EFFECTS OF CLIMATE AND FOOD AVAILABILITY ON FOUR RODENT SPECIES IN SOUTHEASTERN BRAZIL

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Seasonal reproduction of small mammals in the tropics usually is related to annual cycles of rainfall. We examined effects of weather and food availability on reproduction and population ecology of *Nectomys squamipes, Oryzomys intermedius, Akodon cursor* and *Trinomys iheringi*. Each species was studied monthly from February 1993 to January 1995 using mark-recapture methods at Ilha do Cardoso, São Paulo State, Brazil. Average capture rate for each month was used as an index of population size, and survival rate was estimated by the Jolly-Seber method. Direct effects of food availability and rainfall were related to female reproductive activity and survival rate. Path analyses were used to describe quantitatively the hypothesized causal relations among the variables. *N. squamipes* reproduced seasonally, and *O. intermedius, T. iheringi,* and *A. cursor* reproduced all year with peaks during the rainy season. Species responded differently to the environmental factors; however, food availability seems to be the main factor determining reproduction. Abundance of rains appears to diminish survival rate of *O. intermedius.* Survival rate of *N. squamipes* increases with increases in fruit availability.

Key words: *Nectomys squamipes, Oryzomys intermedius, Trinomys iheringi, Akodon cursor,* reproduction, population ecology, Brazil

Proximal causes of variation in population size are the entrance of new individuals into the population by birth or immigration, or their loss due to death or emigration. However, primary causes of population fluctuations are variations in extrinsic factors. Food availability is often an important extrinsic factor influencing abundance and species diversity in a community (Rosenzweig, 1995). However, population regulation must be analyzed in a multifactorial context (Lidicker, 1983, 1988). This study focused on one of the most important determinants of variation in population size: reproduction and its relationship to environmental factors in three species of sigmodontine rodents (*Nectomys squamipes, Oryzomys intermedius, Akodon cursor*) and one species of echimyid rodent (*Trinomys iher-*

ingi) in an area of Atlantic forest of southeastern Brazil.

The Atlantic forest once covered 1,000,000 km^2, but due to human activities, now is ca. 5% of its original size (Lino, 1992). Biological diversity in the Atlantic forest is markedly high due to the variety of climatic conditions, altitude, and latitude present in a continuous strip of woodland along the Brazilian coast. Nevertheless, information about the biology of the species in this area, and the Neotropical region as a whole, remain scarce (Mares and Ernest, 1995).

Small mammals of the Neotropical forest can reproduce throughout the year or have distinct breeding periods (Lacher, 1992). For those species that breed seasonally, many studies have shown the relationships between reproduction and weather (Bergal-

lo, 1994; Bergallo and Cerqueira, 1994; Cerqueira, 1984; Cerqueira and Lara, 1991; Dietz, 1983; Fleming, 1971; Rigueira et al., 1987; Streilein, 1982). In the tropics, seasonal reproduction of mammalian species probably is related to annual cycles of rainfall (Heideman and Bronson, 1990). However, reproduction occurring in rainy periods may be due to higher food availability (Atramentowicz, 1982, 1986; Davis, 1945; Fleming, 1973; Julien-Laferrière and Atramentowicz, 1990), and variation in food availability may in turn be related to weather. Because of this connection, understanding factors that influence reproduction of small mammals is difficult. Nevertheless, the majority of the studies that have examined reproductive biology of small mammals lack a multifactorial model and attribute variation to only one factor (Flowerdew, 1987).

Reproductive studies of small mammals in the field usually are based on condition of females, and there is little information about males (Fernandez, 1989; Fonseca and Kierulff, 1989). This lack of information for males is probably because position of scrotal testes (abdominal or inguinal) is not a good indicator of reproductive condition (Cerqueira, 1984) because it can be subjective.

We sought to answer four following questions. Which environmental factors were related directly to each species' reproduction and survival? What were the direct and indirect effects of rainfall on reproduction? Which environmental and intrinsic factors were related directly to densities of adults, subadults, and juveniles? Can size of scrotal testes be used to determine reproductive periods for each species of rodents?

MATERIALS AND METHODS

Our study and trapping program were carried out in an area of Atlantic forest on Ilha do Cardoso (Cardoso Island, 22,500 ha), located in Cananéia municipality, on the southern coast of São Paulo State, Brazil (25°03'S, 47°53'W). The climate was subtropical, with no water deficit
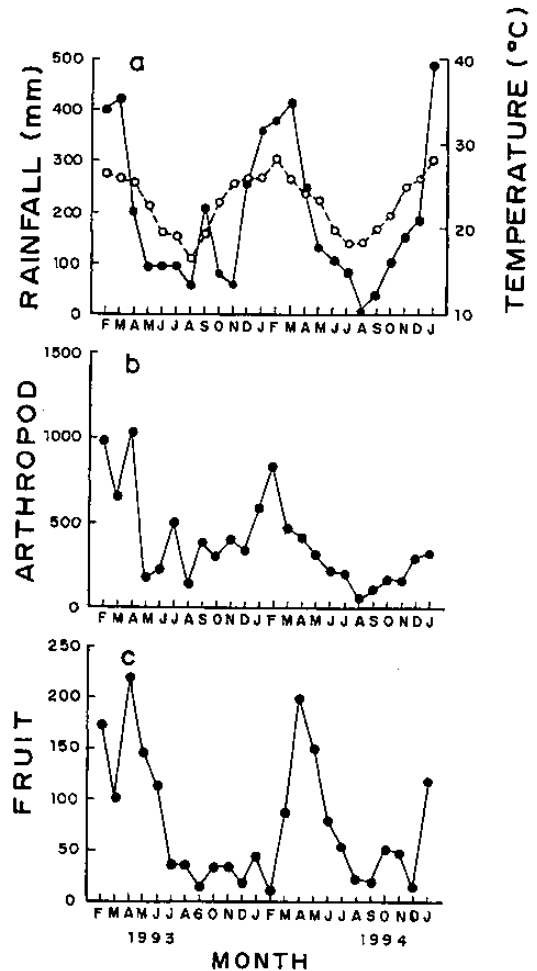

FIG. 1.—Monthly variation in a) mean temperature (dashed line) and rainfall (continuous line), b) availability of arthropods (mm³/0.10 m²), and c) availability of fruits (g/0.096 ha) in Ilha do Cardoso, Brazil, from February 1993 to January 1995.

during winter (June–August) but a surplus in summer (December–February—Funari et al., 1987). More than 70% of the rain fell between December and April during the study period (Fig. 1a). Average temperature was 23.2°C in 1993 and 23.1°C in 1994. The coldest months were August 1993 and July 1994, and the hottest month was February in both years (Fig. 1a). Weather data were obtained from the Climatological Center of Ilha do Cardoso, ca. 4 km from the study area.

The study site, located near a small river (Pe-

requê River, ca. 10 m wide and 1.5 m deep) was in a transition zone between coastal-plain tropical rainforest and montane tropical rainforest. In coastal-plain tropical rainforest, trees were 8–20 m in height and were covered by vines and epiphytes (Barros et al., 1991). The most common tree families were Myristicaceae, Leguminosae, Vochysiaceae, Euphorbiaceae, Monimiaceae, Sapotaceae, and Meliaceae (Barros et al., 1991). The shrub-herbaceous layer was dense and dominated by Heliconiaceae, Marantaceae, and Rubiaceae (Barros et al., 1991). There was little stratification of the montane tropical rainforest, and the most frequent families were Palmae, Rubiaceae, Guttiferae, Apocynaceae, Sapotaceae, Lauraceae, and Myrtaceae (Melo and Mantovani, 1994).

The trapping grid covered 8.8 ha and included the floodplain around the river (5.2 ha) and the montane forest (3.6 ha). The grid was irregular and had eight trails each with 15 trap stations and six trails each with 20 trap stations, spaced 20 m apart, totaling 240 trap stations. Monthly from February 1993 to January 1995, 120 traps were placed at trap stations separated by 40 m during 2 nights. Traps were moved 20 m on the 3rd day, so that the 240 capture stations of the grid could be covered in each 4-day session. Traps were baited with banana or manioc and peanut butter. *Nectomys squamipes, O. intermedius, A. cursor,* and *T. iheringi* were studied with mark-recapture methods.

Captured animals were marked with an ear-perforation code, weighed, measured (length of head and body, hind foot, tail and head), sexed, and released at the capture station. Females were palpated to detect pregnancy. Width and length of scrotal testes of males were measured with vernier calipers; the product of width and length was used as an index of scrotal size.

Resource availability.—Fallen fruits were collected monthly by hand in 80- by 1-m transects along 12 trails in the study site. Mass of fruit collected in each monthly sample was used as an index of fruit availability, during that trap session. Arthropods were collected in 14 cylindrical pit-fall traps (70.9 cm^2 collecting area) left open with an 8:1 water and detergent solution for 72 h every month. Invertebrates collected were fixed in 70% alcohol, and their length, width, and height were measured (Schoener, 1968). The sum of the specimen volume each month was used as an index of availability of arthropods.

Female reproduction.—Percentage of females that were pregnant or had visible nipples (lactating) was used as an index of reproductive activity. Percentages were arcsine transformed for statistical analyses. For *N. squamipes* and *T. iheringi,* we used only the number of pregnant females registered each month. For *O. intermedius* and *A. cursor,* pregnancy detection was more difficult and less accurate than in the larger species (H. Bergallo, in litt.), so we also considered females with visible nipples to be reproducing. Reproductive frequency of females was evaluated relative to fruit and arthropod availabilities and rainfall with multiple regression to determine if those factors were directly influencing reproductive activity of the species. When we had no a priori model to define variation in reproductive parameters, we used the locally weighted least-squares regression (LOWESS) to describe the temporal reproductive patterns (Wilkinson, 1988). Tension was set at 0.5.

Male reproduction.—The index of scrotal size was evaluated relative to size (length of head and body or length of head) and mass measurements with multiple regression to remove the effect of animal size on scrotal size. Residuals from that relationship for each species were averaged monthly to obtain an index of male reproductive condition. To test if that index could be used as an indication of reproductive activity, we correlated it with frequency of pregnant females of *N. squamipes, O. intermedius,* and *A. cursor,* and with the frequency of pregnant females with time lag of 1 month for *T. iheringi,* because gestation in this genus lasts ca. 60 days (Everard and Tikasingh, 1973) and we had recorded fetuses when they were at the minimum size detectable by palpation.

Path analyses.—Frequency of female reproductive activity was related to resource availability and rainfall by multiple regression to evaluate direct effects on reproduction. Multiple regression only identifies direct effects (King, 1993). However, reproductive activity may respond to both direct and indirect effects. Multiple regression techniques have statistical and biological limitations to identify the real influence of factors and examine causal mechanisms (Crespi and Bookstein, 1989; Kingsolver and Schemske, 1991). Path analyses can be used to reduce those limitations, although it has many

of the same statistical assumptions as multiple regression and attributing probability values to individual paths usually is not justified (Petraitis et al., 1996).

The path diagram showing the causal and non-causal relationships among all the dependent and independent variables in the system was based on a priori knowledge (Kingsolver and Schemske, 1991). Studies of small mammals in tropical regions have shown that reproduction is associated with the period of highest rainfall and food availability. Hence, our proposed model for rodent species on Ilha do Cardoso was that rainfall and availabilities of fruits and arthropods directly affect reproductive activity of females. However, because activities and densities of arthropods increase during the rainy season in warmer months due to reproduction of many plants, rain also should have an indirect effect on abundances of arthropods (Janzen, 1973; Janzen and Schoener, 1968; Wolda, 1978). Response of arthropods was not expected to be immediate; there should be a small time lag between change in weather and population response of arthropods (Brown, 1992). Rain also should have an indirect effect through availability of fruits. As availabilities of arthropods and fruit respond to rain with a 1-month time lag (Bergallo, 1995*b*), rainfall also should have an indirect effect on the reproduction of rodents through availability of food.

Effect of rainfall on pregnancy rate should be indirect through fruits and arthropods. However, the direct effect of rainfall was placed in the model to investigate a possible negative effect on reproduction. Rainfall was used in all a priori models as an indication of weather changes. Because temperature, rainfall, and day length are highly correlated, results may reflect the effects of other variables. Path-analysis coefficients indicate the direct contribution of one variable on another when all the others are kept constant (Li, 1975; Pedhazur, 1982). The indirect effect of an independent variable is the product of coefficients along that path. The sum of direct and indirect effects, the effect coefficient, represents the expected change in a variable given the expected variation in the others. Residual variables include all non-measured variables that affect arthropods, fruits, and pregnancy rates (Kingsolver and Schemske, 1991). The residual variable is mathematically equivalent to $(1 - R^2)^{1/2}$, where R^2 (coefficient of determination) is the

proportion of variation that was explained by the path diagram (Kingsolver and Schemske, 1991). Generally, the effect coefficient is estimated by summing the direct effect with various indirect effects. Hence, the effect coefficient refers only to one variable. Nevertheless, rainfall and rainfall with a 1-month time lag were essentially the same variable with the same distributions and magnitudes. In this case, the sum of the effect coefficients of both variables was used as the effect coefficient of rain, independent of when it fell. Path coefficients and their standard errors were calculated by the program EzPath (SYSTAT—Steiger, 1989), after obtaining a matrix of Pearson correlations with all variables that composed path diagrams.

Population ecology.—Population size of each species was estimated as number of captures per month. Population size was estimated separately for age classes (juvenile, subadults, and adults). Population size of each age class was related with population size of the previous age class and food availability with multiple regression to determine direct effects of those factors. We also included in the multiple regression model, average monthly distance traveled between traps for adult age classes of *N. squamipes* and *O. intermedius*. Distance traveled was the maximum distance between captures for an individual within a capture session. The average of distances for each species was used as an index of movement. Distance traveled was an index of dispersal rates; population size of the previous age class was an index of birth rates. Food availability was used in the model to determine if the population size fluctuated according to that factor.

Survival rate between sampling periods was estimated by the Jolly-Seber method (Caughley, 1979). Survival rate was related to availabilities of fruits and arthropods, and rainfall by multiple regression to determine if those factors directly influenced survival in populations. Data were sufficient for this analysis only for *N. squamipes* and *O. intermedius*.

RESULTS

Resource availability.—The index of availability of arthropods was highest in February 1993 and 1994 and April 1993 during the rainy season (Fig. 1b). The lowest values were found in August 1993 and
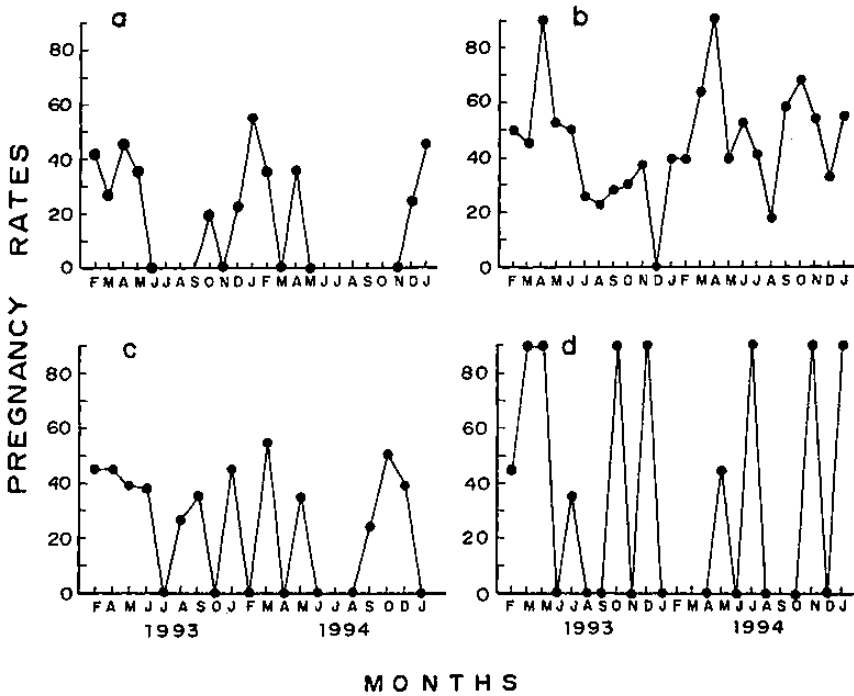
FIG. 2.—Pregnancy rates (arcsine transformed) of a) *Nectomys squamipes,* b) *Oryzomys intermedius,* c) *Trinomys iheringi,* and d) *Akodon cursor* in Ilha do Cardoso, Brazil, from February 1993 to January 1995.

1994 during the coldest and driest months. The index of availability of fruits was highest in April 1993 and 1994 (Fig. 1c). The lowest values were obtained between August and December of both years.

Apparently, the peak of availability of arthropods preceded that of fruits by 1–2 months. Fruits are available up to the beginning of the dry season, by which time availability of arthropods already declined considerably. At the end of the dry season and beginning of the wet season, the availability of arthropods increased whereas that of the fruits reached its lowest value. There were significant relationships between availabilities of fruits and arthropods and rain with a 1-month time lag ($r = 0.622$, $P < 0.001$ and $r = 0.761$, $P < 0.001$, respectively).

Nectomys squamipes.—Female *N. squamipes* reproduced during the rainy season (Fig. 2a). The breeding season was bimodal and was initiated in October 1993

and December 1994 and was finished by May 1993 and April 1994. No female was observed reproducing during the coldest and driest months (mean temperatures $<22°C$). Females with protruding nipples were collected during the same months that pregnant females were recorded and for 2 additional months. Three females collected in October 1994 had visible nipples, possibly indicating the beginning of the breeding season of that year.

About 68% of the variance in female reproductive frequency was explained by the model including availability of fruits and arthropods, and rain ($R^2 = 0.677$, $F = 12.598$, $d.f. = 3,18$, $P < 0.001$). The relationship with all variables was positive. However, availability of arthropods ($P = 0.343$) did not explain a significant fraction of the variance of pregnancy after taking into account availability of fruits ($P = 0.055$) and rainfall ($P = 0.007$).
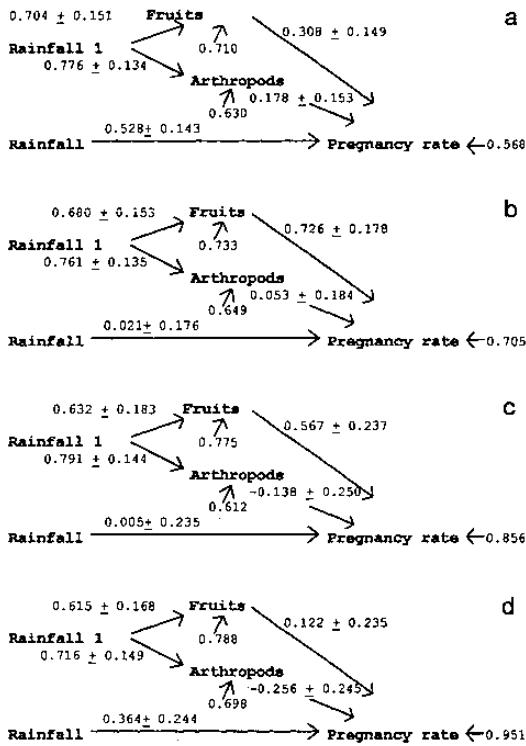
Path analysis indicated that both avail-

FIG. 3.—Path diagrams of the pregnant frequency determinants of a) *Nectomys squamipes,* b) *Oryzomys intermedius,* c) *Trinomys iheringi,* and d) *Akodon cursor* in Ilha do Cardoso, Brazil, from February 1993 to January 1995. There is a time-lag of 1 month from rainfall to availability of arthropods (Arthropods) and availability of fruits (Fruits); there is no time-lag between Rainfall and Pregnancy rate. Path coefficients ± *SE* are presented.
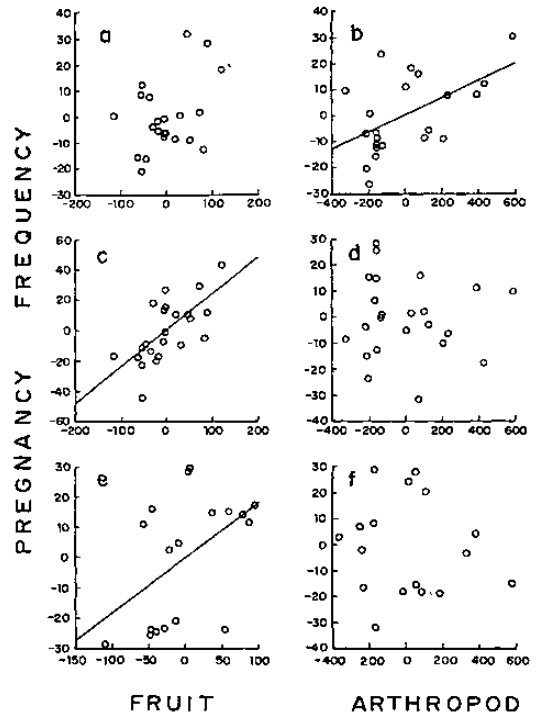

FIG. 4.—Partial regressions between pregnancy frequencies of *Nectomys squamipes* (a and b), *Oryzomys intermedius* (c and d), and *Trinomys iheringi* (e and f) and availabilities of fruits and arthropods in Ilha do Cardoso, Brazil. Partials with regression lines are significants (*P* < 0.05)

abilities of arthropods and fruits were related positively to rainfall (Fig. 3a). The general effect of rainfall on pregnancy was positive, both directly and through availabilities of arthropods and fruits (Fig. 3a). The direct effect of the rain (0.53) on pregnancy was higher than the direct and indirect paths through availabilities of fruits (0.31, 0.22, respectively) and arthropods (0.18, 0.14, respectively). Overall effect coefficient was 0.88, indicating that a change in 1 *SD* in average rainfall will produce a change of 0.88 *SD* in the frequency of pregnant females in the population.

Because rainfall was measured ac-curately than availability of food, it may have obscured a causal effect of food resources on reproduction. There was no positive effect of rain on reproduction in an area where there is no water deficit. Therefore, we repeated the multiple regression for all species without rain. The multiple regression for *N. squamipes* was significant (R^2 = 0.509, F = 9.866, *d.f.* = 2,19, P = 0.001) and availability of arthropods (P = 0.012) explained a significant proportion of pregnancy rate after accounting for the effect of availability of fruits (P = 0.082; Figs. 4a and 4b).

In *N. squamipes,* weight and head and body measurements were correlated positively to size of scrotal testes (R^2 = 0.507, F = 80.334, *d.f.* = 2,156, P < 0.001). Variation accounted for by size of testes after
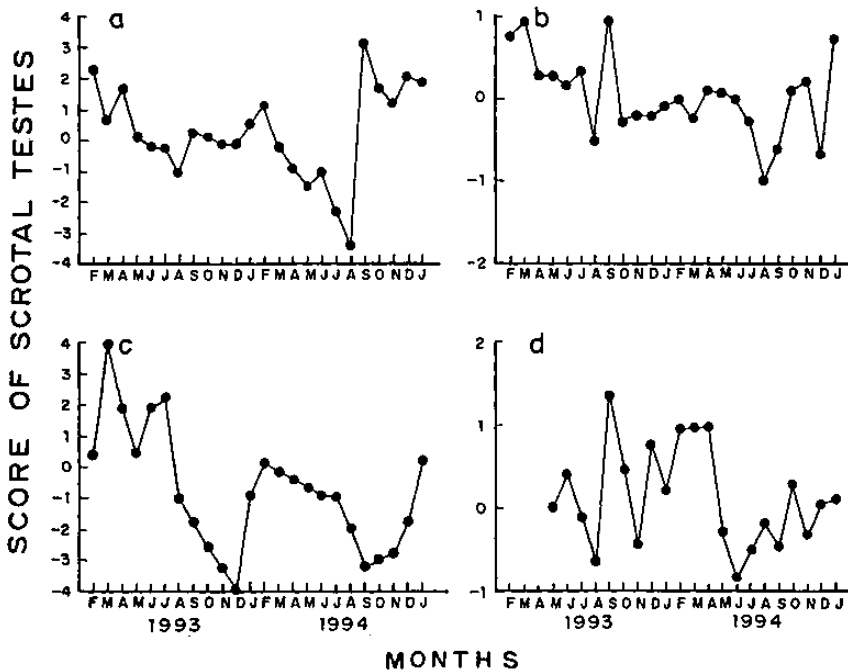
FIG. 5.—Monthly variation in size of scrotal testes independent of animal mass in a) *Nectomys squamipes*, b) *Oryzomys intermedius*, c) *Trinomys iheringi*, and d) *Akodon cursor* in Ilha do Cardoso, Brazil, from February 1993 to January 1995.

removing effects of weight ($P = 0.001$) and head and body ($P = 0.019$) was high. In both years, lowest values in size of testes were observed in August and the highest during the rainy season (Fig. 5a). Size of scrotal testes was correlated positively to pregnancy rate ($r^2 = 0.184$, $F = 4.514$, *d.f.* $= 1,20$, $P = 0.046$).

Densities of adult *N. squamipes* were fairly constant throughout the year (Fig. 6a). Juveniles were collected mainly at the end of the rainy season and subadults during the dry season. Monthly densities ($\bar{X} \pm$ *SD*) were 7.8 $\pm$ 3.5 (range $= 2$–15) for adults, 5.8 $\pm$ 6.9 (range $= 0$–32) for subadults, and 2.4 $\pm$ 2.7 (range $= 0$–11) for juveniles. The proposed model explained a significant proportion of the variance in observed numbers of juveniles ($R^2 = 0.390$, $F = 5.754$, *d.f.* $= 2,18$, $P = 0.012$). Numbers of juveniles were correlated positively to pregnancy rates 2 months before ($P = 0.003$) and correlated negatively to avail-

ability of food ($P = 0.047$). The model also explained a significant proportion of the variance in observed numbers of subadults ($R^2 = 0.594$, $F = 13.898$, *d.f.* $= 2,19$, $P < 0.001$). Both number of juveniles with 2 month time lags ($P < 0.001$, positively) and availability of food ($P = 0.028$, negatively) contributed to the regression. Adult numbers were not correlated to variables in the model ($R^2 = 0.284$, $F = 2.374$, *d.f.* $= 3,18$, $P = 0.104$), but numbers of subadults with 2-month time lags explained a fraction of the variance observed ($P = 0.019$) after taking into account effects of availability of food and distance travelled.

Variation in survival rate was not explained by the model with availabilities of fruits and arthropods, and rainfall ($R^2 = 0.232$, $F = 1.717$, *d.f.* $= 3,17$, $P = 0.201$). However, after accounting for effects of availability of arthropods and rainfall, availability of fruits almost entered the model ($P = 0.053$). Survival rate was re-
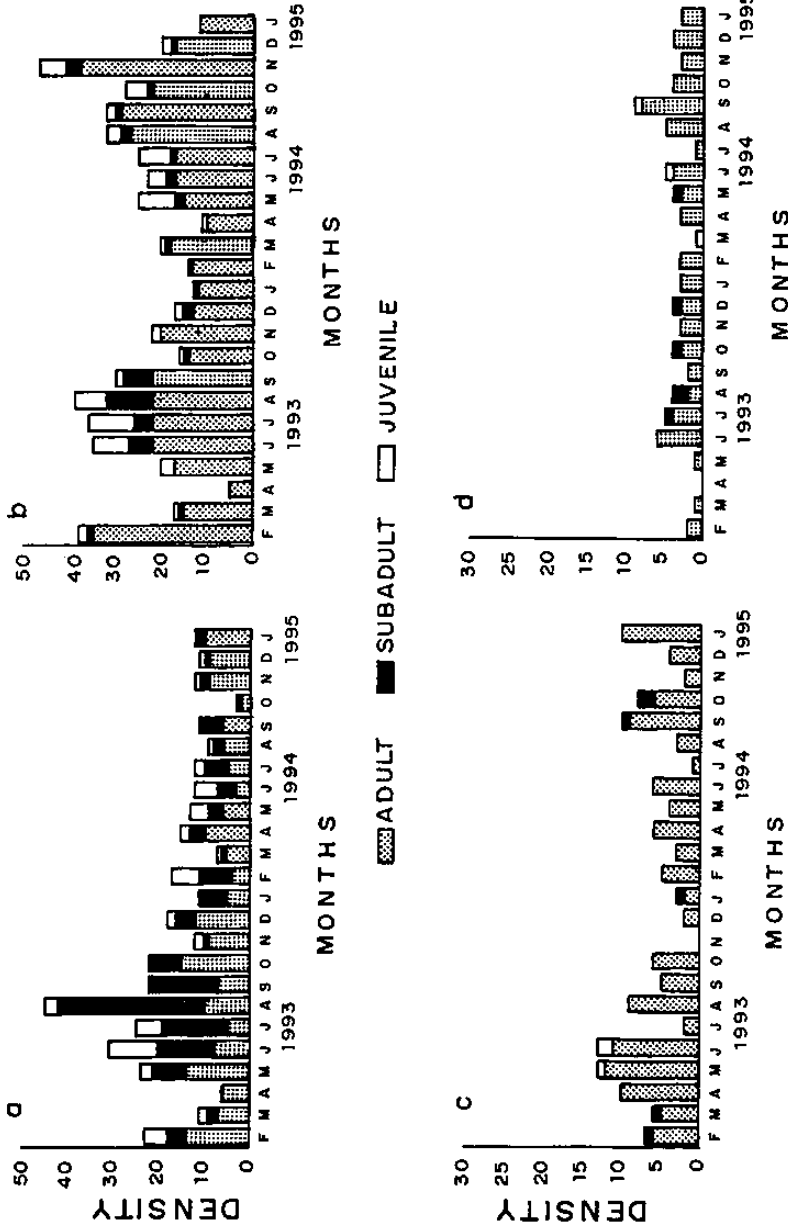
FIG. 6.—Density (individual captured/month) of a) *Nectomys squamipes*, b) *Oryzomys intermedius*, c) *Trinomys iheringi*, and d) *Akodon cursor* in Ilha do Cardoso, Brazil, from February 1993 to January 1995.
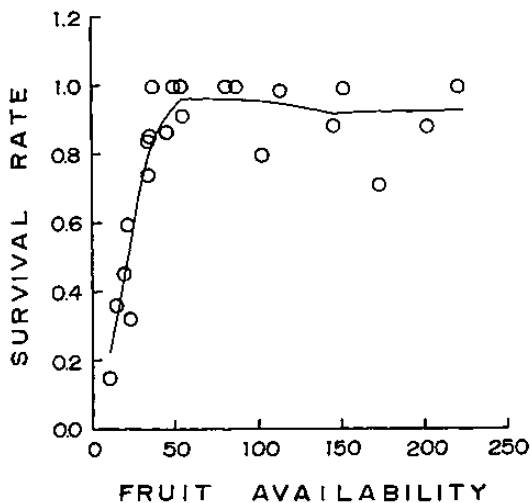
FIG. 7.—Relationship between survival rate of *Nectomys squamipes* and availability of fruits (g/0.096 ha) in Ilha do Cardoso, Brazil. The line was adjusted by LOWESS (tension = 0.5—Wilkinson, 1988).

lated assymptotically to availability of fruits (Fig. 7).

Oryzomys intermedius.—Female *O. intermedius* were observed pregnant or with protruded nipples throughout the year (Fig. 2b). However, there appeared to be a peak in reproductive activity during the rainy season and a decrease in dry and cold months (July–December 1993–1994). Variation in reproductive activity of *O. intermedius* was explained by the model (R^2 = 0.503, F = 6.412, $d.f.$ = 3,19, P = 0.003). Availability of fruits contributed significantly to the model (P = 0.001), but availability of arthropods (P = 0.812) and rainfall (P = 0.920) did not. As indicated by path analysis, direct effects of rainfall and arthropod availability on the pregnancy rate of *O. intermedius* were negligible. Availability of fruits had the highest association with female reproduction (Fig. 3b). The total effect of rainfall on female reproduction was 0.47, but rainfall only had a large effect indirectly through availability of fruits (0.49). The direct effect of the fruit (0.73) was higher than the sum of direct and indirect effects of rainfall. Removal of rain-

fall from the model (R^2 = 0.503, F = 10.113, $d.f.$ = 2,20, P = 0.001) did not change the conclusion that availability of arthropods (P = 0.822) was not significantly related to pregnancy rate (Fig. 4c), but availability of fruits was (P = 0.001; Fig. 4d).

Size of scrotal testes was related to head length (P = 0.003) and mass (P < 0.001) (R^2 = 0.289, F = 55.562, $d.f.$ = 2,273). The lowest values observed of size of testes occurred in August in 1993 and 1994. Peaks occurred in March and October 1993, October and November 1994, and January 1995 (Fig. 5b). Pregnancy rate was not correlated with size of testes in *O. intermedius* (P = 0.205).

Oryzomys intermedius was the most abundant species on the grid. The adult population varied from 5 to 38 individuals with mean ($\pm$ SD) of 18.9 $\pm$ 7.7 individuals captured/month. Adult populations showed peaks during the dry season from June to November (Fig. 6b). Juveniles were collected throughout most of the year but were most common at the beginning of the dry season, with mean of 3.2 $\pm$ 2.9 (range = 0—10; Fig. 6b). Subadults were captured with a higher frequency during the dry season (Fig. 6b) with mean of 1.9 $\pm$ 2.3 (range = 0–10).

The model explained a significant proportion of the variation in number of juveniles captured (R^2 = 0.280, F = 3.885, $d.f.$ = 2,20, P = 0.038), and the pregnancy rate with 1-month time lag had the largest (positive) effect (P = 0.030). Food availability was associated negatively with juvenile numbers, but its contribution to the model was not significant (P = 0.056). The model also explained a significant proportion of the variance in subadult captures (R^2 = 0.554, F = 12.399, $d.f.$ = 2,20, P < 0.001), but availability of food did not contribute significantly to the model (P = 0.674) after accounting for the effect of juvenile captures with 1-month time lag (P < 0.001). Adult captures were related to availability of food, subadult captures, and distance

traveled (R^2 = 0.447, F = 4.847, $d.f.$ = 3,18, P = 0.012). However, only availability of food was correlated positively to adult numbers (P = 0.001), after accounting for effects of subadult captures with a one month time-lag (P = 0.792) and distance traveled (P = 0.672).

Survival rate of *O. intermedius* was not explained with the variables measured. However, the partial regression of rainfall was negative and close to significant (P = 0.073).

Trinomys iheringi.—Pregnancy rate of *T. iheringi* varied considerably in the 24 months of the study (Fig. 2c). Reproductive peaks were observed in February and April 1993 and March and October 1994. Because there was no clear pattern of seasonality in reproduction, we used a LOWESS curve to describe the time series. Peaks in each year occurred at the end of the wet season and the beginning of the dry (Fig. 8a). Pregnancy rates were not correlated with availabilities of fruits and arthropods, and rain (P = 0.213), but the partial regression for availability of fruits (P = 0.047) explained a significative proportion of variation in pregnancy rate after effects of the other variables were removed.

The major effect in the path model was availability of fruits (Fig. 3c), followed by the indirect effect of rain, through availability of fruits (0.36). The effect of availability of arthropods on pregnancy rate was negative and, consequently, so was the indirect effect of rain through availability of arthropods (−0.11). The sum of the indirect and direct effects of the rain was lower (0.25) than the direct effect of availability of fruits.

Multiple regression without rainfall gave similar results to the complete model (R^2 = 0.267, F = 2.731, $d.f.$ = 2,15, P = 0.097). The partial regression of availability of arthropods on pregnancy rate was not significant (P = 0.600) (Fig. 4e), and the partial regression for availability of fruits was positive (P = 0.039; Figure 4f).
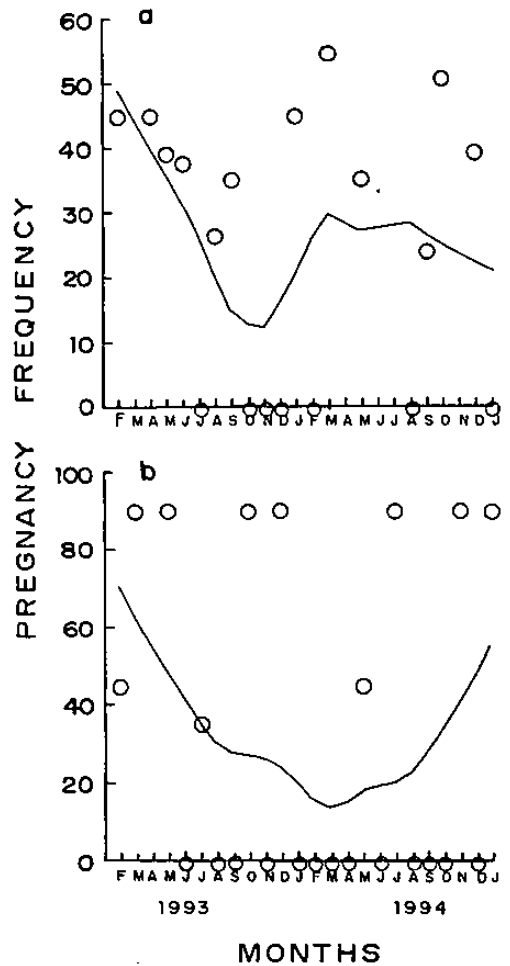
Only mass was significantly related to

FIG. 8.—Tendency curves (LOWESS—Wilkinson, 1988) of the pregnancy frequencies of a) *Trinomys iheringi* and b) *Akodon cursor* in Ilha do Cardoso, Brazil, from February 1993 to January 1995.

size of scrotal testes in *T. iheringi* (R^2 = 0.152, F = 8.451, $d.f.$ = 1,47, P = 0.006). The index of size of testes varied between years, but it was higher from the end of the rainy season to the middle of the dry season in 1993 and 1994 (Fig. 5c). Regression of scrotal testes and pregnancy rate with a 1-month time lag was not significant (r = 0.26, F = 4.20, $d.f.$ = 1,12, P = 0.063). However, the low probability for the null hypothesis indicate a high probability of a type error II.

Few juvenile (n = 3) and subadult (n =

6) *T. iheringi* were collected on the grid (Fig. 6c). Adults were collected throughout the year, except in November 1993, with an average ($\pm$ *SD*) of 5.4 $\pm$ 3.3 individuals/month (range = 0–12). The adult population was higher during the middle to the end of the rainy season in both years and during the end of the dry season of 1994. The model did not explain the variance observed in adult frequency (P = 0.360).

Akodon cursor.—Sexually active female *A. cursor* were observed in different months without any clear pattern (Fig. 2d). Using LOWESS to smooth the time series indicated a decrease in sexual activity in the coldest months between June and August 1993 and 1994 (Fig. 8b). Multiple regression indicated that pregnancy rates were not significantly related to rainfall or availabilities of fruits and arthropods (P = 0.604).

The number of female *A. cursor* captured was too low for a detailed analysis, but we subjected data to the path analysis with the intention of generating, rather than testing, hypothesis. Rainfall appeared to have the greatest effect on pregnancy rates of *A. cursor* (Fig. 3d). The effect of availability of arthropods was negative and consequently, so was the indirect effect of the rain through that variable (-0.18). The coefficient for availability of fruits was negligible (0.07). The total effect of rainfall on female reproduction was similar to the direct effect of availability of arthropods (0.26). Multiple regression of frequency of pregnant *A. cursor* with availabilities of fruits and arthropods was not significant (P = 0.732).

Length of head (P = 0.006) and mass (P < 0.001) explained a significant proportion of the variance in size of scrotal testes for *A. cursor* (R^2 = 0.595, F = 16.865, *d.f.* = 2,23, P < 0.001). Peaks in size of scrotal testes were observed in September 1993 and October 1994 and during the rainy season in 1994 (Fig. 5d). Size of scrotal testes, independent of mass, was not significantly related to pregnancy rates (P = 0.998).

Few juvenile (n = 3) and subadult (n = 6) *A. cursor* were collected (Fig. 6d). The adult capture frequency peaked during the dry season of both years, but none were collected in April 1993 and in March 1994 (Fig. 6d). Fewer adult *A. cursor* were captured than for the other species (3.0 $\pm$ 1.8 individuals/month, range = 0–8).

The model explained a significant proportion of the variation in adult captures (R^2 = 0.304, F = 4.376, *d.f.* = 2,20, P = 0.027). Food availability contributed negatively (P = 0.009) to the model, but subadult frequency with a 1-month time lag was not related to the number of adults captured (P > 0.05). The model may have be an spurious because there was no causal relationship that predicted a negative relationship between food availability and density.

DISCUSSION

Nectomys squamipes and *O. intermedius* had similar reproductive patterns. Pregnancy rates peaked during the rainy season and decreased in the coldest and driest months. *T. iheringi* reproduced at the end of the rainy season and in the dry season. *A. cursor* seemed to reproduce mainly during dry months. Path analysis indicated differences in the details of species-specific reproduction indicating different responses to the food availability and rainfall. However, sample sizes were not large enough to have confidence in minor differences among the path analyses and overall similarities were the most interesting aspect of the study.

The reproductive pattern of female *N. squamipes* is closely related to availability of fruits and rainfall, both by direct and indirect effects. However, a negative effect of rainfall was not predicted by the model. Without rainfall in the model, availability of arthropods became significant. Availabilities of fruits and arthropods are important resource to *N. squamipes* (Ernest and Mares, 1986; Fonseca and Kierulff, 1989). Rainfall may mask the causal effect of availability of arthropods on reproduction due to the lack of precision in their measurement. Seasonal reproduction of *N. squamipes* also was observed by Crespo

(1982), Ernest and Mares (1986), and Bergallo (1994). In all cases, the peak in pregnancy occurred during the rainy season. In the state of Rio de Janeiro, *N. squamipes* seems to reproduce year-round but with increased frequency during the rainy season (Gentile, 1996).

The pregnancy rate of *O. intermedius* peaked just after that of *N. squamipes* when availability of fruits was highest. For female *O. intermedius* that reproduced all year, the highest reproductive rate occurred when availability of fruits was highest during the rainy season. *O. intermedius* in Juréia (ca. 60 km N of Ilha do Cardoso) showed a higher recruitment during the driest months (June–November—Bergallo, 1994), which is in agreement with the frequency of juveniles observed in this study. Births occurred throughout the year in Juréia but peaked in January 1989 (Bergallo, 1995*a*). This result seems to be similar to that found at Ilha do Cardoso, where pregnant females were found all year but with peaks in the rainy season.

Because pregnancy rates of female *O. intermedius* and *N. squamipes* are higher during periods of highest availabilities of fruits and arthropods, young born at the end of the breeding season should enter the population at a time when availabilities of resources are low. This concurs with the observation that growth rates of young *N. squamipes* born at the beginning of the breeding season are higher than those born at the end of the breeding season (Bergallo, 1995*b*). However, growth rates of young *O. intermedius* did not differ between those born at the beginning and those born at the end of the breeding season (Bergallo, 1995*b*).

Trinomys iheringi reproduced at the end of the rainy season and during dry season. A similar result was found in Juréia where frequency of births was correlated negatively to rainfall (Bergallo, 1994). Reproduction of *T.* iheringi seems to occur just after that of *O. intermedius*. Reproduction in both species seems to be related directly to availability of fruits. However, the total effect of rainfall on pregnancy rates of *T. iheringi* was low.

Reproduction in some species of *Proechimys* and *Trinomys* seems to occur throughout the year (Davis, 1946; Fonseca and Kierulff, 1989; Laemmert et al., 1946). Even in species that breed throughout the year, reproductive intensity can vary in response to weather conditions (*P. semispinosus*—Gliwicz, 1984; *T. iheringi*—Bergallo, 1994, this study). Although reproductive females were not captured in every month, reproduction in *T. iheringi* at Ilha do Cardoso probably also occurred throughout the year as observed in Juréia (Bergallo, 1994).

Akodon cursor reproduced throughout the year, and there was no apparent seasonality in pregnancy rates or association with seasonal weather variables included in our multiple regression and path analysis. Lack of significant effects of all variables may be due the small number of individuals captured (type II error). *A. cursor* reproduces seasonally in other areas (Fernandez, 1989; Fonseca and Kierulff, 1989), and reproduction was concentrated in the dry season. In our study, 60% of pregnant females occurred during the dry season, indicating that *A. cursor* in Ilha do Cardoso also may reproduce mostly during dry months.

Size of scrotal testes independent of na individual's mass was a good indicator of pregnancy rates in *N. squamipes* and *T. iheringi*. This indicates that size of scrotal testes may be a good indicator of reproductive activity for those species that have a marked breeding season. Alternatively, *A. cursor* and *O. intermedius* were the smallest species, and testes measurements may not have been taken as accurately as in the largest species. Other factors, such as temperature, may influence whether testes are scrotal and result in a lack of a relationship with pregnancy rates.

Juvenile and subadult capture rates, and presumably densities, are related directly to the size in the previous age classes. There

was a negative association between availability of fruits and juvenile and subadult capture of *N. squamipes* and *O. intermedius*. This probably reflects the fact that pregnancy rates are higher during the peak of food availability. Consequently, young age classes are associated negatively with food availability. Adult densities reached their peak just before and during the breeding season. Densities of adult *A. cursor* were associated negatively with food availability, which is in agreement with observations in other areas (Fernandez, 1989; Fonseca and Kierulff, 1989) that *A. cursor* breeds mainly during the dry season.

Within-year fluctuations in the population appear to be primarily related to variation in pregnancy rates, even for those species that breed all year. As pregnancy rates appear to be related to availabilities of fruits and arthropods, these factors probably regulate within-year population dynamics. A longer study would be needed to determine if they affect long-term dynamics of populations.

Survival rates of *N. squamipes* were high (>0.8) when availability of fruits was >50 g/0.096 ha. However, survival rates decline sharply at availability of fruits <50 g/0.096 ha, suggesting that the individuals were nutritionally stressed. Growth rates of juveniles that are born late in the season are significantly lower than growth rates of juveniles born at the beginning of the season (Bergallo, 1995*b*), which also indicates nutritional stress.

Reproduction occurred during the rainy season in three of the four species, which is in agreement with other studies of tropical small mammals (Bergallo, 1994; Bergallo and Cerqueira, 1994; Cerqueira, 1984; Cerqueira and Lara, 1991; Cerqueira et al., 1989; Dietz, 1983; Fleming, 1971; Rigueira et al., 1987; Streilein, 1982). Nevertheless, the species reproduced sequentially, beginning with *N. squamipes,* followed by *O. intermedius,* and finishing with *T. iheringi. A. cursor* seems to be the only species in which reproduction peaks in the dry season.

This sequence is related closely to dynamics of rainfall and availabilities of fruits and arthropods. Arthropods appear to respond to small variations in weather, but availability of fruits show a more consistent seasonal pattern. Responses of the four rodent species to each factor were different; *N. squamipes* seems to respond more to fluctuations in availability of arthropods and rainfall than *T. iheringi* and *O. intermedius,* whose dynamics can be linked to availability of fruits. Results indicate that reproduction in these species does not suffer a direct negative effect of rainfall but rainfall may have an indirect positive effect through food availability. Unless species live in very dry habitats or habitats subject to flooding, a priori models of population dynamics of small mammals in mesic tropical habitats probably can ignore rainfall as having direct positive or negative effects.

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