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Population biology of *Sigmodon alstoni* (Rodentia: Cricetidae) in the Venezuelan Llanos

Biología poblacional de *Sigmodon alstoni* (Rodentia: Cricetidae) en los Llanos de Venezuela

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ABSTRACT

The population biology of *Sigmodon alstoni* in the Venezuelan savanna of Guárico was monitored between October 1982 and September 1984. Biweekly trapping revealed the existence of a yearly fluctuation in density with an increase phase in the dry season and a decrease phase during the transition into the rainy season and throughout most of the rainy season, and dissapeareance of the animals during the transition between the rainy and the dry seasons. Demographic parameters (survival, reproduction, age structure) were associated with the seasonal pattern of rainfall which renders the llanos extremely dry and flooded intermittently. Changes in habitat due to seasonal rainfall may also be important.

Key words: tropical rodents, rainfall seasonality, population regulation, rodent cycles.

RESUMEN

La biología poblacional de *Sigmodon alstoni* se estudió en los Llanos de Guárico, Venezuela, entre octubre de 1982 y septiembre de 1984. Muestreos quincenales revelaron la existencia de una fluctuación anual de la densidad con una fase de incremento durante la sequía, seguida por un descenso durante la transición a las lluvias y durante las lluvias, y desaparición de los animales durante la transición entre las lluvias y la sequía. Los parámetros demográficos (sobrevivencia, reproducción, estructura de edades) están asociados al patrón estacional de precipitación que transforma a los llanos en zonas muy secas o inundadas en forma intermitente. Cambios en el hábitat debidos a la estacionalidad de las lluvias pueden también ser de importancia.

Palabras claves: roedores tropicales, estacionalidad de precipitaciones, regulación poblacional, ciclos de roedores.

INTRODUCTION

Population biology of rodents has been such a popular subject of study in the temperate areas for many years, that a theory of population regulation has emerged from these studies (see for example Krebs *et al.* 1973, and Krebs & Myers 1974). On the other hand, rodents of Neotropical areas have been neglected until recently when a few studies have started to appear in the literature (Gómez-Núñez 1960; Fleming 1973, O'Connell 1981, Streilein 1982, August 1984, Vivas 1984[a], Cartaya & Aguilera 1985, Vivas & Calero 1985). It is important that the results of such studies on tropical rodents become integrated with the theory of population regulation because they might emphasize aspects previously overlooked. One of the aspects that could prove potentially interesting to look at is the lack of seasonal fluctuations in temperature in tropical areas compared to temperate areas. Many tropical areas are seasonal with respect to rainfall although there is a gradient between almost no seasonality to extreme seasonality. Such extremes include the aseasonal tropical rainforests and the extremely seasonal flooded llanos of Venezuela (Walter & Medina 1971). Such differences between the tropics and the temperate areas may result in completely different demographic strategies if the environment and habitat are the templet upon which demographic strategies are molded (Southwood 1977).

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In an effort to determine how habitat changes influence demography I undertook a population study on the rodents of a seasonally flooded area in the savannas of Venezuela. Previous studies (O'Connell 1981, August 1983, 1984, Vivas 1984[a]) had determined differences in the abundance of rodents in different habitats, and these differences may be associated with differential heterogeneity and complexity in the habitats (August 1983, 1984).

I hypothesized that *Sigmodon alstoni* (Thomas) may have a fluctuating density, tracking the rainfall pattern in the sense of May (1976), as does *S. hispidus* 30 km northeast of the study site (Vivas & Calero 1985). Or, alternatively, that it may adjust its strategy in order to reproduce when resources are available. The above alternatives would imply that the relationship of *S. alstoni* to rainfall might not be linear, but a more complex function where other factors might be involved. Such complex interactions might involve the syntopic species *Zygodontomys microtinus* (Allen), predator-prey relationships with multiple predators (reptiles, birds, and other mammals), abundance of food resources, microhabitat changes and others.

STUDY SITE

The study site was Fundo Pecuario Masaguaral, a cattle ranch, property of Sr. Tomás Blohm, located 45 km south of the city of Calabozo, Guárico State, Venezuela. The coordinates for the ranch are 67°37'W, 8°33'N. Elevation is about 100 meters above sea level (Eisenberg 1979). Masaguaral was chosen as a study site for several reasons: A) It has been protected from fire and hunting since about 1946. B) It is strongly seasonal in rainfall and at the same time is representative of the flooding savannas and very close (approximately 30 km) to the higher savannas which contain other rodent species; thus, there is the possibility of future comparisons without having the inconvenience of a different climate. C) Some data are already available on rodent density (O'Connell 1981, August 1983, 1984). D) Some knowledge, albeit skimpy, is already available on the vegetation (Ramia 1967, Troth 1979).

For the purposes of this study the rainfall data were measured daily *in situ*. I added data for all days since the previous sampling period. This was necessary because the samplig scheme was biweekly, and if monthly values had been used (as customary) they would have covered two (at times three) trapping periods.

The climate in Masaguaral is seasonal. There are mainly two seasons: dry and rainy (figure 1). The dry season spreads between mid-December and mid-May and is characterized by very little rain and very dry cracked soils. It is followed by a short transition period that covers one or two months. The rainy season begins around mid-June and extends to September, and is characterized by extensive flooding in the ranch. It is followed by a transition period that may extend to the first part of December. During this transition period the water evaporates rapidly and the soil is already dry by mid-December.

This report covers part of a study which included two study grids. However, only one grid, Grid A, provided sufficient data on *S. alstoni*

Grid A was located in the Banco-Bajío type of savanna described by Bonnazzi (1962) and Ramia (1967). Banco refers to those areas that never flood in the rainy season and Bajío refers to those areas which do flood in the rainy season. Troth (1979) further subdivided the Bajío formation in Masaguaral into different categories depending on the amount of cover by woody vegetation. Grid A was located in Troth's "Discrete Mata Bajío", which is covered only in parts by patches of woody vegetation, around a *Copernicia tectorum* palm. This particular type of bajío does not flood extensively and in the parts, that do flood the water sheet is only a few centimeters deep. The soil, however, is waterlogged throughout the rainy season.

Grid B was located in the "Shrub Woodland Bajío" of Troth's and floods extensively. Cover is also extensive.

MATERIALS AND METHODS

Each grid had 100 stations, arranged in a 10 by 10 configuration, separated by 10 m in Grid A and 15 m in grid B. The area of Grid A was 1.0 ha and that of Grid B 2.25 ha. Each station had one Sherman live trap (23 by 9 by 8 cm).

The sampling method was that of capture-mark-recapture, and the schedule was similar to that used by Gaines & Rose

(1976). The traps were baited at sunset with a mixture of corn flour and sardines, and checked the next morning between sunrise and 10.30 h to avoid heat deaths and attacks by ants. Traps were left locked open all day, reset at sunrise, and checked again the following morning. Then, the traps were left locked open *in situ* for two weeks until the next trapping period. Sampling began in October 1982 and ended September 1984, with intervals of two weeks in between trapping periods. The first time an animal was caught it was marked in the right ear with numbered and lettered metal ear tags (National Band & Tag Co., Newport, Kentucky). Only one recaptured animal lost its tag and it was retagged on the left ear. It was possible to track its original identity based on sex, weight, and site of capture. Each time an animal was captured, information was recorded on the species, trap station, sex, weight, body length, identification number if a recapture, other characteristics that could aid in future identification, behavior after release, especially where it went for refuge, and lastly, its reproductive condition. Reproductive characteristics were described as abdominal or scrotal testes for the males, and closed or open vagina, small, medium or large nipples, and closed or open pubic symphysis, for the females.

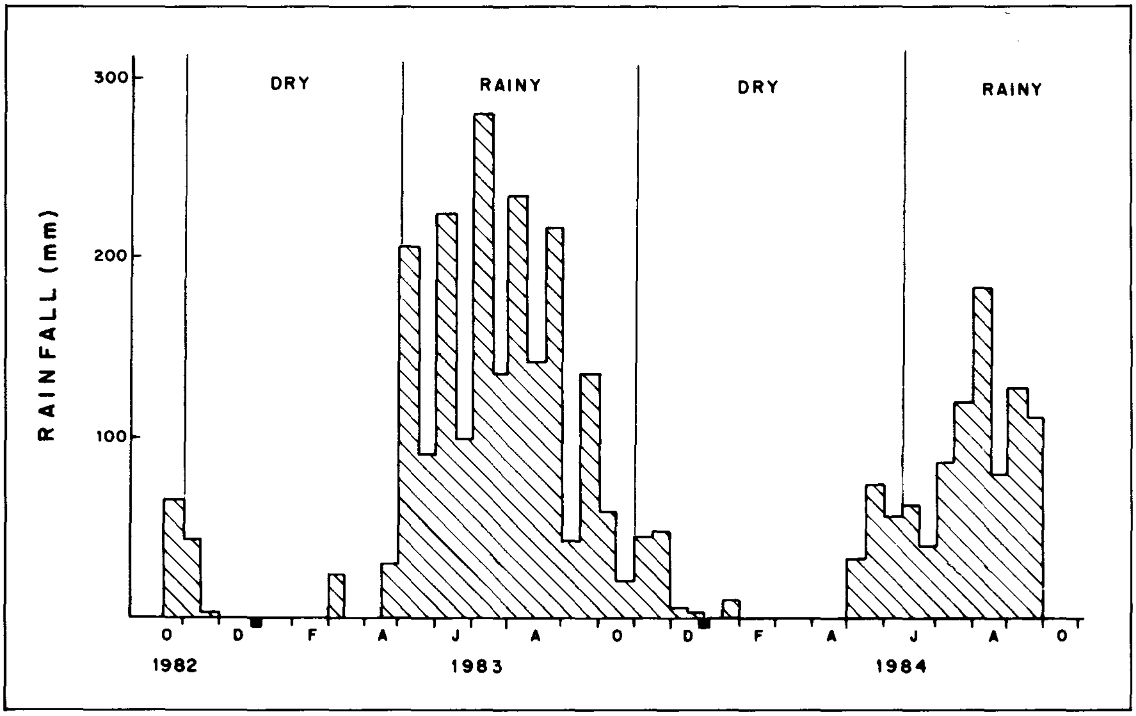

Fig. 1. Rainfall pattern in Masaguaral during the period of study. Values are given biweekly and represent the sum of daily rainfall measured in mm.

Patrón de precipitación en Masaguaral durante el período de estudio. Los valores dados son quincenales y representan la suma de los valores diarios de precipitación medidos en mm.

On each trapping period fecal samples were collected from as many animals as possible in order to determine the dietary patterns. During each climatic season vertical height profiles were determined at each station for microhabitat preference measurements. Indices of importance for each plant species were determined in order to compare resource availability to resource consumption. All these aspects of the study will be reported elsewhere.

RESULTS

Three species of rodents were captured throughout the study: *Zygodontomys microtinus, Sigmodon alstoni,* and *Rhipi-*

domys spp., in order of decreasing density. Results for *Z. microtinus* were reported elsewhere (Vivas 1984)[a] and those for *Rhipidomys* spp. were too scarce to allow description of trends in demographic patterns (it is an arboreal species which is captured very infrequently in ground traps). *Marmosa robinsoni*, a marsupial, was also readily caught and results will be reported elsewhere.

This paper will be refering to the results of Grid A, unless otherwise stated.

Age criteria. The age criteria were determined from a weight-length graph (figure 2). There is no apparent sexual dimorphism in size, but small sample size makes this conclusion tentative. The limits between the age groups are also tentative for no laboratory study is available to corroborate them. A small autopsy study is in progress for this species (Weir & Vivas, unpublished results).

Density pattern. Figure 3 shows the minimum number of animals known to be alive. An increase in density in Grid A was observed at the beginning of the dry season and continued until the transition between the dry and the rainy season, at which point there was a decrease in density.

There were no captures during the transition between the rainy and the dry season. The peak density during 1983 was twice as high as in 1984. The decrease in 1983 started almost inmediately after the peak in May, and in 1984 the density stabilized for almost three months before falling throughout the rainy season. A density of zero animals in the population during the transition between the rainy and the dry season, and the subsequent increase, can be explained by trap shyness and/or emigration of animals to other places during that period, or by mortality (either by natural causes or by predation).

Data for Grid B indicate that *S. alstoni* is very scarce in the shrub Woodland Bajío habitat (figure 3).

Sex ratio. The number of males during 1983 was smaller than the number of females, but the ratio was reversed in 1984 (figure 4). A chi-square analysis indicated a significant difference in number of males to females in 1983 ($p < 0.05$) but not in 1984 ($p > 0.10$).

Further discrimination of the data indicated that the sex ratio was significantly different in the rainy season of both 1983 and 1984 ($p < 0.05$), but non-significant in the dry season of both years ($p > 0.10$).

Age distribution. Only three age classes could be discriminated based on body weights and lengths, and reproductive characteristics. It was necessary to pool all animals from all sampling periods for each month in order to increase sample size; thus the age structure in figure 5 was based on monthly samplings. When an animal was caught more than once in a month, only the weight of its first capture that month

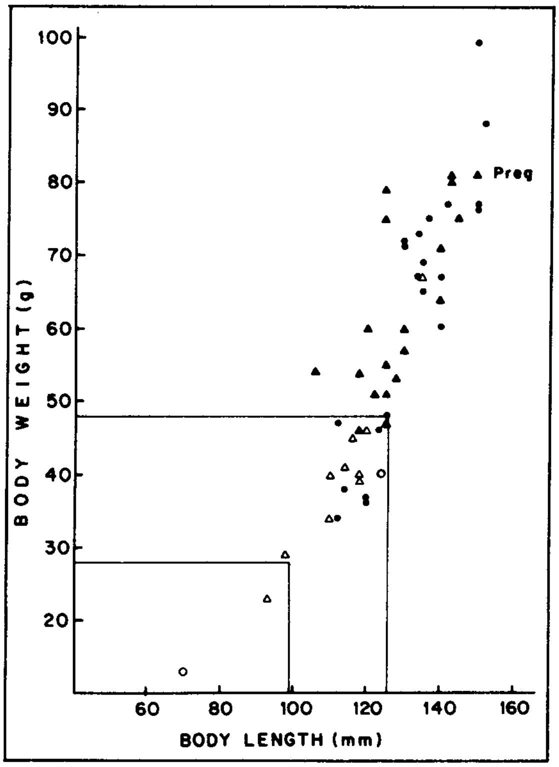

Fig. 2. Age criteria for *Sigmodon alstoni* based on body weights and body lengths of animals captured in Masaguaral. The cut-off points for the different age groups are as follows: 28 g and $\leqslant 99$ mm (juveniles), 29-48 g and 100-125 mm (subadults), and $\geqslant 49$ g and $\geqslant 126$ mm (adults). These criteria are shown as parallel lines to both axes. The symbols are as follows: abdominal testes (○), scrotal testes (●), small nipples (△), and large or medium nipples (▲).

Criterios de edad para *Sigmodon alstoni* basados en peso y longitud corporales de animales capturados en Masaguaral. Los puntos de corte para los diferentes grupos de edad son los siguientes: 28 g y $\leqslant 99$ mm (juveniles), 29-48 g y 100-125 mm (subadultos), y $\geqslant 49$ g y $\geqslant 126$ mm (adultos). Estos criterios se muestran como líneas paralelas a los ejes. Los símbolos son: testículos abdominales (○) testículos escrotales (●), mamas pequeñas (△), y mamas grandes o medianas (▲).

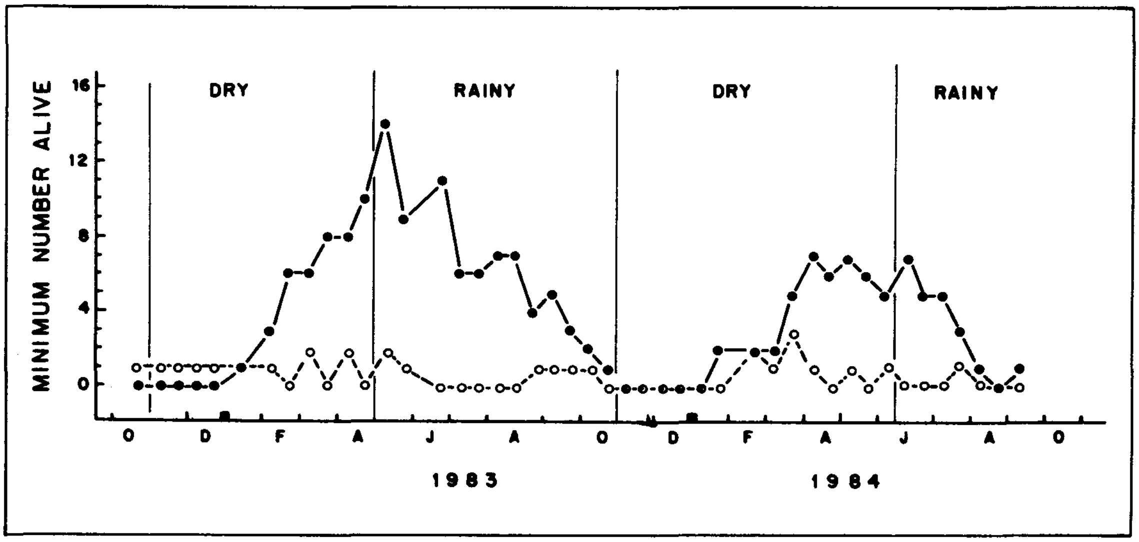

Fig. 3. Minimum number known alive biweekly of *Sigmodon alstoni* in Grid A (●) and Grid B (○) in Masaguaral.

Número mínimo de *Sigmodon alstoni* que se saben vivos en las Cuadrículas A (●) y B (○) en Masaguaral.

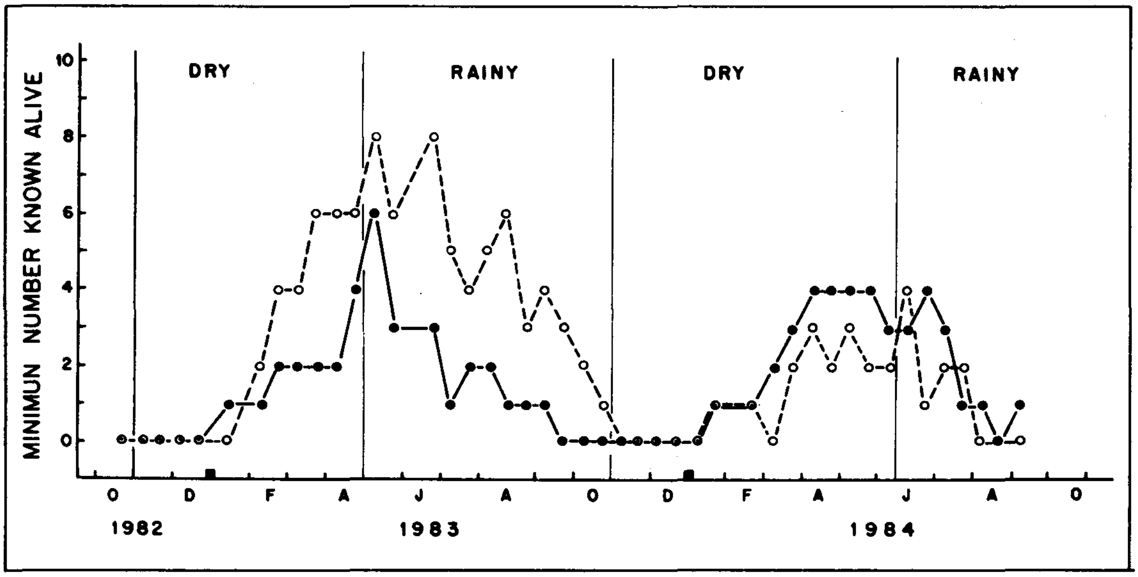

Fig. 4. Minimum number known alive biweekly of males (●) and females (○) of *Sigmodon alstoni* in Masaguaral.

Número mínimo de machos (●) y hembras (○) de *Sigmodon alstoni* en Masaguaral.

was included; in this way the data were not biased by the inclusion of the same individual with different weights at different times in a particular month. Males and females were considered together due to the small sample sizes and the apparent lack of sexual dimorphism in body weights or lengths for this species.

It was observed that the population consisted mainly of adults. Juveniles were few (at least in the trappable population), and were concentrated during the dry season. Subadults were also few and were mainly observed during the dry season and up to the middle part of the rainy season. At the end of the rainy season and the transition into the dry season only adults were found.

Survival. Survival was estimated in the same manner as Gaines & Rose (1976), i.e., for each period t=i the number of animals known to be alive at time t=i–2 that survived to t=i were quantified and presented as percentages. Survival here does not discriminate the causes of disappearance, whether it be predation, natural death or emigration.

The pattern in survival (figure 6) was not clear, although some trends were detected. Survival in the males was generally high during the dry season of both study years, but it followed a decreasing trend (which fluctuated widely) during the rainy season of both years. Survival in the females during the dry season was high in 1983 and it decreased abruptly during the transition into the rainy season of 1984. In the rainy season female survival tended to decrease.

Another aspect of survival is the average length of time that the rodents inhabit the grid. In 1983 this time was 5.5 months, and 3.8 months in 1984. Animals were caught an average of 2.6 trapping periods in 1983, and 2.5 trapping periods in 1984.

Reproduction. Reproductive state is shown in figure 7. All but the juvenile males were in a reproductive state throughout the study, whereas the females varied greatly in their reproductive condition. The females showed moderate reproductive activity with a sudden decrease during the times when juveniles and subadults had higher proportions (see figure 5), i.e., dry season and the transition into the rainy season.

Body weights. Mean body weights per trapping period (figure 8) indicate that the rodents were heavier in the rainy season than in the dry season. This pattern held for males in both years; females did not follow the trend in 1984 (they dissapeared halfway through the rainy season). At-test (table 1) indicated that the differences were statistically significant ($p < 0.05$) for the males in both years and for the females in 1983.

The above pattern was also observed among individual rodents in 1983 (figure 9). Most individuals remained relatively stable in their weight during the dry season, and gained weight in the rainy season. Of course, the small number of individuals that could be followed through both seasons precludes conclusive statements in this respect. In 1984 no individual animals were captured for a long enough period to determine trends.

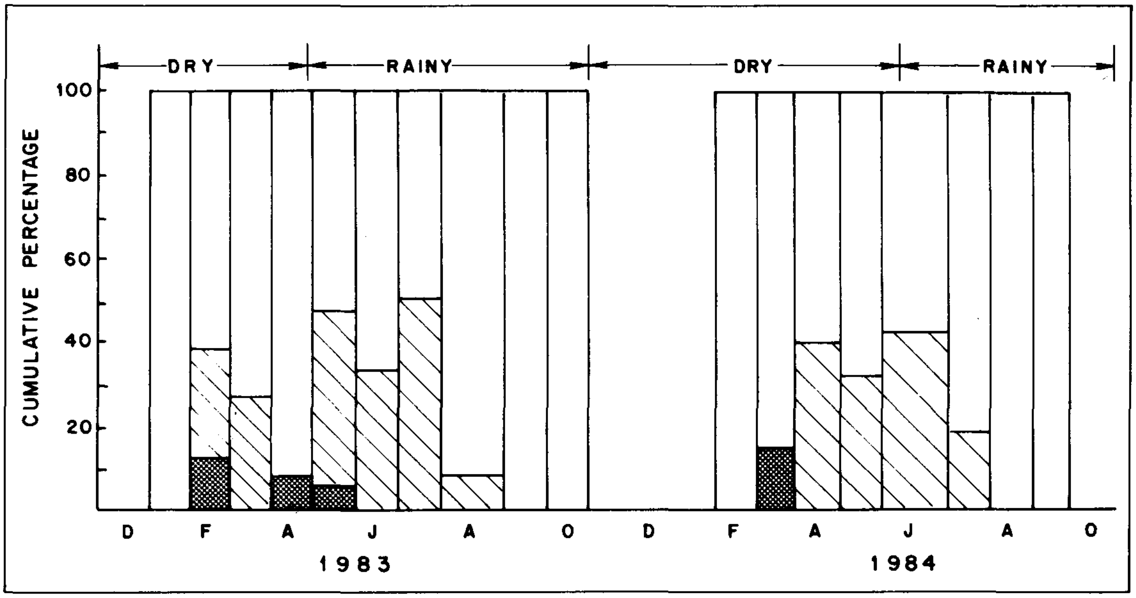

Fig. 5. Monthly changes in age structure of *Sigmodon alstoni* in Masaguaral. Males and females are combined. Stippling indicates juveniles, hatching indicates subadults, with the remainder of each bar indicating adults.

Cambios mensuales en la estructura etaria de *Sigmodon alstoni* en Masaguaral. Los machos y hembras se consideran juntos. El punteado indica juveniles, el rayado indica subadultos, y el remanente de cada barra indica adultos.

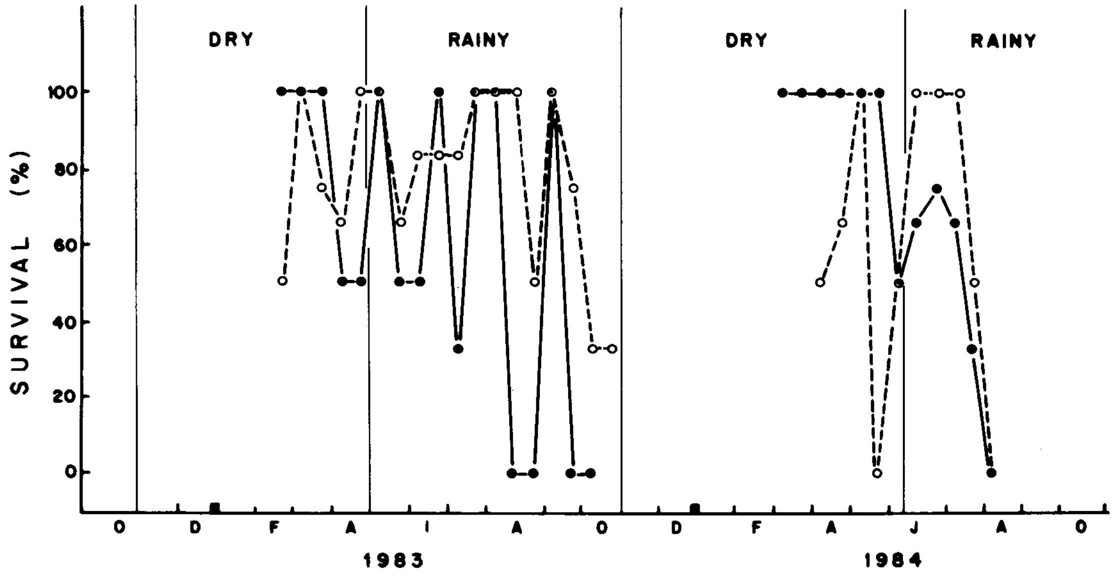

Fig. 6. Biweekly survival of males (●) and females (○) of *Sigmodon alstoni* in Masaguaral.
Sobrevivencia quincenal de machos (●) y hembras (○) de *Sigmodon alstoni* en Masaguaral.

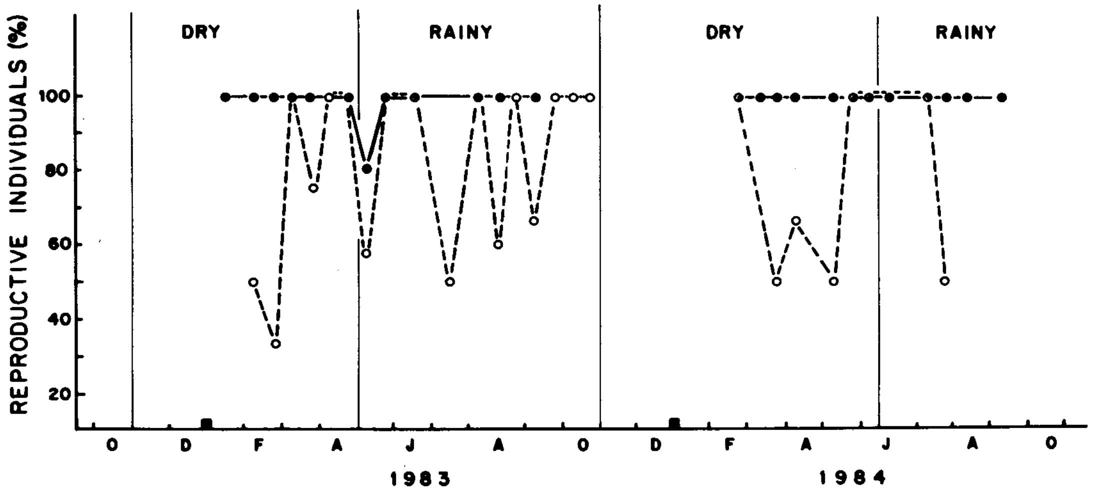

Fig. 7. Reproductive state of males (●) and females (○) of *Sigmodon alstoni* in Masaguaral.
Estado reproductivo de machos (●) y hembras (○) de *Sigmodon alstoni* en Masaguaral.

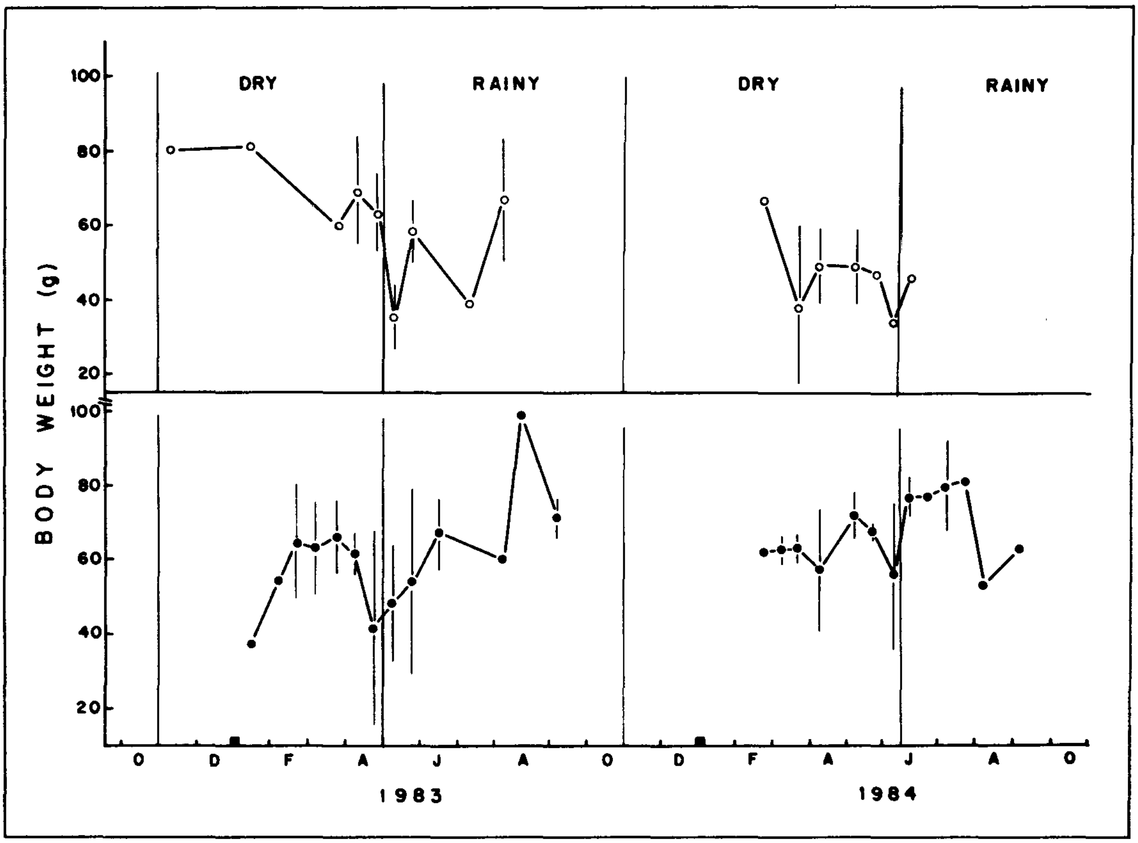

Fig. 8. Pattern of biweekly mean body weights for *Sigmodon alstoni* in Masaguaral. Vertical segments around means denote one standard error. Symbols: males (●), and females (○).

Patrón quincenal del peso corporal medio para *Sigmodon alstoni* en Masaguaral. Las líneas acotadas en torno a las medias representan un error estándar. Símbolos: machos (●), y hembras (○).

TABLE 1

Seasonal means and standard errors of weights and B/W for *Sigmodon alstoni.* The numbers of trapping periods per season are shown in parenthesis (sample size). * = $P < 0.05$; ns = non-significant.

Promedios estacionales y errores estándar de pesos y relación largo/peso corporal de *Sigmodon alstoni.* El número de períodos de muestreo por estación (tamaño muestral) se muestra entre paréntesis. * = $P < 0.05$; ns = no significativo.

YEAR	SEASON	WEIGHT (g)		B/W	
		♂	♀	♂	♀
1983					
	Dry	51.0 ± 11.3 (8)	55.7 ± 8.4 (7)	0.30 ± 0.06 (3)	0.21 ± 0.05 (6)
	Rainy	70.2 ± 17.4 (5)	68.9 ± 17.2 (10)	0.22 ± 0.07 (3)	0.25 ± 0.05 (3)
		(*)	(*)	(*)	(*)
1984					
	Dry	64.1 ± 4.9 (6)	54.0 ± 10.3 (5)	0.23 ± 0.03 (4)	0.26 ± 0.04 (6)
	Rainy	70.0 ± 11.1 (6)	54.2 ± 13.5 (3)	0.18 ± 0.00 (3)	0.26 ± 0.00 (1)
		(*)	ns	(*)	ns

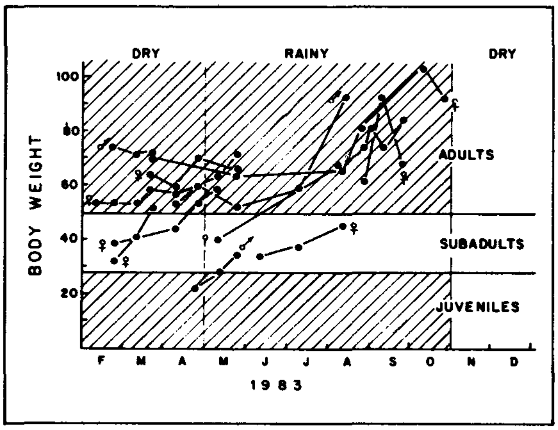

Fig. 9. Change in body weight for some individuals of *Sigmodon alstoni* in Masaguaral, during 1983.
Cambio en el peso corporal de algunos individuos de *Sigmodon alstoni* en Masaguaral durante 1983.

One observation that may be important in the biology of *S. alstoni* is that body weights seem to decrease during the transition period between the dry season and the rainy season.

General condition. An index of general condition (B/W) was calculated for each animal during the study. This index, devised by Heikura (1977) for use on voles, represents the ratio of Body Length (B) to Body Weight (W). The smaller the ratio presumably the better the condition of the individual.

Examination of figure 10 reveals that the males of *S. alstoni* have a better condition during the rainy season than during the dry season. A *t*-test also reveals (table 1) the same pattern in both study years. The females seem to follow the opposite pattern and appear to be better off in the dry season: a *t*-test (table 1) reveals significant differences ($P < 0.05$) between seasons during 1983, but not in 1984.

Home range and habitat preferences. Home ranges were small and most animals were

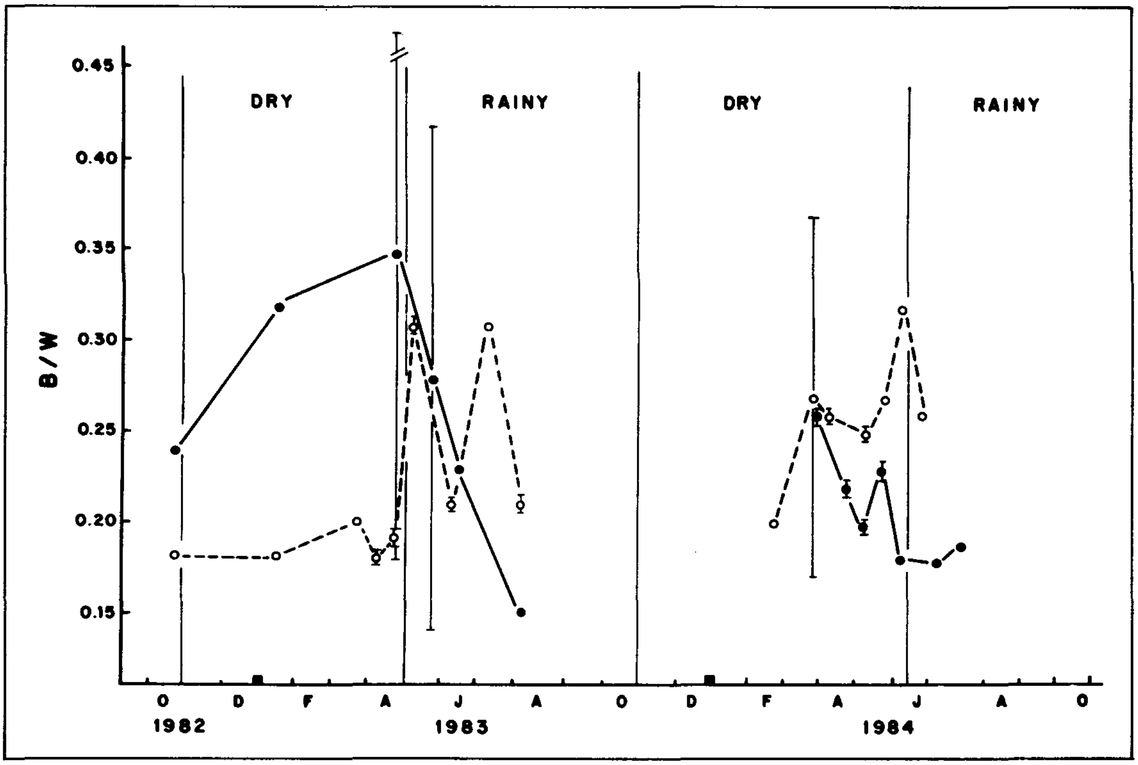

Fig. 10. Mean body length to body weight ratios (B/W) of *Sigmodon alstoni* in Masaguaral. Vertical segments around means denote one standard error. Symbols: males (●), and females (○). High values of the index indicate poor general condition, and viceversa.
Promedios de la proporción largo corporal a peso corporal en *Sigmodon alstoni* en Masaguaral. Las líneas acotadas en torno a las medias representan un error estándar. Símbolos: machos (●), y hembras (○). Valores altos del índice indican una condición general pobre.

caught in traps close to one another. Males were recaptured fewer times per individual than females in 1983 (2.2 vs 3.1 times, respectively), but in 1984 the values were 2.0 and 1.6, respectively.

After determining the home range area with a Model 40 LASICO Compensating Planimeter they were compared by a *t*-test and no significant differences were found ($P > 0.10$) between males and females.

The preferred habitat by both sexes was in the vicinity of the Matas, clusters of woody vegetation (figure 11) growing around one or a few palms (*Copernicia tectorum*). It would seem as if these rodents prefer the ecotone between the Matas and the open savanna, for they were not found inside the Matas very often nor very far into the open savanna.

DISCUSSION

It is obvious that *S. alstoni* in Masaguaral has a very low density, as is indicated by the fact that in 9000 trap-nights only 51 individuals were captured a total of 133 times. That is less than 2% efficiency. This contrasts with the syntopic species *Z. microtinus* of which over 1200 individuals were marked and recaptured about 5600 times in the 18000 trap nights in both grids (Vivas 1984a). The congeneric specie *S. hispidus*, at a distance of only 30 km northeast of Masaguaral has also been documented to have low densities and captured few times (Vivas & Calero 1985). At Barinas, located in the western savannas of Venezuela, *S. alstoni* is present in higher densities than in Masaguaral (Soriano 1977). This observation coincides with Péfaur's (personal communication) data, who, in an intensive trapping in the states of Barinas and Portuguesa, found that *S. alstoni* was moderately abundant.

O'Connell (1981, 1983) reported *S. alstoni* in Masaguaral. She also found very low densities, to the point that the species disappeared from her grid during the second year of the study. An explanation for the low densities she found could be related to habitat preference; in my experience *S. alstoni* is seldom found in woody vegetation areas (as in Grid B) and O'Connell''s grid was more densely covered by that type of vegetation than in this study (personal observation). August (1983, 1984) also reported extremely low densities for *S. alstoni* in Masaguaral in two open-vegetation types of habitats. Ibañez (1980) reported very low densities for *S. alstoni* in the savannas of the state of Apure, Hato El Frio, a place southwest of Masaguaral that floods in the rainy season and where the vegetation is much more open than in Masaguaral.

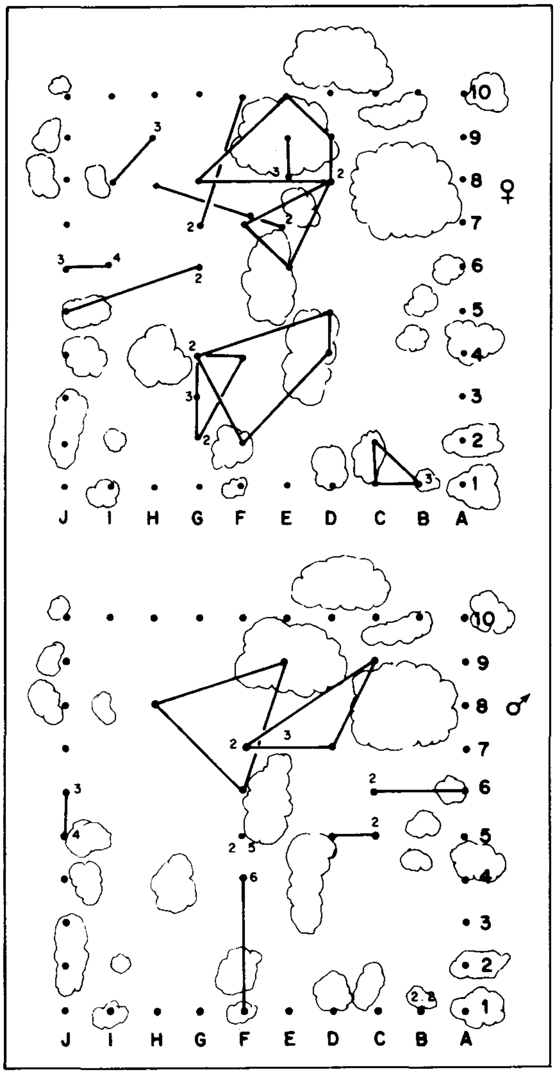

Fig. 11. Home ranges of *Sigmodon alstoni* individuals in Masaguaral as determined by joining the peripheral capture points. The numbers on each capture point indicate the number of times an animal was caught in the trap, and non-numbered dots within the grid indicate single captures.

Ambitos de hogar de *Sigmodon alstoni* individuales, determinados uniendo los puntos más periféricos de captura. Los números en los puntos indican las veces que se capturó un animal en cada trampa. Los puntos dentro del área de trampeo que no llevan número indican una sola captura.

In essence, it would seem from the studies so far undertaken that there is a gradient of increasing density towards the higher llanos of Barinas and Portuguesa and lower density towards the states of Guárico and Apure. The implication of this apparent gradient is that *S. alstoni* in the lower savannas may be occupying marginal ecological habitats or that it is close to the edge of its geographical distribution. Circumstantial evidence for this hypothesis is that only 10 km away from Masaguaral, *S. alstoni* reaches higher density but only in the higher areas in between rice fields (E. Weir, personal communication, who trapped intensively and caught numerous rodents, now deposited at the Simón Bolivar University's Museum of Natural History). Given that rice in the area is grown during the dry season, and the fields are artificially flooded, we could infer that *S. alstoni* requires a more mesic condition than that found during the dry season at Masaguaral, and more like that in the higher llanos. However, the species does not seem to be able to tolerate extensive flooding as is indicated in this study by the low densities towards the end of the rainy season. In fact, Soriano (1977) hypothesized that *S. alstoni* migrates from the bajío areas which flood in the rainy season to the banco areas which do not flood. Although he did not have any emigration data, because he used snap-traps, it is as idea worth testing as I find that in the transition between the rainy season and the dry season the animals simply disappear from the grids and new ones are found in the dry season.

Because *S. alstoni* has no apparent adaptations to survive in very flooded conditions, as does another Sigmodontinae species occurring in the same area, *Holochilus venezuelae*, the above contention that *S. alstoni* requires drier areas than Masaguaral, is plausible. This species cannot swim very well (personal observation), whereas *Holochilus venezuelae* (as do other members of the genus) have interdigital membranes for swimming (Sierra, 1969). *Zygodontomys microtinus* is also an excellent swimmer (August 1984; Vivas personal observation). On the other hand, *S. alstoni* does not seem to tolerate extremely dry areas, as is indicated by its low density even during the increase phase and peak density in the dry season. Besides, it seems not to be adapted to areas of very woody vegetation with extensive cover, as evidenced by ist preference for the ecotone between Mata and savanna (above, and Péfaur, personal communication). Overall it seems as if *S. alstoni* is ill adapted to the savannas of Guárico and Apure, which suffer extreme flooding and harsh dry season alternately.

The above discussion suggests that *S. alstoni* may be a recent invader of the savannas of Guárico and Apure. In fact, the lower llanos as they are today developed between 6000 to 2000 years before present, after the last glaciation (Roa-Morales 1979, 1981). Thus, the Banco-Bajío geomorphological units are relatively recent and probably *S. alstoni* has not yet adapted to the dry-wet extreme seasonality of the lower llanos. That would explain its low densities at Masaguaral and the apparent density gradient towards higher density in the higher llanos of Portuguesa and Barinas. It would also explain why the lower llanos might be marginal ecological habitats for the species.

Sex ratios in *S. alstoni* at Masaguaral present an interesting situation: females were more abundant than males throughout 1983, but not 1984. When sex ratio was discriminated by season, it favored females during the rainy season in 1983 and males in the rainy season of 1984. This fact does not have a simple explanation, but it might be related to the general condition of the animals. According to the B/W index, females were in better condition in the dry season when their density increased, and in worse condition in the rainy season when their density decreased. Males followed, in general, a reversed pattern. Thus, it is plausible that during years with a normal rainfall pattern (like 1983), the females are not affected as much as the males in the increase phase, wich could explain the female-biased sex ratio in 1983. But in years with erratic rainfall patterns (like 1984), females suffer greatly even in the dry season, enough to hamper their increase, which would explain the non-significant sex ratio in 1984. Furthermore, if we consider that during the rainy seasons the females remained in a high reproductive condition, and that juvenile recruitment at that time was extremely low or non-existant, then we could infer that if females are not in good condition they will not reproduce succesfully. If we add that the density of females in 1984 was half of that in 1983, and that the density pattern of the males in both years was about the same, then we can surmise that female condition may be determinant in the success and maintenance of the population, more so than male condition.

The age distribution of the trappable population indicates a bias towards adults, and concentration of juveniles and subadults in the dry season and first part of the rainy season. Because both males and females were reproductively capable all year-round (at least as shown by external reproductive characteristics), it is not possible to know whether there is a definite reproductive season during the dry season. Detailed morphological data is needed to determine age groups precisely, and hormonal studies to determine changes in reproductive activity throughout the year.

The survival pattern is not very clear. What becomes of the rodents during the transition rainy-dry seasons is puzzling. Equally puzzling is where do the new founders come from? If we accept Soriano's (1977) view of a seasonal change in habitat, or that the rodents are searching for unsubmerged habitat of the same type just left, we would have a plausible explanation of why animals disappear part of the year. However, no dispersal studies are available as of now to test this hypothesis. The survival pattern is clear in only one respect: the second year was harsher for *S. alstoni* (as it was for *Z. microtinus*, Vivas 1984). The fact agrees with a more erratic rainfall pattern in 1984 than in 1983 when flooding was more extensive, but less variable. The erratic rainfall pattern of 1984 was translated into a rise and fall of the water level in the grid, decreasing and increasing intermittently the available area for nesting and cover. To the contrary, in 1983 the water level was constantly higher than in 1984, but it was reached through a gradual increase, and it might have allowed the rodents to establish in the higher drier places, permitting moderate recruitment, and thus higher density than in 1984. The longer permanence period of the rodents in the grid in 1983 than in 1984 lends support to this inference, because densities were higher then, when permanence of the water in the grid was longer.

Females had higher survival than the males in the rainy season of 1983. This fact may help explain the female-biased sex ratio during that year and season. Males had very high survival in the dry season of 1984 and low in the rainy season, which may help explain the decrease in density that year and season.

Population density and female survival are apparently related, at least in the rainy season and throughout 1983. Thus, it would be of much interest to determine the ways by which survival may be influencing density. Unfortunately, this will only be feasible when we can keep more precise track of individual animals, hopefully via telemetry.

A study of resource availability and utilization by *S. alstoni* (Vivas, Weir & Gil, unpublished results) suggests that his species tracks its resources. A study on *S. hispidus* (Vivas & Calero, unpublished results) indicates that there is an influence of availability on utilization of resources in response to the phenology of the plant foods. Grazing and trampling of the vegetation was suggested by august (1984) as a possible factor in food depletion. I believe that the influence of these factors on the density of *S. alstoni* is very small, especially because no evidence of overgrazing was detected on or near the study area. In fact, grazing may stimulate increase in primary production if the pressure of grazing is not too large, as occurs in the Serengeti (McNaughton 1985). Besides, the vegetation in the dry season, even though it has lower primary productivity, has a high production of energy-rich seeds which are consumed by *S. alstoni* (Vivas, Weir & Gil, unpublished results).

Both transition periods in between the dry and rainy seasons seem to be critical moments for all *S. alstoni* population parameters: density, survival, reproduction, and age structure. Even morphological or physiological changes may be taking place then, as evidenced by changes in body weight and general condition. Habitat changes which influence cover and resource availability also take place during the transition periods. It then becomes evident that these moments may be very important as selective bottlenecks which may be responsible for triggering events that drive the entire demographic machinery of the species. Thus, it becomes imperative for the understanding of the population biology of *S. alstoni* to carefully monitor events on individuals during the transitions between seasons.

To summarize, *S. alstoni* shows low densities throughout the year, although there are definite increase and decrease phases that may be related to rainfall somehow. The information from this study revealed several clear lines of evidence: 1) *S. alstoni* presents a yearly fluctuation in density, increasing in the dry season and decreasing in the rainy season. 2) The most important population parameters influencing density may be survival and reproduction. 3) Rainfall influences the demographic pattern probably via its effect on habitat reduction during the rainy season. 4) The transition periods in between season seem to be the environmental cues that trigger the demographic events.

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