

Reproductive strategies of female capybaras: dry-season gestation

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Introduction

The life histories and reproductive strategies of vertebrates are closely linked to the pattern of seasonality of the environment in which they live (May & Rubenstein, 1984). In mammals, this allows females to synchronize the energetically costly gestation and lactation with the period in the year when resources are abundant. Depending on the particular strategy and especially on the development of the young at birth, the timing may maximize resources for the mother during gestation or for the young after birth (May & Rubenstein, 1984; Bronson, 1989; Clutton-Brock, 1991). In general, however, lactation requires a greater energy investment than gestation (Oftedal, 1984a).

In some tropical regions, seasons may be virtually non-existent or at least much less marked than in temperate ecosystems. In others, seasonality may be more apparent in rainfall than in temperature and photoperiod. Such rainfall has an important effect on primary production, causing herbivores to adjust their annual cycle of reproduction to the cycle of rains. Thus, there are examples of tropical mammalian herbivores that reproduce only once a year (e.g. the Greater kudu, *Tragelaphus strepsiceros*, at the end of the rains: Perrin & Allen Rowlandson, 1995), although the reproductive season may be longer than in temperate regions (e.g. *Mastomys* rats: Leirs *et al.*, 1994).

The reproductive strategy includes other aspects such as litter size, weight at birth and precocity of the young. More subtle aspects such as the resorption of foetuses and 'manipulation' of the sex ratio of offspring in relation to the mother's condition (Trivers & Willard, 1973) are also part of the reproductive strategy of females. Kozłowski & Stearns (1989) suggest that bet-hedging and selective abortion (or resorption) are alternative, non-exclusive, litter-size manipulation tactics that females may use to optimally allocate their reproductive resources. When bet-hedging, the female starts with the greatest possible litter size and then 'decides' whether to reduce it or not by resorption of embryos according to her assessment of resource availability during gestation. With selective resorption, the female assesses the foetuses themselves and

'decides' how many to carry to term in relation to their individual conditions.

Trivers & Willard (1973) predict that in a species where (i) males have a greater variance in reproductive success than females, (ii) reproductive success in males is correlated with their body weight, and (iii) adult body weight is affected by maternal investment, females in good condition should have a greater proportion of males in their litters than females in poor condition. Tests of the Trivers-Willard hypothesis have met with mixed success (e.g. Austad & Sunquist, 1986 and Gosling 1986 in favour; Armitage, 1987 and Hoefs & Nowlan, 1994 against).

In this chapter, I analyse the reproductive strategy of female capybaras, *Hydrochoerus hydrochaeris*, especially reproductive seasonality and litter-size manipulation, in relation to environmental seasonality and characteristics of the female (age, condition). Since the first two premises of the Trivers-Willard hypothesis are met in capybaras (Herrera & Macdonald, 1993) and the third one is not implausible, a second objective of this chapter is to test this hypothesis in capybaras.

Capybara biology

Capybaras are very large (ca. 50 kg), grazing rodents common in the Neotropical seasonally flooded savannas or Llanos of Venezuela. Their daily routine consists of resting in the morning, wallowing around midday and grazing in the evening and night. Capybaras are invariably found near permanent water holes, which they need for thermoregulation, for escape from predators, for mating, and for feeding since many of the grasses on which they feed are semi-aquatic.

In common with other caviomorphs (South American Hystricomorpha), capybaras are highly precocious (Weir, 1974), weighing 1.5–2 kg at birth (Ojasti, 1973) and able to graze within days or perhaps hours of birth. Gestation length is 5 months (Zara, 1973) and average litter size is 4 (range 1–8). Young from several females join in crèches shortly after birth and females appear to nurse indiscriminately any soliciting young (Macdonald, 1981). Nursing seems to be relatively unimportant since it is seldom observed and nursing bouts are short (Ojasti, 1973). In captivity, weaning occurs at 6 weeks or 3 months (Zara, 1973; Parra *et al.*, 1978). Weir (1974) says that other caviomorphs assume the nursing position long after lactation has ceased, indicating that actual weaning may occur earlier than apparent weaning. Sexual maturity is reached at 1–1.5 years.

Capybaras form stable social groups with an average composition of 3–4

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adult males, 6–7 females and a variable number of young (Herrera & Macdonald, 1987). Males are permanent group members (as opposed to 'floaters') and a rigid dominance hierarchy among them is the salient feature of the social system. The dominant male obtains more matings than any one subordinate, but subordinates as a group may mate more than all dominants (Herrera & Macdonald, 1993). There is a significant correlation between body weight and rank in the hierarchy, with dominant males being heavier than subordinates. However, on average, there is little or no sexual dimorphism in body weight in this species (Ojasti, 1973; Herrera, 1992).

Because of the capybaras' grazing habits and need for water, their reproductive strategy would be expected to be strongly affected by seasons. Indeed, in capybara groups, there is a clear surge in social and mating activity at the beginning of the rains (Herrera, 1986), with a corresponding peak in density of newborn animals 5 months later (September–October). Ojasti (1973) reports that capybaras reproduce seasonally, with 61% of females captured in the wet season being pregnant but only between 20 and 30% being so in the dry months. This is not surprising since the climate in the region is markedly seasonal with around 6 months of rain and 6 months of drought (see 'Study area', below). It is however, interesting that a significant proportion of females are pregnant in the dry months, despite the important lack of resources of this period, which may cause up to 30% density-independent mortality (Ojasti, 1978).

Study area

This study was carried out on Hato El Frío (7° 46' N, 68° 57' W), an 80 000 ha cattle ranch located within the seasonally flooded savannas (Llanos) of Venezuela. In the Llanos, the dry season lasts from November into early April, and the wet season from May until the end of October, the period when 90% of the annual 1600 mm of rain falls (Ramia, 1972). Although the area is apparently flat, there are three physiographical units that differ in their relative heights, soil types and vegetation. At El Frío, a system of dykes, which double as roads, 2–3 m high by several kilometres long, has produced larger reservoirs that limit the effect of the wet-season floods while retaining water for the dry season.

El Frío sustains a large capybara population, numbering between 15 000 and 25 000 animals. An annual cull, based on a quota obtained from Venezuela's Ministry of the Environment, extracts about 20% of the population every year in a commercial operation for meat production (Ojasti, 1991). The slaughter is

carried out in February–March each year. This practice started more than 150 years ago (Humboldt & Bonpland, 1805–37), although it was not until 1968 that it was regulated by the government. Recently, however, because of an apparent reduction in population size due to heavy poaching, smaller or no quotas have been allowed.

Methods

In order to collect data for this project, I took advantage of the annual slaughter, when a large number of capybara carcasses, both males and females, are available for study. During the slaughter, cowboys kill animals with a single selection criterion: size, the lower limit being 35 kg, estimated by eye. Although they attempt to avoid pregnant females, they have little success at this, except perhaps for heavily pregnant ones. This bias in the sample will be taken into account when interpreting results. Fieldwork was carried out in 1990, after 3 years without a slaughter at El Frío. A previous study (Herrera, 1992) has shown that after such a period of time the population can recover to some extent from the effects of the slaughter, at least with respect to mean body size and age distribution.

Two samples were taken during the 1990 slaughter. One consisted of any females killed, from which the proportion of pregnant females was calculated. To increase the number of pregnant females studied, a second sample, selected after pregnancy was detected (by eye) was also collected. From each female, the following data were recorded: body weight to the nearest kilogram, length of one humerus to the nearest millimetre (to assess skeletal size) and age class from the degree of ossification of the humerus epiphyses, following Ojasti (1973). Weights were recorded after cowboys had taken out the digestive and reproductive tracts. Although this was done mainly for practical reasons, the eviscerated weight was considered a better estimate of size and physical condition of the animal, since it is not influenced by the amount of food in the gut or by the weight of foetuses in the case of pregnant females. An index of physical condition was obtained from the residuals of the regression between humerus length and body weight (Berger & Peacock, 1988; Berger, 1992). The best regression was linear because of the small range of weights used.

From pregnant females, the following data were recorded: number of foetuses; weight (nearest 0.1 g or less, depending on size) and length of each foetus (nearest millimetre); sex for foetuses of at least 50 mm (López-Barbella, 1987); and number of resorptions. These were detected either because the foetus was small (relative to others in the uterus), white and without structures, or because the placenta was small and hard. The study of gestation in

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Table 16.1. Comparison of eviscerated weights, humerus lengths and condition indices (see the text) of pregnant and non-pregnant females at El Frio Ranch (Venezuela) in 1990

	Pregnant	Non-pregnant	ANCOVA	
Humerus length (mm)	174.6 (± 6.7) <i>n</i> = 192	176.3 (± 5.9) <i>n</i> = 157	Age	<i>F</i> = 5.93**
			Pregnancy	<i>F</i> = 4.88*
				d.f. = 3, 1, 344
Weight (kg)	42.1 (± 4.3) <i>n</i> = 196	39.1 (± 4.3) <i>n</i> = 153	Age	<i>F</i> = 11.04***
			Pregnancy	<i>F</i> = 53.54***
				d.f. = 3, 1, 343
Condition index	1.59 (± 3.80) <i>n</i> = 190	-1.98 (± 3.43) <i>n</i> = 152	Age	<i>F</i> = 3.38*
			Pregnancy	<i>F</i> = 86.11***
				d.f. = 3, 1, 337

An ANCOVA to test for significance controlling for female age-class is shown.

p* < 0.05; *p* < 0.01; ****p* < 0.001.

capybaras by López-Barbella (1987) permits an estimation of conception date from the size and degree of development of embryos.

Results

From a total of 361 females collected, 290 were from the general sample of females and 71 were those selected because they appeared pregnant. From the first sample it was found that 126 or 43.4% were pregnant. In the following analyses, the total (*n* = 197) sample of pregnant females is used and compared to the sample of non-pregnant (*n* = 164). Sample sizes vary because field conditions did not allow all data to be collected for all females.

Although the skeletal size of pregnant females was on average lower than that of non-pregnant ones, their eviscerated weight was significantly higher than that of the latter (Table 16.1). As a consequence, the condition index was also higher for pregnant females than for the rest (Table 16.1). There were no differences, however, in age class distribution between the two groups of females (Fig. 16.1; $\chi^2 = 5.15$, d.f. = 3, N.S.).

The average number of apparently healthy embryos (hereafter called embryo count) was 4.4 (± 1.5) (*n* = 191, Fig. 16.2) so that the female with zero embryos in Fig. 16.2 corresponds to a female with four resorbed fetuses and no live ones. There was no difference in embryo count among females of

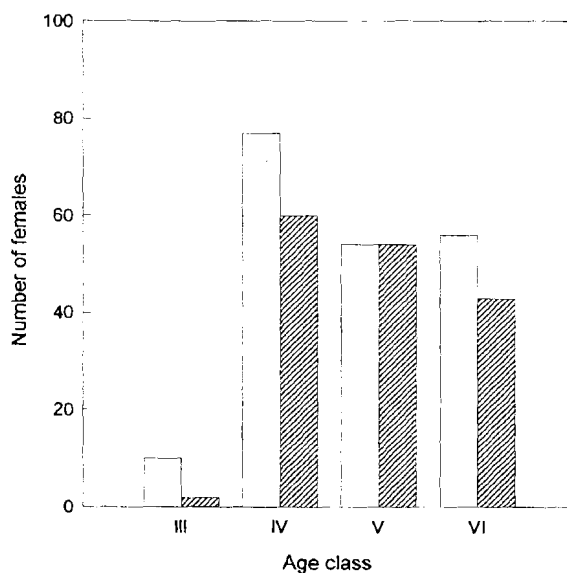


Figure 16.1. Distribution of age-classes (see the text) of pregnant (open bars) and non-pregnant (hatched bars) females collected in February 1990 at El Frio Ranch, Venezuela.

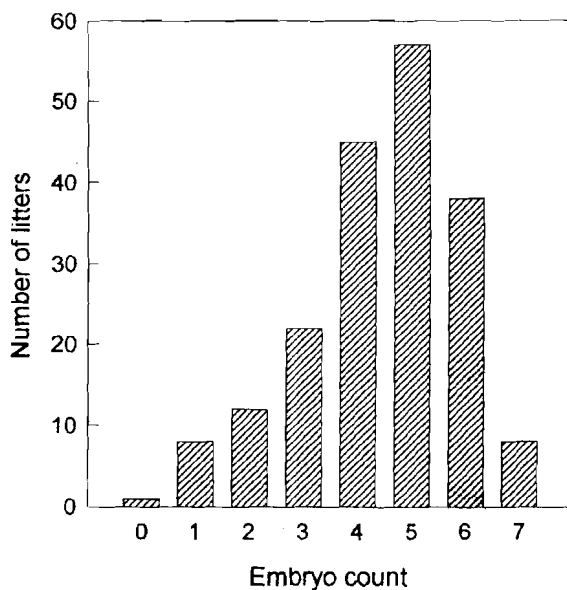
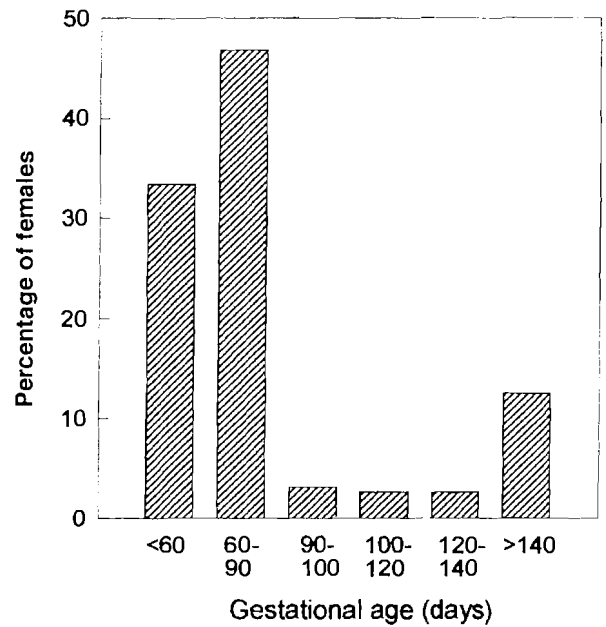


Figure 16.2. Histogram of numbers of apparently healthy embryos (embryo count) in uteri obtained from female capybaras collected in February 1990 at El Frio ranch, Venezuela.

different age classes (Kruskal-Wallis test, $H=4.25$, $d.f.=3$, N.S.) or body condition (partial Kendall's rank correlation coefficient between condition index and embryo count, controlling for mean foetus length, $r_{KP}=-0.084$, $n=151$, N.S.).

Figure 16.3. Distribution of gestational ages of litters of embryos obtained from female capybaras collected in February 1990 at El Frio ranch, Venezuela. $n = 191$.



Seasonality

Mean foetus length in litters was used as an indicator of gestation time. No attempt was made to convert these values to estimates of time since conception because of imprecision in the measurement of very small embryos and because the 'calibration curve' of foetus length and gestation time of López-Barbella (1987) gives a very low resolution since it was made with only five points. These values will nevertheless be used to classify gestations into time brackets.

A third of all the embryos were conceived within the 60 days previous to the sample being taken, i.e. between December and January (dry season), and would have been born between May and June, i.e. during the wet season (Fig. 16.3). Another 48%, with between 60 and 90 days gestation, would have had their litters by the end of April, when the rains start. The rest, less than 20%, would have given birth before the end of the dry season, having mated at the end of the previous wet season or at the beginning of the dry season.

Embryo count was not affected by time of conception (Fig. 16.4; Spearman rank correlation coefficient between mean foetus length and embryo count: $r_s = -0.019$, $n = 158$, N.S.). Neither was there any apparent effect of the progress of gestation on condition or weight of the females (correlation between mean foetus length and female eviscerated weight: $r = 0.013$, d.f. = 149, N.S.; and between mean foetus length and female condition index: $r = 0.019$, d.f. = 153, N.S.).

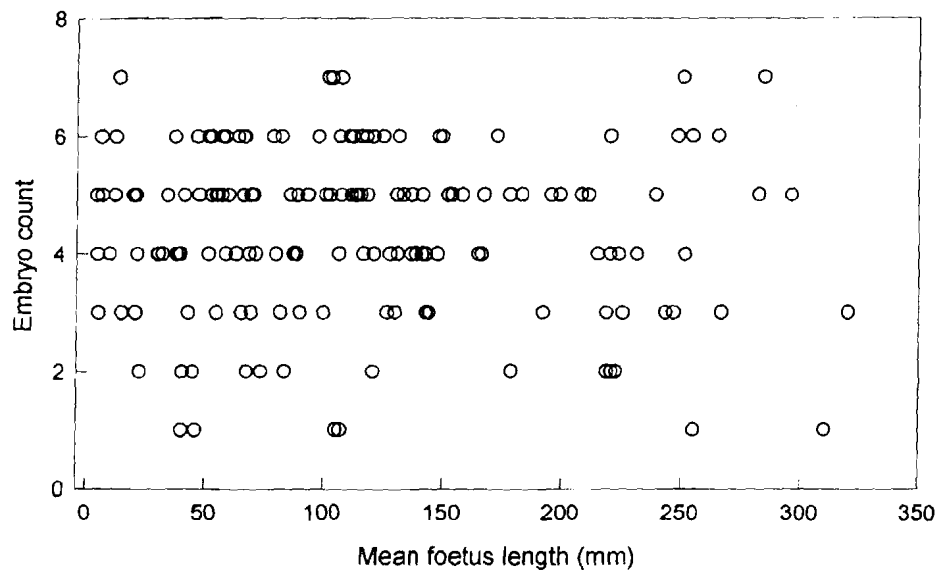


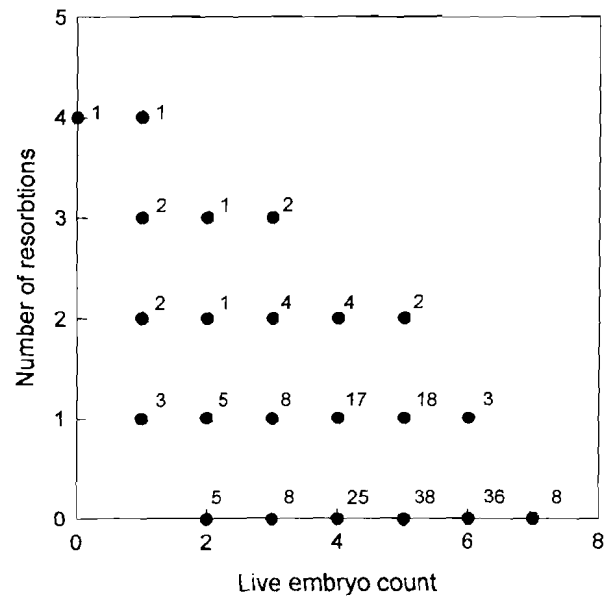
Figure 16.4. Numbers of apparently healthy embryos (embryo count) plotted against the mean length of foetuses (an indicator of gestational age); from pregnant female capybaras collected in February 1990 at El Frio ranch, Venezuela.

Embryo resorption

As many as 74, or 38.7%, of 191 pregnant females had at least one resorbed embryo in their uterus. The number of resorptions varied between 0 and 4 with a mean of $0.54 (\pm 0.82)$ when those females with no resorption are included, and $1.38 (\pm 0.74)$ excluding such females. The mean total embryo count (live embryos plus resorptions) was $4.97 (\pm 1.21)$, with no difference between females with and without resorptions (mean total embryo count with resorptions: $\bar{x} = 4.99 (\pm 1.23)$, $n = 74$; without: $\bar{x} = 4.97 (\pm 1.21)$, $n = 117$; Student's $t = 0.11$, d.f. = 189, N.S.). However, the mean live-embryo count was smaller for females with resorptions ($\bar{x} = 3.59 (\pm 1.43)$, $n = 74$) than for those without ($\bar{x} = 4.97 (\pm 1.20)$, $n = 117$; $t = 7.12$, d.f. = 189, $p < 0.0001$). There was a negative correlation between the number of live embryos and the number of resorptions (Fig. 16.5: $r_s = -0.489$, $n = 191$, $p < 0.0001$).

There was no relation between maternal age and number of resorptions (Kruskal-Wallis test, $H = 2.51$, d.f. = 3, N.S.) or between the mother's condition index and the number of resorptions (ANOVA among females with 1 to 4 resorptions, $F = 1.91$, d.f. = 4, 177; N.S.). Females in later stages of pregnancy did not show more resorptions than those in early stages (Spearman rank

Figure 16.5. Numbers of resorbed embryos plotted against numbers of live embryos obtained from pregnant female capybaras collected in February 1990 at El Frío ranch, Venezuela. Numbers next to dots indicate the number of times each combination appeared in the sample.



correlation coefficient between mean foetus length and number of resorptions: $r_s = -0.076$, $n = 158$, N.S.).

Sex ratio

Overall sex ratio (number of males/embryo count) in uteri did not differ significantly from 0.5 (245 males and 218 females, $\chi^2 = 0.789$, d.f. = 1, N.S.; $n = 105$ litters). Sex ratio of embryos in each uterus showed a small but significant negative correlation with mean foetus length ($r_s = -0.192$, $n = 102$, $p < 0.03$; Fig. 16.6), indicating that older litters had fewer males.

To test the Trivers–Willard hypothesis, I calculated a partial Kendall's correlation coefficient between the mother's condition index and the sex ratio of the embryos in her uterus (keeping mean foetus length constant). The prediction is that the coefficient should be positive (females in better condition should have more males), but in fact it was found to be non-significant ($r_{Kp} = -0.094$, $n = 98$, N.S.; Fig. 16.7). In case the effect was only noticeable at the later stages of pregnancy (after resorptions or abortions), this was calculated for litters at least 100 days old, and found to be non-significant again. To test further for a possible effect of the mother's condition on the sex of the young, the condition index (CI) of females, with all-male embryos (mean CI = 0.206, $n = 10$) was compared to that of females with all-female embryos (mean CI = 3.020, $n = 12$) and although lower, the difference only approached significance (Fig. 16.8; $t = 1.97$, d.f. = 16, $p = 0.066$). To test whether male

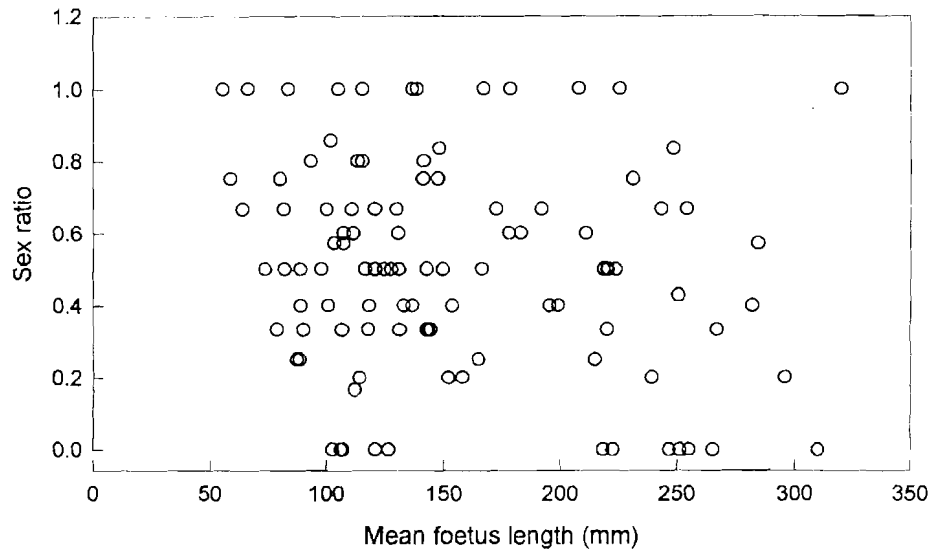


Figure 16.6. Sex ratio of embryos (number of males/embryo count) plotted against their mean length; from female capybaras collected in February 1990 at El Frio ranch, Venezuela.

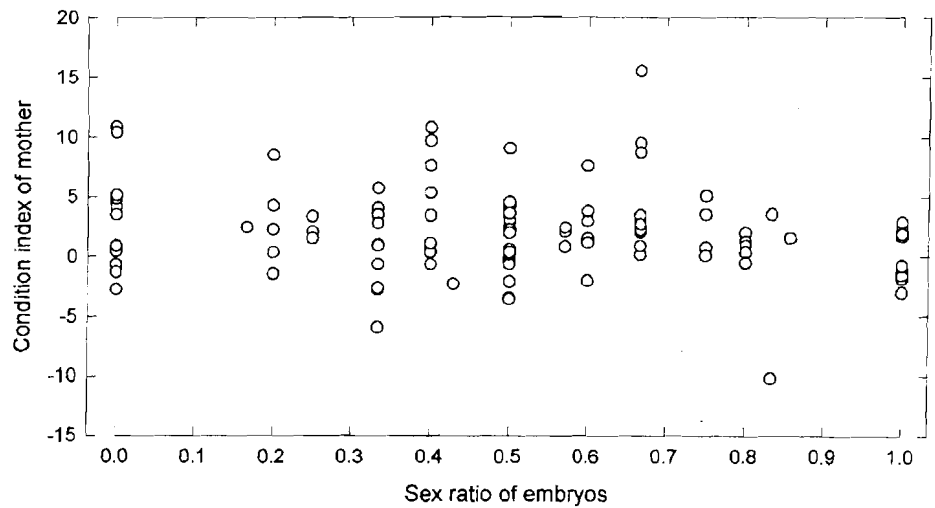


Figure 16.7. Condition index of female capybaras in relation to the sex ratio of the live embryos they carried. Samples collected in February 1990 at El Frio ranch, Venezuela.

Figure 16.8. Condition index of female capybaras carrying all male or all female embryos. n (all male) = 10; n (all female) = 12. Bars are standard errors. Samples collected in February 1990 at El Frío ranch, Venezuela.

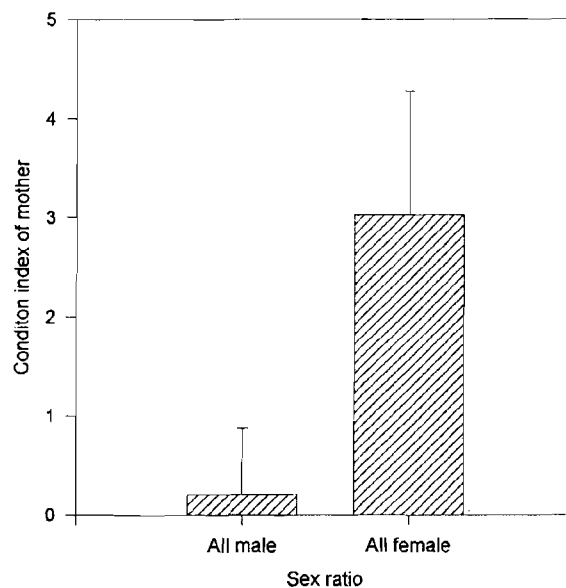


Table 16.2. ANOVA using a randomized block design to compare weights of male and female embryos from capybara females collected at El Frío ranch (Venezuela) in 1990.

Source	d.f	Sum of squares	Mean squares	F-ratio	<i>p</i>
Litter	78	2.2964×10^7	294413.69	202.32	0.000
Sex	1	2093.02	2093.02	1.438	0.231
Error	289	420541.16	1455.16		

'Blocks' are litters in order to control for different degrees of development.

offspring were more costly during gestation than females, I compared the weights of male and female embryos and found them to be not significantly different, using litters as blocks in a random block design ANOVA (to control for the different ages of litters; Table 16.2).

Discussion

Seasonality

The percentage of females found pregnant in the dry season (43.4%) is greater than expected, being exactly twice the value previously reported (21.7% (calculated from data in table 21 of Ojasti, 1973)). This is even more remarkable since this percentage is an underestimate of the actual value because early pregnancies can go undetected, and a certain number of females in late pregnancy are spared from the cull by the cowboys. This result raises two issues: first, the possibility that a number of these females may be having a second litter in the year; and second, the problem of seasonality itself. How can females have a litter at a time of year when water and grasses are dwindling rapidly? In a strongly seasonal environment where 90% of the rainfall falls between May and October (Ramia, 1972), it is remarkable that such a large proportion of females are able to invest in a litter in the dry season, let alone a second one. These points will be discussed in turn.

According to Ojasti (1973), a maximum of 61% of adult females are found pregnant in the wet season. Ojasti's data were obtained from the same ranch in a similar situation, i.e. after a few years without a slaughter, and are therefore directly comparable. If, as seems likely, Ojasti's estimate of the proportion of pregnant females in the wet season is valid, then it is possible that a much smaller proportion are having a second litter in the year. This is hardly surprising given the scarcity of water and grasses at this time.

As to seasonality itself, a number of other factors can help to interpret the large number of pregnant females in the dry season. A relevant result in this sense is the finding that pregnant females were in better condition than non-pregnant ones and that gestational age appeared not to affect the physical condition of mothers. This suggests that those females that become pregnant in the dry season do so because they are in good condition, possibly as a result of storing fat during the wet season. Also, pregnant females were found to be of the same ages as non-pregnant ones, which indicates that females that are reproducing in the dry season are not first-time breeders (if there had been a bias towards younger females) or old females reproducing for the last time. If either of these had been the case, it could have been argued that females were breeding at the wrong time of year. The fact that they apparently are not means that having a litter in the dry season may be a strategy, not an 'error'.

There is one major factor allowing females to be in good condition in order to breed in the dry season. This is the water management system, which retains water into the dry season in large tracts of El Frío and maintains some green

grass for most of the year. The effect of this should be more important in some parts of the ranch than in others, since only a proportion of the ranch is affected by the dykes, but unfortunately no exact locations with description of the habitat were recorded.

It can be inferred from the results (Fig. 16.3) that most pregnant females will give birth during the wet season, thus allowing the young access to good quality grass in the first few months of their life. For females in good condition, to have litters in the early wet season when grass is growing and vegetation offers cover against predators may in fact be an effective alternative to breeding in the wet season. Conversely, the smaller number of females who would give birth in the dry season would be exposed to the high predation pressure faced by newborn capybaras at this time of year (Ojasti, 1973; Herrera, 1986) while having to feed on low-quality grass at least until the rains start. It is not clear how this can be a successful strategy.

The litters

The mean embryo count found in this study ($\bar{x}=4.4$) corroborates previous findings, although it is smaller than the average for the dry season found by Ojasti (1973: $\bar{x}=5.3$). However, the wide range of months when litters would have been born invalidates a strict comparison between the two studies.

Embryo count did not affect the physical condition of mothers, as has been found by other authors (e.g. Samson & Huot, 1995). Apparently, females are able to maintain their condition regardless of the characteristics of the embryos they are carrying. There was no relation between embryo count and age, so older females are not producing larger litters.

A high proportion (38.7%) of females had at least one resorption, which is also higher than previously reported (16.8%) by Ojasti (1973). This is also greater than the values found for deer mice (*Peromyscus maniculatus*) and pocket gopher (*Thomomys bottae*) by Loeb & Schwab (1987). This does not appear to be the result of disease or weakness of females since females with resorbed embryos were in similar condition to females with complete litters. Roberts & Perry (1974) who studied viscachas (*Lagostomus maximus*) and chinchillas (*Chinchilla laniger*) found that resorption in these species and other caviomorphs was common: up to 49% ($n=17$) in viscachas, although they do not give quantitative data for other species. They also conclude that resorbing embryos does not appear to be a result of disease or other problems such as overcrowding.

The facts that full embryo count (live embryos + resorptions) was similar for females with and without resorptions and that females with no resorptions had more embryos than the population average, seem to be more consistent

with bet-hedging than with selective resorption but not conclusively so. The negative correlation between sex ratio and gestational age (as assessed by mean foetal length) suggests that male embryos are selectively resorbed.

Sex ratio of litters

The sex ratio in litters did not differ from 1:1, but it did tend to be biased towards females in more advanced gestations (Fig. 16.6). This may reflect a selective resorption of males. Since these are gestations from the period of the year when food may be scarce, this trend suggests that male embryos – possibly weaker than those gestated in the wet season – are being resorbed because they would benefit their mother less, in accordance with the Trivers–Willard hypothesis. This hypothesis, however, was not supported by the main result of the present study in that there was no correlation between sex ratio and female condition. The latter, if anything, showed a trend – albeit not quite significant – in the opposite direction: females with all-female litters may have been in better condition than females with all-male litters. There is one important caveat to be mentioned in this context. Although the capybara situation appears to comply with the premises of Trivers & Willard (1973), male embryos were no larger than female embryos (Table 16.2) and may not therefore have been more costly, clearly a factor affecting the females' 'decision' whether or not to alter the sex ratio of their litters. Furthermore, the difference in size between dominant and subordinate males is not large (Herrera & Macdonald, 1993), and it may be a product of post-weaning growth. Perhaps males from wet-season gestations are in better condition than those from the dry season. This would imply that females should give birth to more females in the dry season, and this is in fact what the data in Fig. 16.6 suggest: all-female litters are those that will be born within a month after the sample was taken, i.e. before the end of the dry season. Wright *et al.* (1995) propose an alternative to the Trivers–Willard hypothesis based on time of birth rather than the mother's condition. According to this hypothesis, males born early in the breeding season would be at a competitive advantage because they would be somewhat older and larger than those born later.

The results of the present study point to a reproductive strategy of female capybaras based on timing within the dry–wet season alternation: (i) to become pregnant during the wet season, assuring food for the female during her costly gestation; (ii) to become pregnant in the dry season, ensuring that the newborn will have access to good quality forage when the new rains begin. The former is the most common strategy, possibly because gestation may be more costly than lactation. Although opposed to the general trend in mammals (Oftedal, 1984a), this pattern has been found in the capybara's closest relative,

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the guinea pig, *Cavia porcellus* (Ofstedal, 1984b). The second alternative may be less common because it is more risky, since the beginning of the rains is not 100% predictable: any delay in the onset of rains would jeopardize the reproductive effort. As to sex-ratio manipulation within litters, there is a slight trend for females to have female-biased litters if they are to be born in the dry season. The small or perhaps non-existent difference in costs between male and female offspring does not favour a more definite strategy of *in utero* sex-ratio manipulation.

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