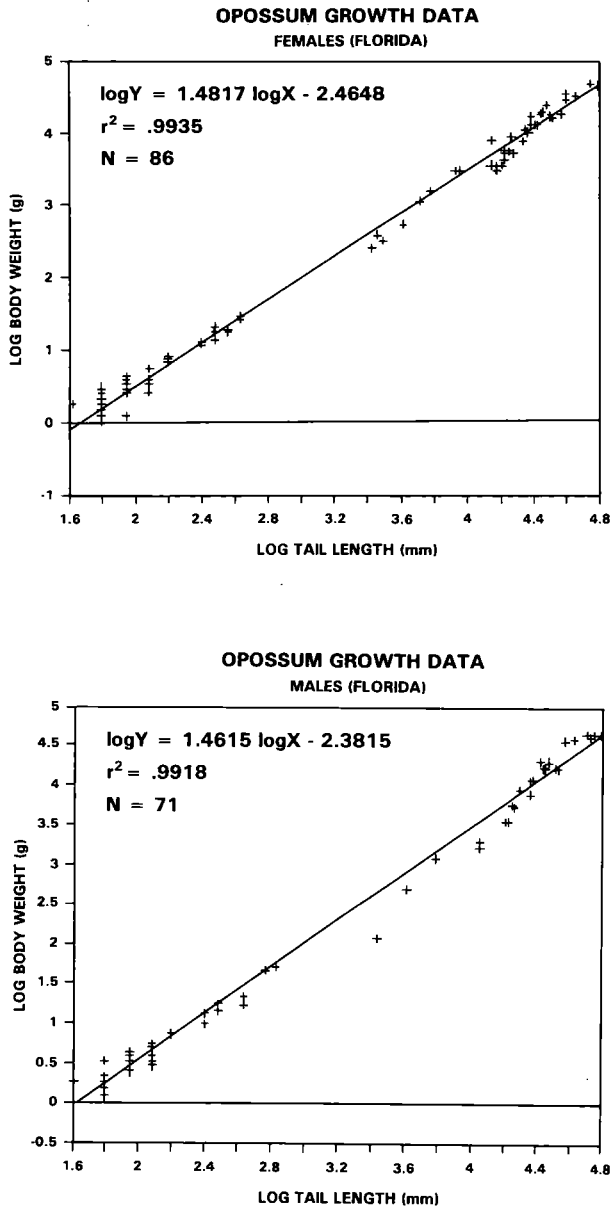
LOG BODY WEIGHT (g)

LOG TAIL LENGTH (mm)

Figure 3. Body weight (mass) of female and male opossum young in the pouch as predicted by tail length (Florida).

(see Table 8). The same trend was evident for provisioned females in Venezuela where 20 of 32 litters were male biased ($p > 0.07 < 0.08$). Females, whether provisioned or not, that are in good condition throughout lactation produce male-biased litters. We can look at these data by comparing control and provision females and looking at females in both groups that gained weight over the interval of lactation. Some control females, of course, gained weight even though they were not provisioned. An inspection of Table 11 indicates that regardless of the treatment, those females that showed weight gains over the course of lactation tended to bias their litters towards males. Of course, the provisioned females were more predictable in terms of biasing the litter to males, by producing not only a greater mass of young at weaning, but also increasing their weight throughout the lactation period. The data for Florida are suggestive of the same trends for Venezuela but we had a smaller sample size.

In Table 8 we examined the litter size and sex ratio for Venezuela and Florida. While there was no difference between control and provisioned females with respect to litter size, the sex ratio was definitely biased toward males at the start of lactation and at the end of lactation for the provisioned females. If we perform a similar analysis comparing first litter with second litter, again we find in the second litter that provisioned females biased their litters toward males (see Table 12).

The sex ratio of litters of older, that is second-year females, in Venezuela was biased toward females (69:95, n=22, $p < 0.04$). Similarly, the proportion of litters that were female biased (14 of 19) was significantly different ($p=0.0318$) from that expected by chance. In Florida, however, there was no sex ratio bias in litters of second-year females (37:35, n=10, $p > 0.4$) or in the number of biased litters (7 of 10, $p=0.172$).

The survivorship of young as a function of treatment is examined in Table 13. For the Venezuelan data, male offspring of provisioned females were recaptured post-weaning significantly more often than males from control litters. The comparison was not significant for the Florida data. We may examine the effect of our treatment on the survivorship of reproducing females. In Table 14 we present data for the three treatment groups suggesting that females who were denied the stress of lactation (DR) tended to survive longer. The differences in survivorship approaches significance for Venezuela. In Table 15 we present "longevity" data based on days from birth until the animal died, thus do not represent calendar ages. These data indicate that in Venezuela, at least, those females that were experiencing delayed reproduction through successive loss of litters tended to live longer than the control females, although the differences are not significant.

Lifetime reproductive effort by females of both species is portrayed in Table 16. The results for Florida and Venezuela are comparable. Most females bear from one to two litters in their lifetime (75% Florida; 89% Venezuela). It

Table 11. Effect of female condition on sex ratio of litters by treatment.

Weight gain or loss between initiation of lactation for 1st and 2nd litters		Number of litters with biased sex ratios		Fisher's exact test
		Male	Female	
VENEZUELA				
Controls	Weight increased	11	3	$p < 0.004$
	Weight decreased	0	5	
Provisioned	Weight increased	10	3	$p < 0.04$
	Weight decreased	1	4	
FLORIDA				
Controls	Weight increased	5	1	$p > 0.20$
	Weight decreased	1	2	
Provisioned	Weight increased	4	2	$p < 0.08$
	Weight decreased	0	4	

Table 12. Litter size and sex ratio analysis by year and 1st and 2nd litters.

Location		Litter size	Sex ratio (M:F)	n
VENEZUELA				
Controls	1984 - 1st litter	7.2	40:52	10
	1984 - 2nd litter	6.7	32:28	9
	1985 - 1st litter	8.4	40:52	11
	1985 - 2nd litter	7.7	20:26	6
Provisioned	1984 - 1st litter	6.1	32:29	10
	1984 - 2nd litter	9.0	45:36	9
	1985 - 1st litter	7.8	49:29	10
	1985 - 2nd litter	8.4	32:27	7
FLORIDA				
Controls	1984 - 1st litter	7.2	19:24	6
	1984 - 2nd litter	7.0	8:6	4
	1985 - 1st litter	6.1	35:26	10
	1985 - 2nd litter	7.6	19:14	5
Provisioned	1984 - 1st litter	7.6	45:31	11
	1984 - 2nd litter	6.7	26:14	6
	1985 - 1st litter	7.7	22:24	6
	1985 - 2nd litter	7.3	7:8	6

Table 13. Recapture rate of independent young.

Location	Treatments		2-sample binomial test
	C	p	
VENEZUELA			
Males	16/71	30/85	$p < 0.05$
Females	20/82	23/70	$p > 0.10$
FLORIDA			
Males	13/29	11/33	$p > 0.10$
Females	18/36	19/34	$p > 0.30$

Table 14. Annual survivorship of female *Didelphis*.

Location	Treatments			Chi-square test
	C	p	DR	
VENEZUELA				$p > 0.05 < 0.1$
Alive	3	1	6	
Dead	15	9	6	
% Alive	17	10	50	
FLORIDA				$p > 0.9$
Alive	6	5	4	
Dead	17	16	9	
% Alive	26	24	31	

Table 15. Longevity (days ± SD) of female *Didelphis*.

Location	Treatments			Test
	C	p	DR	
VENEZUELA	554.4 ± 135.4	506.0 ± 80.8	579.3 ± 100.0	ANOVA
	(n = 16)	(n = 11)	(n = 12)	$p > 0.25$
FLORIDA	559.2 ± 187.3	483.2 ± 76.6	404.7 ± 137.5	*t*-test, C vs. DR
	(n = 12)	(n = 14)	(n = 9)	$p = 0.062$

Table 16. Lifetime reproductive output of female *Didelphis*.

Number of litters reared to 70 days of age	Number of females	
	VENEZUELA (n = 37)	FLORIDA (n = 39)
1	16	12
2	17	17
3	4	6
4	0	3
5	0	1

Table 17. Litter size of delayed reproductives.

Location	Litter size		
	1st litter	2nd litter	3rd litter
VENEZUELA	6.286 (n = 14)	8.214 (n = 14)	8.643 (n = 14)
FLORIDA	6.143 (n = 7)	6.143 (n = 7)	5.714 (n = 7)

Scheffe's test - significant difference between 1st vs. 2nd litter size in Venezuela ($p < 0.05$); 2nd not different from 3rd.
No significant difference in Florida.

would appear that these two species are geared to perform a maximum reproductive effort in the year following their birth.

Females subjected to a reduced lactation time exhibit a tendency on subsequent pregnancies to increase their litter size and then decline in litter size, perhaps due to ovarian senescence. This was evident only in the Venezuelan population (Table 17).

DISCUSSION

We have presented the study of two didelphid species in two rather different environments, although both study sites exhibit seasonal pulses in primary productivity. Both habitats have experienced dramatic changes in vegetative cover during the last 5,000 years deriving from global climatic changes, and to some extent the opossums can be viewed as "pioneers."

The ultimate puzzle is how the female regulates her litter size and the sex ratio. Male opossums appear to have a straightforward reproductive strategy--mate with as many females as possible (Ryser 1992). Females have a different set of priorities--mate with a strong, dominant male; seek and maintain a secure den site in an area which will sustain her through the rearing of her two litters. We have by means of some simple field experiments attempted to clarify some of the issues.

It would appear that in at least two species of *Didelphis* the female has some control over her litter size and the sex ratio of each litter. The exact mechanisms whereby she exercises such control are poorly understood.

A female who has an enhanced food supply will bias her litter towards males. The young of provisioned females achieve higher weaning weights when compared with controls and perhaps a better survivorship potential. Females denied a prolonged lactation will conceive periodically after the loss of the young and often will increase their litter size until age and physiological senescence take their toll. The foregoing conclusion suggest a trade-off between aging and nutritional plane. This is further suggested by an examination of weaning weights of first- and second-litter young (Table 10). Lactation was one to two weeks longer for the second litter, but young were significantly lighter at weaning than the first litter. One should remember that the female *Didelphis* in the year following her birth in seasonal environments has only about 400 days in which to successfully reproduce. Recall that in such seasonal environments a female must invest about 228 days in reproducing two litters. The time frame is tight and pregnancy commences before lactation ceases, a phenomenon also discussed by Kiltie (1988) for other vertebrates.

Reproducing a surplus of males when she is in good physical condition can enhance the spread of 50% of the female's genetic material. The males are polygynous and, although requiring extra energy for their growth, are certain to

inseminate many females should they survive to adulthood (Austad and Sunquist 1986).

These experiments suggest fruitful avenues for future research. *Didelphis* is an excellent model. Females are easily trapped and have a finite and limited opportunity to reproduce.

Didelphis albiventris has not been studied in the same detail as have *D. marsupialis* and *D. virginiana*. What information we do have indicates that it is a habitat generalist with feeding habits quite similar to other species in the genus. In Uruguay, females have an average litter size of 9.4, while farther to the north in Argentina the mean number of young per litter was recorded at 7.1 (Barlow 1965). In seasonal environments, reproduction tends to be highly pulsed and an average of two litters are produced per female in their breeding year. Once again, the seasonality of rainfall and primary productivity appears to regulate the timing of reproduction (Barlow 1965; Crespo 1982; Cerqueira 1984). In captive studies, Cerqueira (1984) found that litter size was maximal in heavier females. Litter size for *Didelphis virginiana* and *D. marsupialis* appears to vary somewhat with latitude. For both species larger litters are born in populations that occur at higher latitudes than populations occurring nearer the equator (O'Connell 1979). In this study provisioned females had slightly larger litters than controls.

A female in excellent physical condition tends to wean young at a higher body weight than females in poorer condition. Weight at weaning may be enhanced by provisioning the lactating female. Provisioned females tend to have litters biased toward males, but control females that maintain excellent body condition also produce litters biased toward the male sex. While there is no apparent difference in the growth rate of pouch young when the sexes are compared during the teat attachment phase, young males are weaned at a slightly heavier weight than their sister siblings. The mechanism whereby a female regulates the size of her litter and the sex bias in the litter is not known. We do know, however, that for *Didelphis virginiana* the number of ova shed exceeds the number of young born and usually the female gives birth to more young than she can possibly rear. The maximum number of young born that has been recorded is 25 and the maximum young that reached the pouch, 21; but the largest permissible litter size is just 13 given the obligate teat attachment phase and the mean number of 13 teats per female (Reynolds 1952; Hartman 1952).

Our field data indicate that on the average a female of either species is able to rear just two litters a year. Less seasonal environments may permit the rearing of a third litter by a larger percentage of females than we found in the Venezuela and Florida study areas. In accordance with laboratory data, females appear to go through one year of reproduction, usually in the year following their birth (Jurgelski 1974). Although some of our females which were delayed in reproduction attempted to produce litters throughout the reproductive season, they were, of course, denied the opportunity to rear a litter. Upon losing her litter a female will usually come into estrus within eight days. Thus a female has the capacity to conceive over a period of about 12 months. But the long lactation time

usually allows the female to only raise two litters in seasonal environments. In northern Venezuela, Cordero (1985) reported that mean maximum longevity for *D. marsupialis* was about 21.8 months. Data from captives are in accord with the results from the field (Jurgelski 1974). Some of our delayed reproductive females lived longer than control or experimental females that reproduced. However, although there is obviously some physiological stress to reproduction the life span of a female is not markedly changed by not reproducing and her reproductive potential is in no way extended. Indeed it appears that the species are geared to produce two litters in the year following their birth whereupon physiological senescence reduces the probability of further reproduction in the following year. Thus the average reproductive output for females of these species in the two habitats is about 14 young. Provisioning or an excellent nutritional intake can bias the sex ratio of the litter toward males and slightly increase the mean litter size, but does not extend the female's reproductive period beyond the single year of maximum reproductive effort. In a way, the females of *Didelphis* behave as if they were "annuals" geared to a single extended season of reproduction.

The bias toward males by healthy females appears to increase the probability that the female will disseminate at least half of her genotype in the next generation. While males do not appear to be more expensive to raise based on the growth data during the teat attachment phase, clearly they are taking more nutrition just prior to weaning given the increase in growth over that displayed by their sister siblings. Post-weaning, the growth of males is appreciably greater than that of females. A large male has the potential to mate many females in the following year, thus it would appear that if a female can afford to produce large, healthy males at weaning she will avail herself of this opportunity. For a further discussion of the phenomenon see Austad and Sunquist (1986).

Didelphis reproduction patterns should not be considered typical for the New World marsupials. Data concerning the life history of the genus *Caluromys* presented by Charles-Dominique (1983) and Charles-Dominique et al. (1981) convince us that within the subfamily Caluromyinae different selective forces may have been at work in shaping life history strategies (Atramentowicz 1982, Perret and Atramentowicz 1989, Eisenberg 1989, Julien-Laferrière and Atramentowicz 1990). The same caution may well be applied to an analysis of the life history of the last extant species of the Microbiotheriidae *Dromiciops australis* (Mann 1958; Marshall 1978). On the other hand, the analysis of reproductive data for some species of *Marmosa* suggests a convergence in life history strategy towards *Didelphis* (O'Connell 1983; Eisenberg 1988). It should be noted that Pine et al. (1985) have established significant evidence that *Monodelphis dimidiata* in the pampas of Argentina may be a near semelparous mammal and approximate in its reproductive strategy the syndrome described for *Antechinus stuartii* (Lee and Cockburn 1985).

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