SUPPORTING THE STUDY OF THE INTRASPECIFIC VARIATION OF LIFE-HISTORY STRATEGIES OF TROPICAL MAMMALS

Fernando A. Cervantes*

RESUMEN

Varios esquemas teóricos han sido propuestos para explicar los patrones de variación de estrategias de historia de vida en mamíferos. Desafortunadamente, no se ajustan a todos los casos y se desconoce si la variación observada es de origen evolutivo o local. Aquí se propone evaluar localmente la variación de los elementos de las tácticas de historia de vida, enfatizando el estudio de los mamíferos tropicales. Especialmente, se deberían comparar distintas poblaciones de una misma especie bajo diferentes circunstancias ambientales. Examinando los parámetros adecuados se comprenderá mejor la magnitud de las diferentes presiones de selección y su influencia en la variación de los patrones de tácticas de historia de vida en mamíferos tropicales.

Palabras clave: demografía, historia de vida, mamífero, tropical, evolución, ecología.

ABSTRACT

Several theoretical schemes have attempted to explain patterns of life-history variation in mammals. However, some cases are not satisfactorily explained and it is unknown to what extent observed life-history variation is the result of both evolutionary and nonevolutionary sources. This manuscript proposes evaluating the nature of the local variance component of life-history traits. Special emphasis will be given to tropical mammals. Attention is focused to comparing and contrasting populations of the same species under different ecological conditions. Examining significant variables will contribute to the better understanding of the role of different environmental pressures in the variation of life-history patterns of tropical mammals.

Key words: demography, life-history, mammal, tropics, evolution, ecology.

LIFE-HISTORY STRATEGIES

The life-history of organisms, like all other phenotypic attributes, represents a series of selective compromises to a suite of environmental variables (Wilbur *et al.*, 1974). A life-history strategy includes such components as age at first reproduction, age-specific fecundity, reproductive life span, age-specific mortality and energetic and behavioral traits (Fleming, 1979; Flowerdew, 1987). However, the demographic parameters represent the major focus of interest in the evolution of life-history strategies since fitness is understood as the number of surviving, reproducing

* Instituto de Biología, Departamento de Zoología, UNAM. Apartado postal 70-153. 04510 México, D.F. México.

offspring an individual produces during its lifetime (Fleming, 1979). These attributes imply a suite of adaptive responses accumulated over evolutionary time. Natural selection will modify each of these components to produce a life-history strategy that results in the highest individual fitness (Wilbur *et al.*, 1974).

Numerous contributions deal with the evaluation of life-history strategies in various organisms (Stearns, 1977). The schemes emerging from broad comparisons have attempted to explain patterns of variation observed in nature and to predict the type of life histories to be expected in different environments and why (Ballinger, 1983). Some attempts have categorized species within general theoretical constructs such as r-K selection which have served to increase the size and delineate the components of the data base necessary for understanding life-history variation. High maximum rate of natural increase, early reproduction, large litter size, semelparity, small body size, and short life span are considered to be components of a r-strategy, and to have evoluved in seasonal or unpredictable environments, while low maximum rate of natural increase, delayed reproduction, small litter size, iteroparity, large body size, and long life span are said to comprise a K-strategy and to have evolved in stable environments (Pianka, 1974; Nichols *et al.*, 1976).

On the other hand, stochastic models predict the evolution of the same combination of life-history traits but for different reasons: when fluctuations in the environment result in highly variable juvenile mortality, then a set of delayed maturity, smaller reproductive effort, and greater longevity should evolve (Murphy, 1968; Schaffer, 1974; Stearns, 1977). This has been called the "bet-hedging" model (Stearns, 1976). The relationship of such environmental variability to variance in life-history parameters is difficult to deduce. Yet, there are several proposed models that illustrate how spatial and temporal heterogeneity of the environment may be critical in life-history evolution (Boyce, 1979; Hastings and Caswell, 1979; Lacey *et al.*, 1983; Ritland and Jain, 1984).

However, the life histories of some well-known organisms are not satisfactorily explained by the theoretical framework mentioned above (Wilbur *et al.*, 1984; Nichols *et al.*, 1976; Armitage, 1981; Dunham, 1982; Berven, 1982). This is proposed to occur when life-history patterns are viewed as the outcome of a minimum number of selective pressures. Moreover, it has been suggested that life-history models are subjected to pleiotropy between life-history characters (Rose, 1983), and this pleiotropic effet as the condition of a life-history trait influencing another or more related life-history traits. According to this hypothesis, these component characters are not generally autonomous of one another, and hence, antagonistic pleiotropy may lead to abundant genetic polymorphism for life-history attributes. Therefore, both the detailed studies and analysis of specific populations, and the consideration of many environmental dimensions seems essential to identify causal mechanisms and provide complete understanding of the evolution of life histories (Wilbur *et al.*, 1974; Armitage, 1981). This becomes more important as the development of similar life-history tactics may evolve from different natural selection pressures.

A general hypothesis tested in ecological studies of natural populations is that life histories of species are adaptive and hence explicable in evolutionary terms (Van

Devender, 1982). However, some workers have addressed the problem of geographical and ecological variation in life-history traits within a species (Western, 1979; Ballinger, 1983; Berven, 1982). Researchers frequently use data from several localities to infer geographic patterns in life-history attributes. Observed variation is usually assumed to be adaptive and correlated with environmental differences at the sites. Yet, annual and local variations in demographic characters can have important effects on populations (Van Devender, 1982).

One of the facts that restricts our understanding of life-history diversity is that it is not known to what extent observed life-history variations are a result of evolutionary processes and to what extent these variations reflect nonevolutionary sources. Ballinger (1983) proposed a model to evaluate the nature of life-history variations combining them to assess their relative importance and providing an initial test of the model. He pointed out that phenotypic variation (Vp) is the sum of the variation due to genetic and environmental factors:

$$V_p = Vg + Ve.$$

Ultimate factors represent a cause-effect pathway mediated through the genetic system (Vg), while proximate factors result in a direct response to environmental stimuli (Ve). He also suggested that genetic variance be divided into evolutionary components of Vy and Vc such that

$$Vp = Vy + Vc + Ve + Vr.$$

Component Ve represents the proximal environmental source of variation as before, and Vr is the residual variance left unexplained by the other variance components (omitted before as is often customary). Component Vy is the phylogenetic variance which represents genetic variation resulting from phylogenetic and design constraints (constraints of phenotypic variation which result from limited genetic information contained in a particular phylogenetic lineage or the constraints of design which result from what is developmentally possible). Component Vy would tend to be manifested by characteristics that are extremely conservative through evolutionary time. Component Vc is the "ecotypic variance" which represents the genetic variation resulting from adaptations to specific environmental conditions.

According to this model, a nested analysis of variance can be used to determine the variance associated with each variance component:

$$Pijkl = U + Yi + Ej(i) + Ck(ij) + Rl (ijk),$$

where P is the life-history character of interest; U is the overall mean value of that character; Yi is the phylogenetic and design background within which P is constrained; Ej is the proximal environmental component; Ck is the genetic component that reflects the adaptation of P to specific ecological conditions (location); and Rl is a random variable.

The major sources of variation in life-history traits then include: 1) those proximal variations of the environment that alter allocations in the time and energy budget, and 2) those genetic factors that, through evolution, have resulted in different adaptive patterns to maximize fitness or have affected morphological or developmental characteristics that canalize or constrain life-history traits (Ballinger, 1983).

Stearns (1983) examined a large data set of mammalian life-history traits using multivariate statistical methods, and concluded that not only do life-history traits

co-vary along more than one significant dimension in mammals but size and phylogeny have significant independent effects on patterns of covariation in life-history attributes. Other than this reference very little (e.g. Bekoff and Daniels, 1984; Bekoff, Diamond and Mitton, 1981; Eisenberg, 1981; Krohne, 1981) has been discussed about the nature of patterns of life-history variation in mammals. The question whether the life-history traits observed are more predictable or best explained by a knowledge of phylogenetic, adaptive, or proximate factors, has not certainly been explored, although it seems certain that all factors are involved (Ballinger, 1983). Evaluations of the nature of the variance components of the life-history traits in many mammalian species are needed before the patterns of life-history variation in mammals can be adequately understood.

Most of the theoretical framework has been developed after analyzing empir ical research undertaken under temperate conditions. Few data have benn produced examining tropical mammals. The richness of mammalian species and habitats in the tropics must have yielded patterns of life-history tactics that along with the mentioned above may significantly contribute to understand better the role of proximate factors in the variation of life-history traits of mammals.

TROPICAL MAMMALS

The extreme variance of the climatic conditions during the winter has played a signficant role in shaping the ecological and evolutionary responses of temperate mammals to the seasonality and stress of the environment. Very drastic fluctuations in the availability of resources represent a major constraint in these northern areas. However, variations in temperature and food resources in the Neotropics are less (Janzen and Wilson, 1983). The humidity conditions may vary significantly however, and the consequent seasonal rainfall patterns affect the populations of mammals. By far, the harshest period is the dry season, especially in places such as the neotropical dry forest of the Central American Pacific lowlands where the moisture levels have their minimum values during several months.

For example, the wet-dry seasonality has a strong effect on the reproductive pattern of tropical mammals, many of which are seasonal breeders (Fleming, 1975). However, it has been shown that the demographic responses of some tropical rodents to seasonality are strongly related to a taxonomic component. *Liomys adspersus* (Heteromyidae), *Oryzomys capito* (Cricetidae), and *Proechimys semispinosus* (Echyimidae) live in the same habitat but have quit different reproductive strategies (Fleming, 1971).

Dry season populations peaks also occur in rodents and insectivores inhabiting tropical savannas, and seasonal variations in survivorship have been reported in several tropical species of small mammals (Delany, 1978; Fleming, 1971, 1975). Rats (*Rattus rattus* in Venezuela and *Proechimys semispinosus* in Panamá) born in the dry season survive better than those born in the wet season. Seasonal changes in food availability may play an important role in seasonal survival variation in these two rodents. Similarly, March-born individuals of *Lophuromys flavopunctatus* in Uganda have a maximum lifespan of 12 months whereas those born in September live only 8 months or less. Moreover, individuals of *Rattus exulans* on Kure atoll,

Hawaii, first captured in late winter or summer when food levels were highest, survived better than those first captured in early winter.

Furthermore, most of the published information on the reproductive ecology of neotropical bats agrees with the fact that the frugivorous and insectivorous species have a seasonal pattern of reproduction corresponding to seasonal food availability (Fleming, 1972; Heithaus, Fleming and Opler, 1975; August and Baker, 1982).

Switching of food resources by nonspecialist mammals is a response to seasonality i the tropics. Some rodents and insectivores may feed upon items such as fruits, flowers or green parts during the wet season, but seeds are their main source fo food in the dry season (Janzen and Wilson, 1983). Wilson (1981) showed that the bat *Micronycteris hirsuta* feeds on different fruit items during the dry season while gleans insects from the foliage during the rest of the year.

On the other hand, some Costa Rican mammals like other animals, migrate locally to escape seasonal effects (Janzen and Wilson, 1983). In areas of deciduous forests traversed by strips of evergreen vegetation along everflowing rivers, howler monkeys, *(Allouatta palliata)*, spread out over the tropical deciduous forest during the rainy season and retreat to the riparian vegetation in the dry season. It is also believed that some species of bats in the dry forest of the pacific lowlands of the Guanacaste province, Costa Rican, move up to tens of kilometers to locate riparian trees in flower, fruit or both. Often, food scarcity in one area r ay be synchronized with food abundance in other areas. Insect populations in open hillsides are high during the wet season, buty very low during the dry season. In adjacent shady riparian habitats, however, insects are abundant during the dry season (Janzen and Schoener, 1968; Janzen, 1973).

The climate may play an important role under that ecological conditions. There are great differences between the physical climate in the deciduous forest and the climate in an immediately adjacent strip of evergreen riparian forest (Janzen, 1976). Near the end of a dry season, a station in the Costa Rican riparian forest had soil temperatures 6.5°C cooler, air temperatures 5.5°C cooler and relative humidity 20% higher than a station 62 m away in the deciduous forest. In addition to food availability, this may explain why the animals move into the riparian forest as the dry season progresses. To have this large difference in mean annual temperature for two weather stations in Costa Rican, they have to be almost 1,000 m apart in elevation.

However, the differences between the decidous and riparian forest largely disappear during the rainy season (Janzen, 1976). At the peak of the rainy season, two stations from these habitats differed by less than 1°C in soil temperature, 3°C in air temperature, and 21% in relative humidity. This difference in humidity is biologically different from the same difference at the bottom of the scale of humidity, which is where the difference ocurrend in the dry season.

There is also a striking difference between the floristic composition of the deciduous and riparian habitats. Janzen (1976) lists the tall evergreen trees of the riparian forest and the canopy of deciduous forest trees. These differences may result in a wide variation of resource availability, among the most important may be food, nesting sites, and shelter.

Therefore, it seems that during the dry season the more shaded, and cooler

riparian forest appears to be of great biological importance as a refuge for animals from the open drier, more iluminated, and hotter deciduous forest. The linear oases might funtion as dry-season sites of mammalian concentration due to the proximity of water, shade, fruit, foliage, and animal preys.

While it is well known that large and medium size mammals move in and out of the riparian habitats, the case of non-volant small mammals is not clear, but they are less likely to migrate locally. Small tropical rodents have small home ranges (Fleming, 1974; French, 1975; O'Connell, 1981; August, 1981). Some examples (Fleming, 1974) show that individuals occupy home ranges relatively stable in size and location for extended periods (one year or more). However, there are seasonal differences in distances moved among capture sites probably related to food availability (Fleming, 1974; O'Connell, 1981; D. Janzen, pers. comm.). Furthermore, there are several species of tropical rodents that maintin populations at the same place through the year in the deciduous tropical dry forest (Genoways, 1973; pers. obser.). Additionally, in the dry forest most of the species and biomass of edible seeds, by species and also biomass, fall in the last month of the rainy season and the first three months of the dry season (Fleming, 1974). This suggests that instead of moving into the riparian zone, the small mammals (mostly seed eaters) may take advantage of the high supply of food resources in the dry areas. Unfortunately, there are no data about the availability of food resources in the riparian forest (other than insects).

It is feasible then that populations of some nonvolant, small mammals species spread throughout both the dry and riparian areas and remain throughout the year in their same headquarters. However, comparative studies of different ecological conditions in tropical species of rodents have rarely been done. This would be a good example to follow the variation of life history-traits of the same species under contrasting selective pressures. Bat populations also would be useful tools to dilucidate the phenomena here discussed. High numbers of individuals under contrasting conditions must be monitored. The analysis of the populational responses and life-history heterogeneity associated with diverse habitat conditions in local populations of the same species of mammal would contribute to the knowledge of life-history variations. This is a topic to research in order to understand the role of different environmental pressures on the variations of the life-history patterns found in mammals.

Empirical studies of temperate species of small mammals have yielded significant amount of data to build the theoretical basis of the knowledge on life-history tactics. Unfortunately, research on life-history traits of tropical mammals has been left behind. Experimental testing of predictions and hypotheses derived from life-history models is encouraged. Bellinger's model may well be hard to test. However, it shows the need to carefully examine proximate variation of life-history traits what it is strongly recommended here, especially for populations of tropical mammals at intraspecific level. New predictions and hypotheses must be tested under tropical conditions. The life-history traits of most importance to examine are those related to population fluctuations, reproductive strategy, survival, longevity, body size, and environmental stability (e.g. seasonality of climate and food availability).

More detailed demographic studies of populations of selected species ocurring

ın contrasting tropical habitats are thus needed to gain insight into the life-history variation of tropical mammals. The results provided from this approach will greatly contribute to the better understanding of the nature and evolution of life-history strategies of mammals.

In México, preserved tracts of tropical vegetation provide attractive opportunities to examine different habitats under tropical conditions: from tropical evergreen forests, through mangrooves, cloud forests, and deciduous forests to grasslands and dunes. Several protected areas are managed by forestry and biological stations for research (e.g. "La Mancha", Veracruz, "Chamela", Jalisco, "El Tormento", Campeche, "Los Tuxtlas", Veracruz) where field work may be largely supported.

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