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Consequences of Habitat Fragmentation on Age Structure and Life History in a Tortoise Population[1]

ABSTRACT

We studied changes in a population of red-footed Amazonian tortoises, *Geochelone carbonaria*, consequent to isolation in an insular forest fragment. Altered age structure, population density, and body growth rate are shown here for the first time to be associated responses. Age structure was strongly biased toward juveniles and growth rates were reduced compared to the mainland. Our data suggest that density-dependent processes induced by habitat fragmentation changed demography and life history parameters in a scant 16 years.

Key words: age structure; body growth rate; Geochelone carbonaria; *habitat fragmentation; life history traits; top-down vs. bottom-up; tortoise; tropical dry forest; Venezuela.*

Numerous effects of fragmentation on animal populations have been documented in an extensive literature (Faarborg *et al.* 1995, Robinson *et al.* 1995, Laurance & Bierregaard 1997). Documented effects include presence or absence of particular species in fragments of different size, increases and decreases in population density, enhanced or depressed reproductive success and survival, increased or reduced predation rates, and of course accelerated extinction (George 1987, Leigh *et al.* 1993, Terborgh

et al. 1997, Rao 1999, Shahabuddin & Terborgh 1999, Davies *et al.* 2000, Zanette *et al.* 2000, Terborgh *et al.* 2001). Evidence exists that some levels of top-down control are responsible for these changes. Less attention has been paid to the effects of fragmentation on demography and structure of persistent populations. The hyperabundance of certain animal populations surviving in forest fragments has been attributed to an absence of predation. A direct link between "predation relaxation" and hyperabundance, however, has seldom been conclusively demonstrated, just as reduced mortality from sources other than predation has seldom been ruled out (Rao 1999).

Life-history theory predicts that changes in the environment and adaptive responses to these changes both influence population processes and tend to vary the density and age structure of a population (Ricklefs 2000). Those changes may stimulate further evolutionary responses, consequently affecting life history traits. Here, we demonstrate that fragmentation resulting in habitat isolation has changed the age-specific mortality rates in a population of red-footed Amazonian tortoises (*Geochelone carbonaria*) producing altered age structure, population density, and body growth rate.

This study was conducted on 350 ha Danto Machado (DM) Island and the adjacent mainland surrounding Lago Guri, a 4300 km² hydroelectric impoundment created in 1986 in east central Venezuela (7°21′42″N, 62°52′47″W). The island was created as a consequence of the hydroelectric impoundment; thus, it was 16 years old by the time of this study. At its closest approach, the margin of Danto Machado lies *ca* 2 km from the nearest point on the mainland. The tortoise population on DM was compared to that at a control site 4 km to the south on the mainland (M1). A second sample of mainland tortoises (M2) came from the town of El Manteco, 30 km to the east. This sample was composed of 22 confiscated poached animals. People from El Manteco usually feed on tortoises they catch in nearby forests. The National Guard (police) personnel frequently appropriate poached tortoises and keep them in captivity for a few months before they are released. Tortoises used in this study had been seized by the National Guard just 15 days before we measured them. All of them were initially collected by the same person. The entire study area (DM, M1, and M2) is covered by 15 to 20 m tall semi-deciduous tropical dry forest (Huber 1986). DM can be considered a fragment of the original forest (Terborgh *et al.* 1997, Rao 1999, Shahabuddin & Terborgh 1999, Terborgh *et al.* 2001).

Tortoises were captured on Danto Machado in three areas of 6.2, 15.5 and 1.4 ha. These areas were searched daily from May to July 2000. Searches were conducted mainly during the afternoons when tortoises were more active. An 11 ha plot on the mainland (M1) was searched during June 2001. Searches at both DM and M1 sites were carried out during the beginning of the rainy season under the same climatic conditions. Each sampled area was surveyed for six to seven days. Teams of two or three people searched the mainland site (M1) for 51 person-hours. Every individual tortoise captured was marked on the carapace and released at the same site. The Schnabel method for few recaptures was used to estimate population size in each sampled area (Krebs 1999). Fire is also a major cause of mortality in tortoises (Coe *et al.* 1979), and so we also checked every individual for burn scars on the shell.

The age structure of both the DM and M1 populations was determined by counting the annuli on the dorsal scutes of the carapace. Body growth parameters were estimated by measuring annuli length and fitting a von Bertalanffy model to the data sets. Both methods are well developed and have been used to age tortoises and turtles reliably in previous studies (Germano 1988, 1998). Growth data collected in such a way is equivalent to a longitudinal sample (*i.e.*, a measurement of each individual every year along its growth period). A von Bertalanffy model for length of the form $LC = a(1 - b \, EXP(-k \, T))$ was fitted to the data using the nonlinear regression module of Systat. In this module, LC is the length of the carapace at any time; T is the age of the individual; a is the asymptotic size; b is a parameter related to size at birth; and k is the rate of approximation to the asymptotic size or intrinsic rate of growth. The von Bertalanffy model has proved to be useful in modeling indeterminate growth. Support-plane confidence intervals were constructed for the growth parameters (Schoener & Schoener 1978).

Seventy-four tortoises were captured on DM during 147 person-hours of searching over 39 days for an average capture rate of 0.6 individuals/hour (maximum 4.5 individuals/hour). Mark–recapture was used to estimate the population of all three sample areas combined at 205 individuals (95% ci = 125–256 individuals) or 12.9 individuals/ha (95% ci = 6.51–17.09 individuals/ha). Despite daily sampling efforts on M1 being 1.7 times higher than on DM (6.35 vs. 3.75 person-hours in DM), 29 tortoises were discovered for a capture rate of 0.57 individuals/hour. The population estimate for M1 was 61 tortoises, which is equivalent to 5.51 individuals/ha (95% ci = 3.64–6.15 individuals/ha).
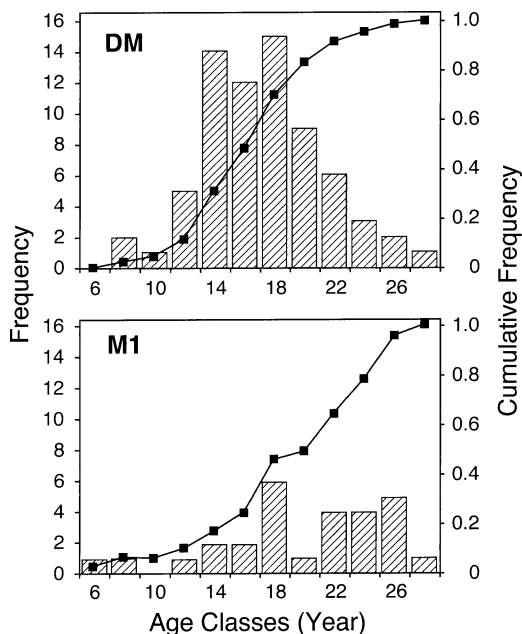
FIGURE 1.   Age structure of tortoise populations on Danto Machado Island (DM) and the mainland (M1). On DM, 50 percent was under 16 years of age; 70 percent was 2 years old or less by the time the habitat fragment was created in 1986; and on the mainland, 25 percent of the population was younger than 16 years.

At both DM and M1, recapture distances ranged between 0 and 200 m from the original point of capture, being in most cases less than 60 m. All tortoises recaptured on DM were caught within the original sampling area, with the first recapture recorded 25 days after the first individual had been marked. In contrast, the first recapture at M1 occurred 5 days after sampling started.

When comparing DM and M1 populations, the proportion of individuals under 16 years old was not independent of site ($G_1 = 4.7$, $P = 0.031$). Fifty percent of the tortoises found on DM were younger than the island (≤ 16 years old; Fig. 1a), despite the well-known difficulty of finding young tortoises (Dodd *et al.* 1994, Anderson *et al.* 2001). At the mainland site, these age classes represented only 25 percent (Fig. 1b). Body growth rate of DM tortoises was significantly lower than that of the M1 population (Table 1) despite the fact that 5 individuals from DM were discarded from the sample because they were probably too old and their annuli were too worn to count. This may have biased the growth rate of DM tortoises toward higher values. DM tortoises' growth rate was also lower when compared with pooled M1 and M2 data. Growth rate of tortoises from the M2 population did not differ from that of the M1 population. Only two individuals from M1 were discarded because their annuli were too worn.

Densities of *G. carbonaria* on DM were higher than in the M1 plot. In a previous study conducted in Brazil and using similar methods, Moskovits (1988) determined the abundance of *G. carbonaria* and *G. denticulata* to be 1.02 individuals/ha and 0.2 individuals/ha, respectively, or 1.25 individuals/ha overall (95% ci = 0.78–3.18). On DM, *G. carbonaria* densities were ten times higher than the two species combined in Brazil.

If the high density of tortoises on DM were merely a lingering consequence of an artificially high concentration of animals created by rising water as the impoundment filled in 1986, the population would have been biased toward older individuals. On the contrary, the high proportion of juveniles suggests an increase in the reproductive success of the adult population and/or a decrease in juvenile mortality subsequent to the isolation of DM. Typically, turtles and tortoises suffer high mortality rates early in life but become almost invulnerable to predators later as they increase in size and shell hardness (Auffenberg & Iverson 1979, Pritchard & Trebbau 1994). On DM, some potential predators of tortoise

TABLE 1. *Von Bertalanffy body growth parameters for Danto Machado Island (DM), mainland site 1 (M1), and mainland site 2 (M2) male tortoise populations. Few females from both mainland sites were available for analyses. (a) Maximum asymptotic body size measured as linear carapace length (LCL; cm); (b) size at birth; (k) rate of approximation to the asymptotic size; b and k are dimensionless parameters; 95% support-plane confidence intervals for growth parameters are shown.*

| | Growth parameters | | |
Sites (N)	a	b	k (95% ci)
DM (44)	31.57	0.816	0.051 (0.049, 0.053)
M1 (18)	34.20	0.899	0.093 (0.084, 0.102)
M2 (22)	32.60	0.892	0.111 (0.099, 0.121)
M1 and M2 pooled data	33.40	0.897	0.101 (0.096, 0.106)

eggs (*Tupinambis* sp.) and newborns or juveniles' predators (*Caiman crocodylus*, *Leopardus* spp., *Eyra barbara*, and *Nasua nasua*) are scarce or absent but are common on the mainland, based on ten years of observations in the area.

Fire is a frequent event on the mainland, while rare on the island. In the last ten years, fire has burned mainland forests in 1993, 1995, 1998, and 2001. In contrast, only one fire event was documented on DM since 1990 and that was in 2001, one year after our sampling at that site. Examination of tortoise carapaces from DM and the mainland showed that the presence of burn scars was not independent of site ($G = 16.8$, $P = 0.0008$). On M1, 27.6 percent of the tortoises had burn marks versus 1.3 percent in DM.

The available evidence suggests that a decrease in the mortality caused by either fire or predation of tortoise eggs and/or juveniles, or a combination of both, occurred subsequent to the isolation of DM. The resulting increase in juveniles has raised the local density of *Geochelone* substantially over densities recorded in mainland populations, probably having strong effects on body growth rate via density-dependent processes. Once free from major sources of mortality, the DM population may now be controlled primarily by resource availability. Although not yet reflected in the age structure, the effects of bottom-up forces may become apparent in future studies. Despite this tortoise population being clearly under the effect of top-down forces, other non-trophic factors such as fire are also affecting it. Our data suggest that the structure of terrestrial ecosystems also may be determined by other non-trophic interactions not considered by the top-down versus bottom-up debate.

Density dependence of body growth has been reported previously for turtles and tortoises (Bjorndal *et al.* 2000) due to competition for limiting resources. As the age of maturity is highly dependent on rate of body growth (Bourn & Coe 1978, Stearns & Koella 1986, Shine & Iverson 1995), we can expect future changes in other life history traits of the island population given that present conditions are maintained.

Previous reports on low growth rates in turtles or tortoises have come from highly abundant populations, giving the wrong impression that this is the rule rather than the exception. For example, Aldabra tortoises (*Geochelone gigantea*) showed body growth rates of 0.05 (Bourn & Coe 1978), very similar to that reported by us on DM. Free of predators, Aldabra tortoises have reached population densities of 26.9 individuals/ha (Bourn *et al.* 1999). In contrast, *Gopherus agassizii*, living at low densities, reached growth rates of 0.112 to 0.114 (Germano 1994), similar to that reported by us for *G. carbonaria* on M1 and M2. Low body growth rates seem to be a by-product of living in high density areas where predators are absent and hence populations are limited by resources. We suggest that in the case of tortoises, this characteristic is the product of habitat fragmentation and isolation. Changes in life history traits like those reported here occur at the phenotypic level. Nevertheless, what is being modified is the rate of body growth that may affect the age at maturation and the clutch size, egg mass, and reproductive success as it has been demonstrated not only in tortoises but also in other species with indeterminate body growth. Therefore, we predict that habitat fragmentation will have a strong influence on the selective pressures that shape the evolution of life history traits.

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Gregarious Oviposition and Clutch Size Adjustment by a *Heliconius* Butterfly[1]

ABSTRACT

Female *Heliconius hewitsoni* butterflies were found to aggregate during oviposition, producing multi-parent egg clutches. This behavior occurred when host plants were locally plentiful, indicating that females chose to oviposit gregariously. Collective clutch size correlated with host growth rate and with the number of females contributing to a clutch. Eggs did not positively bias host plant growth. Collective clutch size adjustment may represent a mechanism for facilitating larval aggregation while reducing intraspecific competition.

Key words: communal oviposition; intraspecific competition; larval aggregation; Passiflora; *social oviposition*

BUTTERFLIES ARE AN IMPORTANT SYSTEM FOR STUDYING THE BEHAVIORAL ECOLOGY of clutch laying and larval aggregation (Stamp 1980, Godfray *et al.* 1991). An exceptional aspect of butterfly clutch laying is that some butterflies produce collective egg clutches through gregarious oviposition behavior (Mallet & Jackson 1980, Godfray *et al.* 1991, Sourakov 1997, Prokopy & Roitberg 2001). Previous descriptions of this behavior, however, consist of only a few observations with quantitative data. This study documents gregarious oviposition in the butterfly *Heliconius hewitsoni* in terms of spatial and temporal aggregation of ovipositing females in nature, and relates these data to population-wide patterns of collective clutch laying in the context of host plant availability.

Heliconius hewitsoni occurs in lowland rain forests of southwestern Costa Rica and western Panama (Longino 1984, DeVries 1987). Individuals have small home ranges and display predictable patterns of daily movement (Reed, pers. obs.). Larvae of *H. hewitsoni* feed solely on the liana *Passiflora pittieri*, and gregarious oviposition behavior has been previously noted in this species (Longino 1984; Duckett 1989; L. E. Gilbert, pers. comm.).

This study was conducted near La Sirena field station, Corcovado National Park, Costa Rica, where I observed butterflies at four *P. pittieri* sites (8°28.68′N, 83°35.41′W; 8°29.04′N, 83°35.48′W; 8°28.83′N, 83°35.46′W; and 8°28.81′N, 83°35.11′W) during the wet season of July and August 2001. I numbered all females with a Sharpie pen and recorded the identity of ovipositing individuals, the total number of eggs laid during an event, shoot length at the time of oviposition, the time of the first oviposition, the approximate time of the final oviposition, and, for a subset of females, individual clutch contributions.