

Catastrophes, disturbances and density-dependence: population dynamics of the spiny pocket mouse (*Heteromys desmarestianus*) in a neotropical lowland forest

Rob Klinger¹

Section of Evolution and Ecology, University of California, Davis, California 95616, USA
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Abstract: Capture–mark–recapture methods were used to study the influence of density-dependent and density-independent factors on population dynamics of the spiny pocket mouse *Heteromys desmarestianus* in a lowland forest in Belize. Fourteen trapping sessions were conducted in six 0.5-ha grids at irregular intervals from July 2000 to March 2005. Responses by *H. desmarestianus* to four disturbance events depended on the type and magnitude of the events. Although fluctuations in density were strongly related to fruit availability, the disturbances tended to magnify direct and delayed density-dependent effects on reproduction and juvenile survival. A catastrophic flood in July 2000 eliminated the entire population, but by September 2001 population density had increased from 34.4 individuals ha⁻¹ immediately pre-flood to 42.5 individuals ha⁻¹. Indirect effects from a hurricane in October 2001 had greater and longer lasting influences on demographic rates than direct effects from less severe floods in August 2002 and September 2003. Fruiting ceased for almost 2.5 y after the hurricane, resulting in extremely low juvenile survival and a decline in density from 46.8 individuals ha⁻¹ in January 2002 to 23.0 individuals ha⁻¹ in January 2004. Fruiting began again in January 2004, and after several subsequent pulses of reproduction and generally higher rates of juvenile survival the population reached a maximum of 77.3 individuals ha⁻¹ in March 2005. Inferences from the study, especially on the duration of delayed-density-dependent effects, must be made cautiously because of the irregular trapping intervals resulting from the unplanned disturbances. However, the results indicate that population dynamics of many tropical small-mammal populations will be driven by direct and indirect effects from density-independent events that amplify density-dependent influences on demographic rates.

Key Words: density-independence, floods, hurricanes, resource limitation, rodents, small mammals, tropical forests

INTRODUCTION

Over the last 10 y a better understanding has emerged of factors influencing the population dynamics of small-mammal populations in the tropics (Keesing 2000, Leirs *et al.* 1997, Madsen & Shine 1999). Demographic rates in particular appear to have a strong relationship with rainfall, in all likelihood because of its influence on seasonal and annual production of food (White 2004, Wright *et al.* 1999). However, other density-independent factors can also have an important influence on mammal abundance. For instance, disturbance events have both direct and indirect effects on animal populations in tropical ecosystems, including alteration of resource

production, change in vegetation structure, and increased mortality (Beck *et al.* 2004, Briani *et al.* 2004, Keesing 2000, Klinger 2006).

Besides density-independent factors, small-mammal population dynamics are often driven by strong density-dependent effects (Leirs *et al.* 1997, Lima & Jaksic 1998). Density-dependent effects are generally considered to be the outcome of predation (top-down process), competition, or resource availability (bottom-up processes) (Hixon *et al.* 2002). Predation does not appear to have an effect on dynamics of tropical small-mammal populations as important as in temperate and sub-arctic systems (Hanski *et al.* 2001, Keesing 2000, Vibe-Petersen *et al.* 2006). However, variation in abundance of mammals in the tropics is known to be strongly related to changes in seasonal and inter-annual production of food (Adler 1998, Curran & Leighton 2000, Wright *et al.*

¹ Email: rcklinger@ucdavis.edu

1999), while both inter- and intra-specific competition appear to be related to population dynamics of small mammals in African savannas and grasslands (Keesing 2000, Leirs *et al.* 1997).

It is reasonable to expect that different density-independent events may often influence density-dependent rates of survival and reproduction, and hence population dynamics, in different ways (Lima & Jaksic 1999). Specifically, variation in food abundance is often a result of density-independent events (Walker *et al.* 1991, White 2004), and reproduction appears to be the demographic parameter affected most by variation in food resources in tropical small mammals (Adler 1998, Duquette & Millar 1995, Fleming 1974). This suggests that: (1) the relative influence of reproduction and survival on population dynamics will likely depend on variation in the type, severity, duration, and extent of density-independent events; (2) density-dependent effects on demographic rates should be most pronounced during periods of food shortage; and (3) reproduction will often have a stronger effect on population dynamics than survival.

Four unforeseen natural disturbance events over a 5-y period provided an opportunity to examine the interaction between density-independent and density-dependent factors on the population dynamics of the spiny pocket mouse *Heteromys desmarestianus* in a lowland tropical forest in northern Central America. There has been little systematic study of small-mammal population dynamics in the Neotropics (Sanchez-Cordero & Fleming 1993), and no studies have explicitly examined how demographic rates respond to interactions between density-independent and density-dependent factors. Therefore, the objectives of the study were to describe the direct and indirect effects of the disturbances on the population dynamics of *H. desmarestianus*, analyse the relative contribution of survival and reproduction to changes in the population, and determine the degree to which availability of food resources was related to density-dependent feedback on stage-specific demographic rates.

METHODS

Study area

The study was conducted from July 2000 to March 2005 in the south-eastern section of the Bladen Nature Reserve (BNR), Toledo District, Belize. The BNR is located within the south-eastern region of the Maya Mountains, approximately 30 km inland from the Caribbean Sea and 80 km north of Belize's southern border with Guatemala (16°33'N, 88°43'W). The reserve is 350 km² in area and contains the headwaters of the Bladen Branch of the Monkey River. The river's floodplain widens into broad, alluvium-covered benches on the valley floor in the south-

eastern part of the watershed. The main ridges adjacent to the study site are generally < 300 m in elevation, but the slopes are rugged and steep.

Annual rainfall is typically 2500–3000 mm, with 67–81% of the precipitation falling during the wet season (June–January; Belize Foundation for Research and Environmental Education unpubl. data). Temperatures are relatively constant throughout the year, with mean annual daily minimum and maximum of 24 °C and 30 °C, respectively. The flora and fauna of the BNR remain entirely intact, with most of the vegetation comprised of evergreen tropical forest (Brewer *et al.* 2003).

Species

Heteromys desmarestianus Gray (Heteromyidae) is a granivorous/frugivorous, burrowing rodent that occurs in moist forest habitats throughout Central America (Sanchez-Cordero & Fleming 1993, Schmidly *et al.* 1993). It is often considered to be the most abundant small mammal in many lowland forests of Central America (Klinger 2006, Sanchez-Cordero & Fleming 1993). Home range size of *H. desmarestianus* in Costa Rica was estimated to be approximately 100 m², and breeding (mean litter size = 3.1) can occur year-round (Fleming 1974, 1983; Sanchez-Cordero & Fleming 1993). *Heteromys desmarestianus* consumes a wide variety of fruits and seeds in the BNR (Brewer & Rejmánek 1999), but the large seeds of the palm *Astrocaryum mexicanum* Liebm. (Arecaceae) are known to be a particularly important year-round food resource (Brewer 2001).

Disturbances

Three major floods and a Category 4 hurricane (maximum sustained winds of 210–249 km h⁻¹; US National Oceanic and Atmospheric Administration National Hurricane Center, <http://www.nhc.noaa.gov/2001iris.html>) occurred in the BNR from 2000–2003 (Klinger 2006). The first flood occurred in July 2000 and covered 100% of the floodplain for 72 h. The second flood occurred in August 2002 (duration = 6 h, 25–50% of floodplain covered) and the third in September 2003 (duration = 8 h, 50–75% of floodplain covered). The last flood to occur in the reserve (3–4 h duration) was in 1997 (S. Brewer, J. Marlin, pers. comm.).

Hurricane Iris made landfall in Belize on 9 October 2001, with maximum sustained winds > 225 km h⁻¹. High winds in the BNR were sustained for approximately 6 h (J. Marlin, BFREE, pers. comm.). The magnitude of damage to the forest in the BNR was severe and extensive, with 75–100% of the trees in most areas sustaining defoliation, the crown removed, or being uprooted

(Klinger 2006, J. Meerman, unpubl. data). There are no records to confirm when the last hurricane hit the BNR, but it is known that the reserve has not been seriously affected by one since the 1930s (US National Oceanic and Atmospheric Administration National Hurricane Center, <http://www.nhc.noaa.gov>).

Trapping

Mark–recapture trapping was conducted in six permanent 0.5-ha plots from July 2000 to March 2005. The plots were established at randomly selected locations on the valley floor. Distance between the plots was 125–375 m. A 10 × 10 grid with trap stations spaced 7 m apart was arranged within each plot. A single Sherman live trap (Model XLK; 8 cm × 10 cm × 38 cm) was placed at each station and baited with a mixture of whole peanuts, kernels of corn (*Zea mays* L.) mixed with peanut butter, and a slice of banana or plantain. The traps were kept open throughout the day and evening and checked once per day each morning.

Trapping was originally scheduled to be conducted in each of the six grids in each of three equally spaced trapping sessions (Pollock *et al.* 1990) each year from 2000–2003. However, financial and logistical constraints associated with the four disturbances resulted in trapping being conducted irregularly in each of 14 trapping sessions from July 2000 to March 2005. Trapping was conducted for 5–6 d per grid in each session from 2001 to 2005 (September 2001, January 2002, May 2002, September 2002, January 2004, February 2004, March 2004, April 2004, August 2004, October 2004, December 2004, March 2005). It was only possible to trap four grids in July 2000 because of the flood, but an additional trapping session in August (starting 3 d after the flood) was added to make an immediate assessment of the flood's impact on the population of *H. desmarestianus* and other small-mammal species (Klinger 2006). Fifty traps were placed at alternate stations (14-m intervals) in each of the four grids and checked each morning for 3 d during this abbreviated trapping session.

All captured individuals were ear-tagged, weighed, evaluated for reproductive condition (females pregnant, lactating, or not active; males with testes descended or not), and assigned to an age class (adult, subadult or juvenile based on pelage, weight and reproductive status). Individuals with grey pelage were classified as juveniles. Males without descended testes, no juvenile pelage, and > 50 g were classified as subadults, while females > 50 g with no evidence of having been reproductively active and no juvenile pelage were classified as subadults. Males with descended testes and females ≥ 65 gm or showing evidence of reproductive activity (e.g. lactating or a perforated vagina) were classified as adults. Size and pelage

colour made identification of juveniles obvious. Inspection of recapture data confirmed that adult males were reproductively active throughout the year (testes did not become abdominal after they descended), and all captured females that produced litters were correctly identified as adults in subsequent trapping sessions even when they were not reproductively active. Therefore, the likelihood that adults were misclassified as subadults was low.

Fruit and seed availability

A systematic count of fruiting trees and climbers was done weekly in each plot within 3–4 wk of the beginning or end of each trapping session. When a fruiting tree or climber was found a count was made of the number of fruits or seeds on the ground in four 1-m² quadrats. A single quadrat was located randomly along each of four 3-m transects oriented in the four cardinal directions from the main trunk of the tree or the main stem of the climber. The mean of the four counts was used as the estimate of fruit abundance for that species in that plot, and estimates were summed as the index for all fruiting tree and climber species in the plot.

The number of *Astrocaryum mexicanum* infructescences per tree was counted along five randomly selected 2.5 × 7-m transects spanning each plot. Counts were done within 2 wk of the beginning or end of each trapping session.

Data analysis

Capture–mark–recapture analysis. Demographic parameters were estimated with capture–mark–recapture (CMR) models using the software program MARK (White & Burnham 1999). The parameters included population size (N), recruitment (f , the number of new individuals per capita at time t relative to individuals in the population at $t - 1$, including in situ reproduction and immigration), residency (γ , also known as a seniority parameter, the probability of an individual in the population at time t being present at $t - 1$), population rate of change (λ , calculated as Φ_t/γ_{t+1}), survival rates for adults (Φ_A), subadults (Φ_S), and juveniles (Φ_J), as well as the transition rates of juveniles → subadults (Ψ_{JS}) and subadults → adults (Ψ_{SA}).

The robust-design model was used to estimate population size (N) (Kendall *et al.* 1997, Pollock *et al.* 1990). Population size was standardized as density (individuals ha⁻¹), $D = N/A_e$, where A_e = the effective trapping area of the grid. The mean maximum distance moved between traps was used to estimate A_e (Wilson & Anderson 1985). The software program RDSURVIV was used to evaluate fit of the global model (time variation

between trapping periods for N , Φ (overall probability of survival), Γ' (immigration) and Γ'' (emigration), and time variation between and within primary periods for probability of capture (p) and recapture (c) to the data and to determine the best starting model (Kendall *et al.* 1997).

Estimates of f , λ , and γ (standardized as monthly rates) were derived for the 2001–2005 data from reverse-time CMR models (Nichols *et al.* 2000, Pradel 1996). Goodness-of-fit of the most general reverse-time CMR model to the data was tested with the program RELEASE (Nichols *et al.* 2000). Multistate models (Hestbeck *et al.* 1991, Nichols *et al.* 1992) were used to estimate Φ_A , Φ_S , Φ_J , Ψ_{JS} and Ψ_{SA} (standardized as monthly rates). Program MSSURVIV (Hines 1994) was used to test the goodness-of-fit of the most general multistate model to the data. Because sample sizes in some periods were low, estimates of Ψ_{JS} and Ψ_{SA} were highly variable ($CV \geq 100\%$) or could not be derived for some intervals. Therefore, estimates of these two parameters were held constant over time. Estimates of λ , γ , Φ_S and Φ_J were not made for the interval September 2002–January 2004 because the period of time between trapping periods would have made the estimates meaningless. An estimate of Φ_J in the period between December 2004 and March 2005 could not be made because of the low number of juveniles captured in December.

The effects of direct density-dependence (density in the current trapping period, time t), delayed density-dependence (density in the previous trapping period $t-1$), and food availability on the estimates of γ , f , Φ_A , Φ_S and Φ_J were analysed with generalized linear models (GLM) using the logit link function (McCullagh & Nelder 1989). Food availability variables included the mean number of infructescences ha^{-1} of *Astrocaryum mexicanum* (Astro), Astro in the previous trapping period (Lagastro), the mean number of tree and climber species in fruit (Fruitspec), the mean of the index of fruit availability (Fruitden), and Fruitspec and Fruitden in the previous trapping period (LagSpec and LagFruit, respectively). The relationship between the food availability variables and abundance of *H. desmarestianus* was analysed with GLM using a logit link (McCullagh & Nelder 1989). The analyses excluded the interval September 2002–January 2004 because of the long period of time between trapping periods. Model selection was based on Akaike's Information Criterion (AIC); candidate models were ranked by ΔAIC (the difference between a given model and the best supported model) and AIC weight (a relative measure of support for the model). Estimates for all parameters were derived by model averaging (Burnham & Anderson 2002).

Sex, age class and active breeding proportions. Likelihood-ratio Chi-square tests (Fienberg 1987) were used to analyse changes between periods in the proportion of individuals classified as adults, subadults and juveniles. Profile analysis (Tabachnik & Fidell 1996) was used to evaluate changes in the proportion of reproductively

active adults (R), the index of fruit density, and the mean number of infructescences per individual for *A. mexicanum* between the trapping periods. The data from July 2000 were omitted from the profile analysis because only four grids were trapped during that period. Proportions of R in the profile analysis were transformed by $\arcsine\sqrt{R}$.

GLM using the logit link was used to analyse the relationship between the proportion of breeding adult females R_t and direct (D_t) and delayed (D_{t-1}) density-dependence. Significance of the regression was evaluated by determining if the Wald confidence limits for the regression coefficients included 0 or not. The proportion of variance explained by D_t and D_{t-1} was estimated by the correlation between the observed and predicted values ($R^2_{corrected}$). Estimates of D from July 2000 and September 2002 were omitted from the analysis of delayed density-dependence because the interval between those and the next trapping period was too long for density-dependent effects to be present.

RESULTS

There were 4564 captures of 1180 individuals. Recapture rates within each primary period were high, with a mean of 81.0% of the individuals captured more than once (range = 57.5–99.2%). The mean number of captures per individual within the primary periods was 2.46 (range = 1.87–3.31). Probability of capture (p) varied between periods from 0.26 to 0.60 (mean = 0.43, SE = 0.04) and c from 0.26 to 0.61 (mean = 0.44, SE = 0.04). The goodness-of-fit test of the global robust-design model indicated that it fitted the data well ($\chi^2 = 912$, $P = 0.998$), as did goodness-of-fit tests of the reverse-time CMR ($\chi^2 = 13.1$, $P = 0.947$) and multi-state models ($\chi^2 = 8.28$, $P = 0.991$). The robust-design starting model included time variation for Φ and N , no time variation for Γ'' and Γ' , and time variation between but not within primary trapping periods for p and c (Appendix 1).

The density of *H. desmarestianus* fluctuated widely during the course of the study (Figure 1). The July 2000 flood had a catastrophic effect on the population; no *H. desmarestianus* was captured in the trapping period immediately after the flood. However, by September 2001 density was 42.5 individuals ha^{-1} (Figure 1). Relative to September 2001, density increased 24% in the first 4 mo after the hurricane but then decreased 47% to a low of 25 individuals ha^{-1} by September 2002. When trapping resumed in January 2004, 3 mo after the most recent flood, density was approximately the same as in September 2002. Density increased 100% January–February 2004 ($\lambda = 2.03$; Table 1) and 57% April–August 2004 ($\lambda = 1.38$; Table 1). There was a decrease in density during the latter part of the wet season of 2004, but by March 2005 the population had attained its highest level of the study (Figure 1). The overall mean

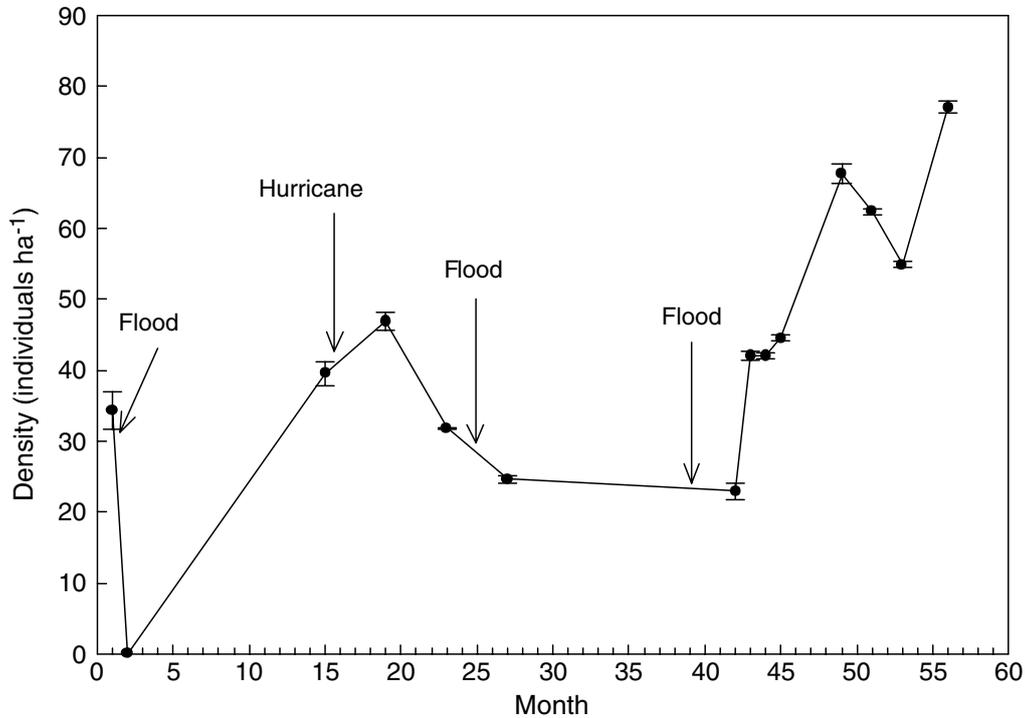


Figure 1. Density estimates (\pm SE) for the spiny pocket mouse *Heteromys desmarestianus* in the Bladen Nature Reserve, Belize. Trapping was done in 14 irregularly spaced intervals: July 2000 (Month 1), September 2001, January 2002, May 2002, September 2002, January 2004, February 2004, March 2004, April 2004, August 2004, October 2004, December 2004 and March 2005.

monthly rate of population change (geometric mean λ) from September 2001–March 2005 was 1.028 (Table 1).

Fruits were observed on only one species of tree (*Spondias mombin* L.; Anacardiaceae) in January 2002 (Figure 2a), and these were almost exclusively on branches that had broken off the trees during the hurricane and fallen to the ground. The amount of fruit on the branches at that time was very high and the index of fruit availability was 50% greater than in September 2001 ($F_{1,5} = 20.9$, $P = 0.006$; Figure 2b). No trees or climbers were observed producing fruit from January 2002 to September 2002; casual observations indicated that this pattern persisted through 2003. Trees and climbers began

producing fruit again in January 2004, with a subsequent increase in the index of fruit availability of almost four-fold by March 2005 ($F_{1,5} = 13.8$, $P = 0.014$; Figure 2b).

The number of infructescences ha^{-1} for the palm *Astrocaryum mexicanum* decreased 65% between September 2001–January 2002, but then increased rapidly over the next 9 mo (Figure 2c). In May and September 2002 virtually all *A. mexicanum* palms had at least one infructescence, and production increased from 1.1 to 2.4 infructescences per individual ($F_{1,5} = 20.7$, $P = 0.006$). Production by *A. mexicanum* returned to pre-hurricane levels by May 2002. Production remained relatively constant from September 2002 through

Table 1. Demographic parameters for the spiny pocket mouse *Heteromys desmarestianus* in the Bladen Nature Reserve, Belize. Parameter estimates are standardized as monthly rates (mean \pm 1 SE). Parameters are λ = finite rate of population change, Φ = survival, γ = seniority, f = recruitment (reproduction + immigration). Trapping occurred in September 2002 and January 2004, but estimates of the parameters for that interval were not done because of the duration of time between the two periods (see text for full explanation).

Interval	λ	Φ	γ	f
September 2001–January 2002	1.07 \pm 0.037	0.835 \pm 0.040	0.770 \pm 0.032	0.872 \pm 0.053
January 2002–May 2002	0.889 \pm 0.033	0.720 \pm 0.039	0.811 \pm 0.031	0.690 \pm 0.047
May 2002–September 2002	0.903 \pm 0.031	0.887 \pm 0.040	0.973 \pm 0.022	0.390 \pm 0.107
September 2002–January 2004				
January 2004–February 2004	2.03 \pm 0.256	0.780 \pm 0.089	0.380 \pm 0.053	1.26 \pm 0.252
February 2004–March 2004	1.02 \pm 0.083	0.746 \pm 0.070	0.723 \pm 0.056	0.283 \pm 0.074
March 2004–April 2004	1.08 \pm 0.093	0.687 \pm 0.074	0.623 \pm 0.049	0.407 \pm 0.077
April 2004–August 2004	1.38 \pm 0.073	0.740 \pm 0.050	0.528 \pm 0.034	1.17 \pm 0.083
August 2004–October 2004	0.928 \pm 0.027	0.739 \pm 0.034	0.789 \pm 0.027	0.821 \pm 0.034
October 2004–December 2004	0.923 \pm 0.033	0.821 \pm 0.038	0.880 \pm 0.029	0.439 \pm 0.059
December 2004–March 2005	1.19 \pm 0.049	0.762 \pm 0.046	0.630 \pm 0.029	0.923 \pm 0.057

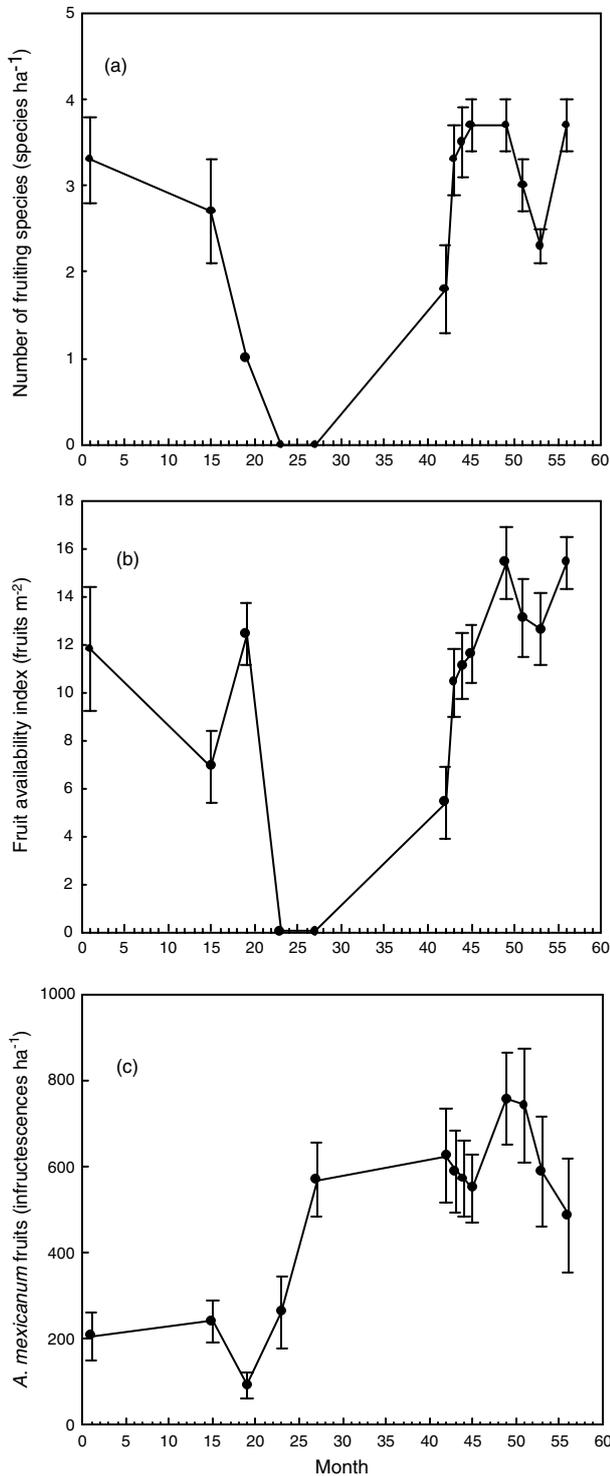


Figure 2. The number of fruiting trees and climbers (\pm SE) (a); index of fruit availability for trees and climbers (\pm SE) (b); the number of infructescences (\pm SE) on the palm *Astrocaryum mexicanum* (c) in the Bladen Nature Reserve, Belize. Counts were done in 14 irregularly spaced intervals; July 2000 (Month 1), September 2001, January 2002, May 2002, September 2002, January 2004, February 2004, March 2004, April 2004, August 2004, October 2004, December 2004 and March 2005. A hurricane occurred in October 2001 (Month 16).

October 2004, with a mean of 1.8 infructescences per individual (Figure 2c). Production dropped 33% to a mean of 1.2 infructescences per individual from December–March 2005 ($F_{1,5} = 22.6$, $P = 0.005$).

Three models that included the influence of the fruit-availability covariables on abundance of *H. desmarestianus* had stronger support than the best-fit robust-design model with only time variation (Appendix 1). Ratios between model likelihoods indicated that the three best supported models had 3.5–6.5-fold more support than the model with just time variation and > 75-fold than the other models. Density of *H. desmarestianus* had a positive relationship with all fruit-availability covariables for both the period at time t and $t - 1$ (Appendix 1). There was no support that abundance of *H. desmarestianus* was influenced to any significant degree by availability of *A. mexicanum* seeds (Astro and Lagastro). The value for Δ AIC between models including availability of *A. mexicanum* seeds and the best-fit model incorporating fruit density was > 13.9.

The proportion of *H. desmarestianus* in the three age classes varied greatly between trapping periods (likelihood-ratio $\chi^2 = 183$, $P < 0.0001$; Figure 3). The proportion of adults increased linearly from 66% in September 2001 to 98% in September 2002. No juvenile animal was captured in May 2002 and only one in September 2002, and no subadults in September 2002. The proportions of individuals in the three age classes remained relatively constant January–October 2004 (Figure 3). Juveniles and subadults decreased 27% from October–December 2004, but then increased 32% December 2004–March 2005; adults showed opposite trends.

Survival probabilities for the three age classes are given in Table 2. Juvenile survival probabilities were highly variable, ranging from a low of 0.007 from May–September 2002 to 0.71 from April 2004–August 2004 (Figure 3). The mean for ψ_{JS} over the duration of the study was 0.86 (SE = 0.09). Probabilities of subadult survival were relatively high, ranging from 0.72 to 0.94, with a mean value for ψ_{SA} of 0.97 (SE = 0.03). Survival probability for adults was less variable than juveniles and subadults, with a mean of 0.76 (SE = 0.06) over the duration of the study. Models with direct and delayed density-dependent effects and food availability on monthly survival probabilities for adults had virtually no support relative to models with just time variation (Appendix 2). However, three models for subadult and juvenile survival that included effects of direct and delayed density-dependence and food availability had much stronger support than models with just time variation (Appendix 2). There was no clear distinction between the three best models that included effects of direct and delayed density-dependence and food availability (Δ AICc = 2.28), but they indicated that subadult and

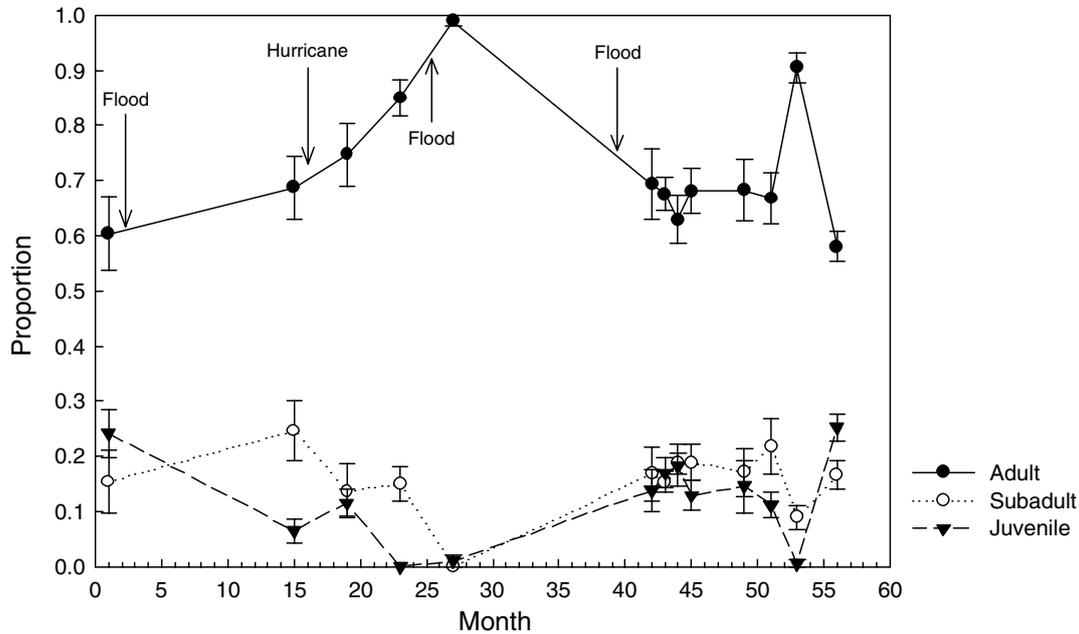


Figure 3. The mean proportion of individuals (\pm SE) in three age classes for the spiny pocket mouse *Heteromys desmarestianus* in the Bladen Nature Reserve, Belize. Solid line = adults, dotted line = subadults, dashed line = juveniles. Trapping was done at 14 irregularly spaced intervals; July 2000 (Month 1), September 2001, January 2002, May 2002, September 2002, January 2004, February 2004, March 2004, April 2004, August 2004, October 2004, December 2004 and March 2005.

juvenile survival rates were related to different factors. Juvenile survival had a negative relationship with density ($t - 1$) and a positive relationship with the index of fruit density. Subadult survival had a negative relationship with density (t) and a positive relationship with Astro.

Resident animals generally comprised a large proportion of the population and contributed relatively more to λ than recruits ($\gamma_{t+1}/1 - \gamma_{t+1}$); values of γ were generally 2–18 times greater than $1 - \gamma$, the exceptions being the interval January–February 2004 when $1 - \gamma$ had > 2.7-fold the influence on population growth as γ (Table 1). Estimated values of f declined by 50%

September 2001–September 2002, but were particularly high January–February 2004 (Table 1). Models for γ and f that included the effects of direct and delayed density-dependence and food availability relative to the model with just time variation had no support ($\Delta AICc > 124.6$).

There were significant differences in the pattern of reproductively active male and female *H. desmarestianus* (Wilks' $\lambda = 0.058$, $F_{7,4} = 9.20$, $P = 0.024$). The mean percentage of reproductively active adult males approached 100% in all periods except May 2002 (Figure 4). The mean percentage of reproductively active adult females reached a low of 36.0% in May 2002, but

Table 2. Apparent probability of monthly survival (Φ ; mean \pm 1 SE) for three age classes of the spiny pocket mouse *Heteromys desmarestianus* in the Bladen Nature Reserve, Belize. Estimates for subadults and juveniles were not done for the interval September 2002–January 2004 because of the duration of time between the two periods. Estimates of juvenile survival could not be made for the interval December 2004–March 2005 because only two juveniles were marked in December 2004.

Interval	Φ Adults	Φ Subadults	Φ Juveniles
September 2001–January 2002	0.871 \pm 0.034	0.724 \pm 0.071	0.682 \pm 0.127
January 2002–May 2002	0.718 \pm 0.035	0.819 \pm 0.067	0.616 \pm 0.105
May 2002–September 2002	0.876 \pm 0.035	0.915 \pm 0.066	0.007 \pm 0.001
September 2002–January 2004	0.738 \pm 0.055		
January 2004–February 2004	0.825 \pm 0.085	0.791 \pm 0.150	0.618 \pm 0.163
February 2004–March 2004	0.718 \pm 0.064	0.932 \pm 0.076	0.593 \pm 0.132
March 2004–April 2004	0.676 \pm 0.070	0.927 \pm 0.072	0.383 \pm 0.127
April 2004–August 2004	0.707 \pm 0.034	0.813 \pm 0.050	0.714 \pm 0.080
August 2004–October 2004	0.750 \pm 0.048	0.794 \pm 0.077	0.519 \pm 0.129
October 2004–December 2004	0.791 \pm 0.034	0.946 \pm 0.042	0.560 \pm 0.108
December 2004–March 2005	0.758 \pm 0.037	0.698 \pm 0.112	

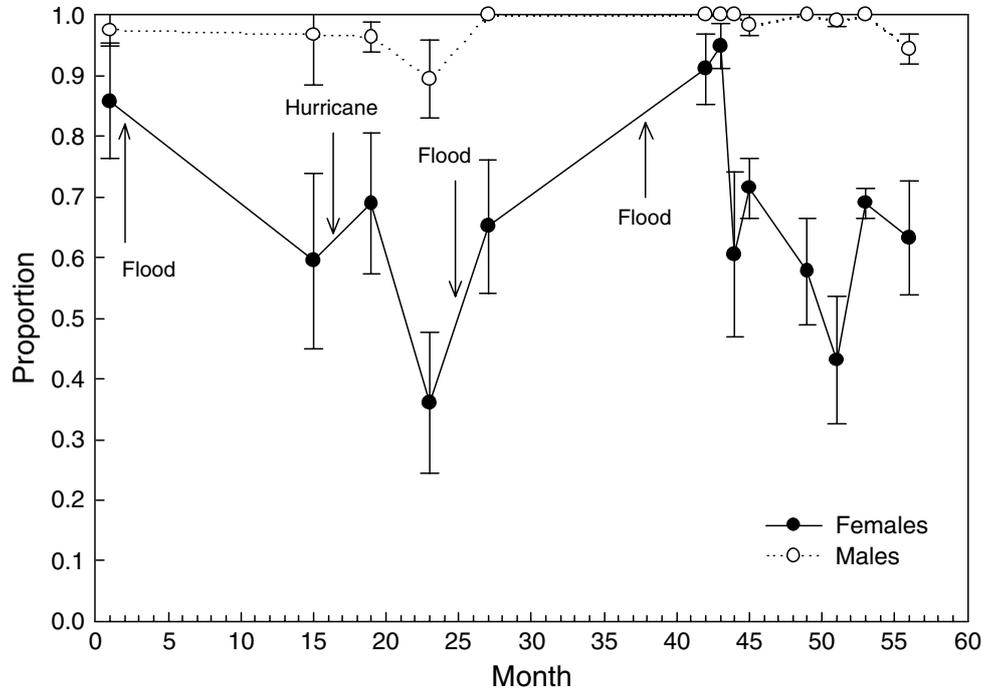


Figure 4. The mean proportion (\pm SE) of reproductively active adult spiny pocket mice *Heteromys desmarestianus* in the Bladen Nature Reserve, Belize. Dotted line is for males, solid line for females. Trapping was done in 14 irregular spaced intervals; July 2000 (Month 1), September 2001, January 2002, May 2002, September 2002, January 2004, February 2004, March 2004, April 2004, August 2004, October 2004, December 2004 and March 2005.

then ranged from 86.9–92.9% in January and February 2004 when $\lambda > 2$ (Figure 4). The proportion of reproductively active females had a negative relationship with delayed density-dependence (parameter for $D_{t-1} = -3.77$, $SE = 1.56$, Wald 95% confidence interval = -6.89 to -0.64). However, the proportion of variation explained by the relationship was low ($R^2_{\text{corrected}} = 0.12$).

DISCUSSION

The disturbances in the BNR had direct and indirect effects on the population dynamics of *H. desmarestianus*. Not only did these appear to amplify density-dependent processes, but the disturbances did not act independently on the population of *H. desmarestianus*. Rather, they interacted with each other and density-dependent processes to influence population dynamics through different demographic mechanisms (Lewellen & Vessey 1998).

Density-dependent effects

Both reproduction and survival of *H. desmarestianus* were subject to density-dependent effects. These effects were expressed as interactions between demographic parameter (reproduction or survival), the type of density-dependence (direct or delayed), and age class. Interactions at the demo-

graphic level varied within phases of population increase and decrease and were expressed at the population level as high rates of increase and moderate rates of decrease in population size. Population increases were due primarily to increased female fecundity while population decreases were due primarily to low juvenile survival.

Low abundance of potential competitors (Klinger 2006) and the high survival of subadults and adults argue against interspecific competition or predation playing major roles in the population dynamics of *H. desmarestianus*. The relationship between food availability and abundance of *H. desmarestianus* indicates that density-dependent effects were most likely an outcome of resource availability and intraspecific competition (Hixon *et al.* 2002). Periods of population growth were strongly related to increased food resources, and during these periods the proportion of female *H. desmarestianus* that produced litters was often large. However, density-dependent effects tended to rapidly reduce the proportion of pregnant females, even when food resources were relatively high. The result was population growth occurred in relatively brief but pronounced pulses. This not only suggests that population growth in many tropical small-mammal populations is limited by an interaction between intraspecific competition, food availability and population density, but that the amount of food per reproductively active female will put an upper bound on rates of increase (Adler 1998, Duquette & Millar 1995).

Survival of adult *H. desmarestianus* had no relationship with density-dependent effects. Survival of subadults was influenced by direct density-dependent effects, but it was at least as high as that of adults and a high proportion made the transition to the adult stage. In contrast, survival of juveniles was subject to delayed density-dependence and strongly influenced by food availability. This was especially apparent in the year after the hurricane when fruiting of all species except *A. mexicanum* ceased and there were few if any juveniles in the population. As with female reproduction rates though, it appeared that per capita rather than absolute food availability had the greatest influence on survival of juvenile *H. desmarestianus*. The index of food availability and density of *H. desmarestianus* were both relatively high between August and December 2004, but juvenile survival declined severely when fruit production decreased during this period. Interference competition, exploitation competition, or their joint occurrence could explain, at least in part (see below), this pattern.

Inferences regarding the magnitude and duration of delayed density-dependent effects on the population dynamics of *H. desmarestianus* must be made cautiously because the irregular trapping intervals likely biased estimates of these effects. Standardizing demographic parameters to monthly rates helped reduce this bias to a degree, and the bias was not severe enough to mask their importance. Indeed, studies in other systems indicate that influences on population dynamics from delayed density-dependence can persist for as long as 1 y (Lima & Jaksic 1999). While it is reasonable to conclude that both direct and delayed density-dependence influenced the population dynamics of *H. desmarestianus* in the BNR, it would be inappropriate to try and assess the degree to which different time lags influenced specific demographic rates.

Hurricane effects

In contrast with other vertebrates, very little is known about hurricane effects on small mammals (Klinger 2006, Waide 1991). Although the hurricane had a strong impact on the entire Bladen River watershed, it appeared to have little if any direct negative impact on *H. desmarestianus*. Direct mortality due to the hurricane was probably low because *H. desmarestianus* is a burrowing rodent and can find shelter below ground. However, there was substantial evidence that the hurricane had large indirect effects on both survival and reproduction, primarily as a result of changes in food quantity and type. The virtual cessation of food production amplified density-dependent feedback on reproduction and juvenile survival, bringing about a decline in abundance that lasted until fruit production began to increase almost 2.5 y after the hurricane. The occurrence of the floods

in August 2002 and September 2003 may have been additive mortality factors, but the decline in juvenile survival in 2002 began 6 mo prior to the flood and density in January 2004 was not significantly different from September 2002.

Seeds of *A. mexicanum* were the only food source available to *H. desmarestianus* once the pulse of *Spondias mombin* fruit in the first 2–3 mo following the hurricane had ended. Although intraspecific competition for *A. mexicanum* seeds may have played a role in the marked decrease in juvenile survival in the year after the hurricane, the size of the *A. mexicanum* seeds may also have been a critical factor. Removal rates for *A. mexicanum* seeds were high in the 9 mo after the hurricane (R. Klinger, unpubl. data) and I hypothesize that the increased production of seeds was high enough to sustain adults and subadults. However, the small size of juvenile animals (< 50 g) likely prevented them from harvesting, caching and eating the relatively large seeds of *A. mexicanum* (17 g vs. 5 g for *Spondias mombin*).

The relationship between hurricane effects on food availability and fecundity of female *H. desmarestianus* was characterized by a complex interaction with density-dependent effects. The decrease in overall food availability after the hurricane increased the intensity of density-dependent effects on reproduction by adult female *H. desmarestianus*. In general, per capita recruitment dropped precipitously through 2002 and was not compensated for by other demographic mechanisms, such as increased survival. It is possible that if fruiting had occurred patchily, emigration resulting from source-sink dynamics (Beck *et al.* 2004, Yunker *et al.* 2002) could have compensated, to a degree, for the decrease in fertility. But the hurricane impacted the entire region, and the fruiting failure occurred throughout much of the entire Bladen River watershed. Estimates of γ in all three periods in 2002 were very high, indicating that emigration was a minor component of the demography of *H. desmarestianus* during this period. So, despite high survival for adult and subadult *H. desmarestianus*, low recruitment from the combined effects of reduced fertility and survival of juveniles resulted in a pronounced decrease in abundance.

The relationship between reproduction, density, and fruit production observed from September 2001 to September 2002 was also observed from January 2004 to March 2005. When fruit production began to increase in January and February 2004 and density of *H. desmarestianus* was low, the proportion of females in active reproductive condition was very high and density of *H. desmarestianus* doubled in a month. Then, despite a steady increase in fruit production, the proportion of reproductively active females went into a general decline through October 2004 as density increased. The consistently strong effects of food availability on the

demography of *H. desmarestianus* reinforce findings of other studies noting the importance of bottom-up forces on demography of tropical small mammals (Adler 1998, Duquette & Millar 1995). However, the patterns also underscore how rapidly density-dependent effects can limit the strength of bottom-up forces.

Flood effects

In contrast with the indirect effects of the hurricane, effects from the floods on the population dynamics of *H. desmarestianus* were direct but more variable and of shorter duration. The degree of influence the floods had depended not so much on the simple occurrence of flooding, but the intensity and duration of the individual events and how these interacted with density-dependent processes.

The July 2000 flood had a catastrophic impact on the population of *H. desmarestianus* in the floodplain, the critical factor being the long period of inundation (3d). Nevertheless, the rate of population recovery following this catastrophe was quite rapid. Density was approximately 25% higher in September 2001 than immediately prior to the flood. Individuals dispersing from the surrounding hillsides in the initial months after the flood were undoubtedly the most important factor for the re-establishment of the population. The relatively high proportion of subadults in the population in September 2001 indicated that reproduction by immigrants recolonizing the floodplain had initially been high. However, the proportion of reproductively active females was approximately 30% lower in September 2001 than in July 2000, suggesting that density-dependent effects on female reproduction limited population growth rates.

The floods that occurred in 2002 and 2003 had inundation periods much shorter than the flood in 2000 (several hours vs. several days) and did not appear to have as severe an effect on abundance of *H. desmarestianus*. Survival of adults and subadults after the August 2002 flood remained high, and almost all subadults survived and made the transition to the adult age class. Because the inundation period of the 2003 flood was similar to that in 2002 it is reasonable to expect its effects would also have not been very severe. However, this interpretation must be made cautiously because there were no density estimates for 2003. It is also important to note the lack of fruit production in 2003 would confound potential flood effects on abundance of *H. desmarestianus* with that of reduced food resources.

Conclusions

Despite limitations due to the irregular trapping intervals, there was clear evidence that the population dynamics of *H. desmarestianus* over the 5-y period of this study

were due to complex direct and indirect interactions between disturbances, food availability and density-dependent processes. Similar to studies of small mammals in other systems (Leirs *et al.* 1997, Lima & Jaksic 1998), the population dynamics of *H. desmarestianus* in the BNR were influenced by both density-dependent and density-independent factors. However, whereas studies in other systems have emphasized how climatic variation influences biotic interactions (Lima & Jaksic 1999, Meserve *et al.* 2003), the present study shows that the influence of climatic factors may be overridden or greatly modified in systems that are prone to disturbances. This is a strong indication that models of the demography and dynamics of populations of small mammals in disturbance-prone systems will need to explicitly include disturbance type and regime. Specifically, the period of time on which disturbances leave an imprint on population dynamics will not just depend on direct effects, but also on the severity, extent and duration of indirect effects on key resources and how they influence age-specific demographic processes.

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Appendix 1. Robust design capture-mark-recapture models for estimates of survival (Φ), probability of capture (p), probability of recapture (c), and abundance (N) between primary periods for the spiny pocket mouse *Heteromys desmarestianus* in the Bladen Nature Reserve, Belize. The starting model was $\Phi(t)$, $p(t(.))$, $c(t(.))$, $N(t)$, where the symbol $(t(.))$ indicates time variation for p and c between primary periods but constant within primary periods, while the symbol (t) indicates time variation for N and Φ between primary periods. Temporary emigration was random and constant between periods [$\Gamma''(.) = \Gamma'(.)$] for all models. Fruitspec is the mean number of tree and climber species fruiting, Fruitden is an index of fruit availability, Lagspec is the mean number of tree and climber species fruiting in the previous trapping period, Lagdensity is the index of fruit availability in the previous trapping period, Astro is the mean number of infructescences ha^{-1} of *Astrocaryum mexicanum*, and LagAstro is the mean number of infructescences ha^{-1} of *Astrocaryum mexicanum* in the previous trapping period. AIC is the Akaike Information Criterion, ΔAIC is the difference between a given model and the best supported model (the model with the lowest AIC value), AIC weight is an absolute measure of support for the model, Model Likelihood is the AIC weight of a model divided by the AIC weight of the best model and is a relative measure of the degree of support for a model, and Deviance is the difference in likelihood of a given model to the most general model. Models are ordered from best supported to least supported.

Constrained Models: $\Phi(t)$, $p(t(.))$, $c(t(.))$	AIC	ΔAIC	AIC Weight	Model Likelihood	Deviance
N(Fruitden + Lagdensity)	440.3	0	0.411	1.000	1273.6
N(Fruitspec + Fruitden + Lagspec + Lagdensity)	440.9	0.6	0.304	0.739	1270.1
N(Fruitspec + Fruitden + Lagdensity)	441.6	1.3	0.218	0.530	1272.8
N(t)	444.1	3.8	0.062	0.150	1261.6
N(Fruitden)	450.2	9.9	0.003	0.007	1285.5
N(Lagdensity)	450.6	10.3	0.002	0.006	1285.9
N(Astro)	454.2	13.9	0.000	0.001	1289.6
N(LagAstro)	454.9	14.6	0.000	0.001	1290.2
N(Astro + LagAstro)	455.5	15.2	0.000	0.001	1288.8

Appendix 2. Models for the probability of apparent monthly survival (Φ) for three age classes of the spiny pocket mouse *Heteromys desmarestianus* in the Bladen Nature Reserve, Belize. Trapping was conducted in 13 periods from July 2000–March 2005. A = adult age class, S = subadult age class, and J = juvenile age class. AIC is the Akaike Information Criterion, ΔAIC is the difference between a given model and the best supported model (the model with the lowest AIC value), AIC weight is an absolute measure of support for the model, Model Likelihood is the AIC weight of a model divided by the AIC weight of the best model and is a relative measure of the degree of support for a model, and Deviance is the difference in likelihood of a given model to the most general model. Density is abundance of *H. desmarestianus* (individuals ha^{-1}), Lagdensity is abundance in the previous trapping period, Fruitden is an index of fruit density, Lag Fruitden is the index of fruit density in the previous trapping period, Astro is the density of *Astrocaryum mexicanum* infructescences, and LagAstro is the density of *Astrocaryum mexicanum* infructescences in the previous trapping period. Models are ordered from best supported to least supported.

Model	AIC	ΔAIC	AIC Weight	Model Likelihood	Deviance
$\Phi A(t)$, $\Phi S(\text{Astro})$, $\Phi J(\text{Fruitden})$	3368.9	0	0.295	1.000	1223.1
$\Phi A(t)$, $\Phi S(\text{Density} + \text{Astro})$, $\Phi J(\text{Lagdensity} + \text{Fruitden})$	3370.1	1.2	0.158	0.536	1220.2
$\Phi A(t)$, $\Phi S(\text{Density})$, $\Phi J(\text{Lagdensity})$	3371.1	2.2	0.094	0.319	1225.4
$\Phi A(t)$, $\Phi S(t)$, $\Phi J(\text{Density})$	3371.9	3.0	0.064	0.219	1209.6
$\Phi A(t)$, $\Phi S(\text{Astro})$, $\Phi J(t)$	3372.3	3.4	0.053	0.181	1214.1
$\Phi A(t)$, $\Phi S(\text{Density} + \text{Lagdensity})$, $\Phi J(\text{Density} + \text{Lagdensity})$	3372.6	3.7	0.045	0.151	1226.9
$\Phi A(t)$, $\Phi S(t)$, $\Phi J(\text{Fruitden})$	3372.7	3.8	0.044	0.151	1210.4
$\Phi A(t)$, $\Phi S(t)$, $\Phi J(\text{Lag Fruitden})$	3372.7	3.8	0.044	0.150	1210.4
$\Phi A(t)$, $\Phi S(t)$, $\Phi J(\text{Lagdensity})$	3372.7	3.8	0.043	0.145	1210.4
$\Phi A(t)$, $\Phi S(t)$, $\Phi J(\text{Density} + \text{Lagdensity})$	3373.1	4.2	0.036	0.121	1208.7
$\Phi A(t)$, $\Phi S(\text{AstMex} + \text{LagAstro})$	3374.3	5.4	0.020	0.067	1214.1
$\Phi A(t)$, $\Phi S(t)$, $\Phi J(\text{Fruitden} + \text{Lag Fruitden})$	3374.5	5.6	0.018	0.061	1210.1
$\Phi A(t)$, $\Phi S(\text{Density})$, $\Phi J(t)$	3374.7	5.8	0.016	0.054	1216.6
$\Phi A(t)$, $\Phi S(\text{Density} + \text{Lagdensity})$, $\Phi J(t)$	3374.7	5.8	0.016	0.054	1214.5
$\Phi A(t)$, $\Phi S(\text{LagAstro})$, $\Phi J(t)$	3375.0	6.2	0.014	0.046	1216.9
$\Phi A(t)$, $\Phi S(\text{Fruitden})$, $\Phi J(t)$	3375.4	6.5	0.011	0.038	1217.2
$\Phi A(t)$, $\Phi S(\text{Lagdensity})$, $\Phi J(t)$	3375.7	6.9	0.010	0.032	1217.6
$\Phi A(t)$, $\Phi S(\text{Lag Fruitden})$, $\Phi J(t)$	3376.2	7.4	0.007	0.025	1218.1
$\Phi A(t)$, $\Phi S(t)$, $\Phi J(t)$	3376.3	7.5	0.007	0.024	1201.5
$\Phi A(t)$, $\Phi S(\text{Fruitden} + \text{Lag Fruitden})$, $\Phi J(t)$	3377.2	8.3	0.005	0.016	1216.9
$\Phi A(\text{Density})$, $\Phi S(t)$, $\Phi J(t)$	3386.7	17.9	0.000	0.000	1230.7
$\Phi A(\text{Density} + \text{Lagdensity})$, $\Phi S(t)$, $\Phi J(t)$	3388.5	19.6	0.000	0.000	1230.3
$\Phi A(\text{Lagdensity})$, $\Phi S(t)$, $\Phi J(t)$	3389.6	20.7	0.000	0.000	1233.5