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DYNAMICS OF A SUBTROPICAL POPULATION OF THE ZEBRA LONGWING BUTTERFLY *HELICONIUS CHARITHONIA* (NYMPHALIDAE)

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Abstract

We studied the population dynamics of the zebra longwing butterfly, *Heliconius charithonia* (Nymphalidae), in a 0.05 ha garden in Miami, Florida, for 2 years to answer the following questions: (1) How stable is a suburban, subtropical population of this widespread neotropical butterfly? (2) What are the major factors influencing its population dynamics? (3) What are the implications of adult mobility regarding gene flow within and between fragmented urban populations of this species? A mark-recapture study indicated that adult population size averaged 59 individuals (range: 9-115 individuals). Peak numbers occurred in mid-wet season (September) in 1996 and in the late dry and early wet seasons (April through June) in 1997. Fluctuations in size of the adult population paralleled changes in biomass of the larval food plant, *Passiflora incense*. Population sex ratio was consistently male-biased (68% males). Reproduction occurred year-round, and parasitism by a trichogrammatid wasp killed about 50% of *Heliconius* eggs throughout the year. Recruitment of adults from chrysalises produced in the garden and deaths, rather than immigration and emigration, accounted for most numerical changes. Both males and females apparently adjust their home range locations in response to changes in the biomass of *Passiflora* plants. Females search these plants for suitable oviposition sites, and males search them for female pupae (mates). In addition to relatively high mortality from egg parasitism, fluctuations in the number of suitable oviposition sites and amount of larval food limited recruitment into the adult butterfly population. High adult mobility probably results in substantial gene flow within and between populations of this butterfly in urban south Florida.

Key Words: population dynamics, food limitation, egg parasitism, *Heliconius charithonia*

Resumen

Estudiamos la dinámica poblacional de la mariposa “cebra de alas largas”, *Heliconius charithonia* (Nymphalidae), en un jardín de 0,05 ha en Miami, Florida, por dos años para responder a las siguientes preguntas: (1) Qué tan estable es una población suburbana subtropical de esta mariposa neotropical ampliamente distribuida? (2) Cuáles son los principales factores que influencian su dinámica poblacional? (3) Cuáles son las implicaciones del movimiento de adultos en el flujo de genes dentro de y entre poblaciones urbanas fragmentadas? Un estudio de marca-recaptura indicó que el tamaño de la población adulta promedió 59 individuos (rango: 9-115 individuos), con picos en la mitad de la estación lluviosa (Septiembre) de 1996 y al final de la estación seca e inicio de la estación lluviosa (Abril a Junio) de 1997. Las fluctuaciones en el tamaño de la población adulta fueron paralelas a los cambios en biomasa de la planta huésped del estadío larval, *Passiflora incense*. La proporción de sexos en la población fue consistentemente sesgada hacia los machos (68% machos). La reproducción ocurrió durante todo el año, pero una especie de avispa tricogrammatidae parásita mató alrededor del 50% de los huevos de *H. charithonia* producidos en el año. Más que la inmigración y emigración, el reclutamiento de adultos, a partir de crisálidas producidas en el jardín, y la mortalidad controlaron el tamaño de la población. Tanto machos como hembras aparentemente modifican sus ámbitos hogareños en respuesta a cambios en la biomasa de las plantas *Passiflora*. Las hembras visitan estas plantas en búsqueda de sitios óptimos para la oviposición, mientras que los machos lo hacen para buscar pupas hembras (parejas para reproducción). Además de la relativa alta mortalidad causada por el parasitismo de los huevos, las fluctuaciones en el número de sitios óptimos para la oviposición y la cantidad de comida para las larvas limitaron el reclutamiento hacia la población adulta de mariposas. La alta movilidad de los adultos probablemente resulta en un flujo sustancial de genes dentro de y entre las poblaciones de esta mariposa en el sur de la Florida.

Translation provided by the authors.

Butterflies of the genus *Heliconius* are common and conspicuous members of forest habitats throughout the neotropics. Studies of their population dynamics indicate that *Heliconius* butterfly populations (i) occur in low population densities (<5 per ha), (ii) have biased sex ratios (usually towards males), (iii) reproduce year-round, (iv) have maximum adult lifespans ranging from 90 to 180 days, and (v) contain individuals that exhibit home range behavior (Ehrlich & Gilbert 1973; Cook et al. 1976; Saalfeld & Araujo 1981; Quintero 1988; Gilbert 1991; Ramos & Freitas 1999). Compared with most temperate butterflies, species of *Heliconius* are low density, long-lived insects with extended reproductive lifespans. The degree to which *Heliconius* populations are genetically open or closed has been controversial. Brazilian workers (e.g., Romanowski et al. 1985; Haag et al. 1993; Silva & Araujo 1994) have reported that populations of *Heliconius erato* are 'insular' and inbred whereas Mallet (1986) suggested, based on mark-recapture data, that individuals of *H. erato* in Costa Rica disperse considerable distances and are not likely to be inbred.

What are the structure and dynamics of *Heliconius* butterfly populations near the northern geographic limits of the group? As has been reported for some species of temperate butterflies (e.g., Thomas et al. 1994; Shreeve et al. 1996; Van-Strien et al. 1997), are subtropical populations more variable in size than tropical populations? Are mortality rates higher and reproductive seasons shorter in northern populations? To answer these questions, we studied the dynamics of a population of the zebra longwing butterfly, *Heliconius charithonia* L. (Nymphalidae), for two years in Miami-Dade County, Florida. *H. charithonia* is widely distributed in the southeastern United States, the West Indies, and Central and northern South America (Opler & Krizek 1984). According to Gilbert (1991), this species is more common in disturbed than in undisturbed sites and prefers seasonal tropical sites to evergreen forests. *H. charithonia* is a phylogenetically advanced member of its genus the larvae of which are feeding specialists on non-woody, short-lived species of *Passiflora* (passion vines) found in successional habitats. Adults tend to collect smaller, less nutritious pollen grains than less-advanced heliconiines. Pupal mating occurs in this species, and females lay their eggs gregariously on fresh shoots. Larvae are non-aggressive and feed on older leaves only after fresh shoots are depleted.

MATERIALS AND METHODS

Study Site

This study was conducted for two years (mid-December 1995 to mid-December 1997) in a 0.05-ha. garden in suburban Miami, Florida (25°49'N, 80°17'W). Most observations were made in a 15-m × 20-m section of the garden, which was planted in 'butterfly' plants, including *Pentas lanceolata*, *Stachytarpheta fruiticosa*, and *Hamelia patens*, that provided nectar and pollen for adults. One individual of *Passiflora incense*, a non-native (hybrid) larval food plant (Vanderplank 2000), was planted at the base of a clothes pole that served as an arbor in January 1995. By late 1995 rhizomes of this plant had spread over a relatively large portion of the 300 m^2 intensive study area, and new stems emerged continuously throughout the study. Prior to 1 August 1997, we did little to control the growth of *Passiflora* in the garden. By that date, however, vines had overgrown much of the study area, and we removed >95% of the *Passiflora* biomass. A native *Passiflora* (*P. suberosa*) occasionally 'volunteered' in the garden but was quickly eliminated by *Heliconius* herbivory.

The climate of Miami includes a 5-month dry season (November-April) and a 7-month wet season (May-October). About 75% of Miami's average annual rainfall of 1,420 mm falls during the wet season. Annual rainfall was above average in 1996 and 1997 and totaled 1,466 and 1,795 mm, respectively. During the study, lowest temperatures of 2-3°C occurred on one day each in January and February 1996 and January 1997, and highest temperatures of 34°C occurred in June 1996 and July and August 1997. In this study, we recognize two seasons per year: dry season (1 November-30 April) and wet season (1 May-31 October).

In addition to *H. charithonia*, two other species of heliconiid butterflies frequented the garden. The gulf fritillary, *Agraulis vanillae* (L.), was present in low numbers (but sometimes in equal abundance to that of the zebra longwing) during most of the study. Its larvae co-occurred with those of *H. charithonia* on *Passiflora* vines. Much less common than the gulf fritillary was the julia, *Dryas iulia* Clench, which apparently did not oviposit in the study area.

Methods

Size of the adult population feeding, ovipositing, and mating in the garden was estimated by mark-recapture methods. One morning each week, butterflies were captured with hand nets and released during a period of 1.5-2 h. Captured individuals were marked by writing a number on the outside surface of both hindwings with a Sharpie® Extra Fine Point permanent marker. At an individual's initial capture, we noted its sex, wing length, and wing wear condition. On subsequent captures, we recorded ID number and wing wear condition. We measured wing length to the nearest 0.5 mm with a plastic ruler as the distance from the bottom of the left hindwing to the tip of the left forewing. We scored wing wear condition in one of five categories: 0 = no wear (bright, intense color), 1 = early wear (color less intense but still bright), 2 = medium wear (color faded but wings still opaque), 3 = extensive wear (color very faded and wings partially transparent), and 4 = extreme wear (little color, wings extensively damaged). Butterflies were retained for ca. 5 min at each capture. At approximately weekly intervals between 4 July 1996 and 24 March 1997, we counted the number of adults night-roosting on a *Citrus* tree in the garden after sunset.

We surveyed 2-10 major *Passiflora* stems, depending on availability, for heliconiid eggs, larvae, and chrysalises once each week Throughout the study the "clothes pole" plant was the largest *Passiflora* stem and was always surveyed for immature life stages. Other stems ≥1 m in length were surveyed whenever they contained fresh growth. We could not distinguish between the eggs of *H. charithonia* and *A. vanillae*, so our egg counts include both species. Number of larvae in each of three size categories (<1/3 maximum length (= "small"), >1/3 but <1/2 maximum length (= "medium"), and >1/2 maximum length (= "large") was recorded separately for both heliconiid species. Finally, we searched each plant for zebra longwing chrysalises and counted and marked each one with a small spot of fingernail polish to distinguish "new" from "old" chrysalises.

We estimated egg mortality due to parasitism by trichogrammatid wasps between 6 October 1996 and 21 November 1997 in two ways. First, every two weeks between 6 October 1996 and 10 May 1997 we removed 15 randomly chosen eggs from new leaves or stems and placed each one in a labeled 1.5 mL microcapillary tube. Eggs were examined daily and the fate of each egg (no larvae or parasites emerged, larva emerged, parasitic wasps emerged) was recorded for two weeks. Because all larvae emerging from eggs were those of *H. charithonia*, these mortality estimates are not confounded by the presence of *A. vanillae*. Second, six times in 1997 (twice in April and May, once in July and November) a series of 4-109 eggs on 1-14 plants was marked with a dot of ink on the leaf next to each egg. For the next 2-9 days the status of each egg was scored as "parasitized" (egg turned dark gray), hatched (egg shell empty), or "gone." Number of small larvae of *H. charithonia* and condition of the leaf bearing the eggs (intact or chewed) also were recorded every day.

To estimate the amount of *Passiflora* biomass present in the study area each week, we took notes on the condition of each stem (i.e., each ramet) that we surveyed. Each stem was given one of the following "condition" scores: 0 = chewed back to ground level; 1 = new or regrowth ≤1 m long; 2 = a medium-sized, non-flowering plant; 3 = a large, flowering plant; and 4 = a very large, flowering plant. These scores represent the approximate greatest length (in m) of each stem. The sum of the scores of stems was multiplied by 2 to represent the approximate biomass of *Passiflora* foliage (in m^2) present in the intensive study area each week.

Population Estimation

Capture-recapture data were analyzed in a set of models implemented in program TMSURVIV; J. Hines, unpublished), a modification of program SURVIV (White 1983) developed to compute estimates under the transient models of Pradel et al. (1997). Transient models represent a generalization of the standard Cormack-Jolly-Seber model (Cormack 1964; Jolly 1965; Seber 1965) developed for open populations (i.e., populations that can experience gains and losses between sampling periods). The generalization basically involves the possibility of different survival probabilities for animals captured in any sampling period, *i*, depending on whether or not the animal has been captured previously (i.e., whether the animal is marked or unmarked).

The most general model contains three kinds of parameters indexed by both time (sampling period, *i*) and sex (*s*):

$\varphi_i^{(s)}$ = the probability that a marked butterfly of sex *s* in the population at time *i* survives and is present in the area exposed to sampling efforts in period *i*+1;

$\gamma_i^{(s)}$ = the ratio of survival probabilities (*i* to *i*+1) of unmarked to marked butterflies of sex *s* (in a population with transient individuals, this ratio is the probability that an unmarked butterfly is a transient);

$p_i^{(s)}$ = the probability that a butterfly of sex *s*, in the population at time *i*, is captured at *i*.

The zebra longwing butterfly data set contained 97 sampling occasions, and the most general model thus contained a very large number of parameters. Several reduced-parameter models were created by eliminating one or more sources of variation in model parameters. For example, models with $\gamma_i^{(s)} = 1$ incorporated the assumption of the standard Cormack-Jolly-Seber model that survival probability does not depend on mark status. Some models incorporated the assumption of parameters constant over time (e.g., $p_i^{(s)} = p^{(s)}$), and others assumed equality of parameters for males (*m*) and females (*f*) (e.g., $p_i^{(m)} = p_i^{(f)} = p_i$). Although most sampling was conducted on a weekly basis, this was not strictly true, and the time intervals separating successive sampling periods varied. For this reason, the time constraint, $\varphi_i^{(s)} = \varphi^{(s)}$ makes little biological sense. However, the hypothesis of equal survival per unit time is reasonable, so we reparameterized survival in the model as $\varphi_i^s = (S_i^{(s)})^t$, where *t* denoted the time period (in weeks) separating sampling periods *i* and *i*+1. Thus, we effectively scaled survival probability to a weekly time interval, and the hypothesis of equal weekly survival over time, $S_i^{(s)} = S^{(s)}$, is biologically plausible.

We fit 14 different models to the data and followed the general suggestions of Lebreton et al. (1992) for model notation. Model ($S_i^{(s)}, p_i^{(s)}, \gamma_i^{(s)}$), the general model of Pradel et al. (1997), was the most general model in our model set. All three classes of parameter include the subscript *i*, denoting full time variation, and the superscript *s*, denoting sex-specificity of parameters. Absence of a superscript or subscript indicates that the source of variation is omitted from the model parameterization. For example, model ($S^{(s)}, p^{(s)}, \gamma$) includes no time-specificity for any parameter (denoted by absence of subscripts, *i*), and no sex-specificity either for γ. We considered models that assumed equal survival probabilities for previously marked and unmarked butterflies (the Cormack-Jolly-Seber model assumption), and denoted this assumption as $\gamma = 1$. Thus, model ($S, p, \gamma = 1$) denotes a simple 2-parameter model in which survival and capture probability are constant over time and the same for males and females and survival is the same for marked and unmarked butterflies.

The software, TMSURVIV, provides maximum likelihood estimates of the parameters and associated estimates of variances and covariances under each model. Adequacy of fit of the most general model was judged using a parametric bootstrap approach. Under this approach, capture history data were simulated under the general model by treating the parameter estimates as true values. The general model was then fit to each simulated data set, and maximum likelihood estimates obtained. The standard G^2 goodness-of-fit statistic was also computed for each simulated data set. We ran 100 simulations and compared the G^2 statistic from the actual data analysis with the distribution of statistics from the simulated data sets to test for fit. In the event of poor model fit, we followed the approach recommended by White & Burnham (1999) of estimating a variance inflation factor, $\hat{c}$, as the ratio of the observed G^2 to the mean of the G^2 values from the simulations. In the event of poor model fit, variance estimates were obtained using a quasi-likelihood approach (e.g., Burnham et al. 1987; Lebreton et al. 1992) as the product $\hat{c}\, v\hat{a}r\, (\hat{\theta})$, where $\hat{\theta}$ is the maximum likelihood estimate of parameter θ under the selected model, $var\,(\hat{\theta})$ is the associated model-based variance estimate, and $\hat{c}$ is the variance inflation factor associated with lack of model fit and estimated as described above.

Model selection was based on QAICc values, Akaike's Information Criterion adjusted for lack of fit (quasi-likelihood) and sample size (Burnham & Anderson 1998). AIC can be viewed as an optimization criterion useful in model selection (Akaike 1973; Burnham & Anderson 1998). The criterion places value on good fit of the model to the data and on describing the data with as few parameters as possible (Burnham & Anderson 1992, 1998; Lebreton et al. 1992).

Population size was not a model parameter but was estimated using the numbers of butterflies caught at each period ($n_i^{(m)}$ = number of males; $n_i^{(f)}$ = number of females; $n_i^{(m)} + n_i^{(f)} = n_i$ = number of butterflies of both sexes combined) in conjunction with the associated estimates of capture probability ($p_i^{(s)}$). Specifically, population size and its associated variance were estimated as:

$$\hat{N}_i^{s} = \frac{n_i^{(s)}}{\hat{p}_i^{(s)}} \qquad (1)$$

$$v\hat{a}r(\hat{N}_i^{(s)}) = \frac{(n_i^{(s)})^2\; var\,(\hat{p}_i^{(s)})}{(\hat{p}_i^{(s)})^4} + \frac{n_i^{(s)}(1-\hat{p}_i^{(s)})}{(\hat{p}_i^{(s)})^2} \qquad (2)$$

Confidence intervals for $\hat{N}_i^{(s)}$ were approximated using the approach of Chao (1989; also used and recommended by Rexstad & Burnham (1991)). The estimation is based on the estimated number of butterflies not detected, $\hat{f}_{0,i}^{(s)} = \hat{N}_i^{(s)} - n_i^{(s)}$. The ln ($\hat{f}_{0,i}^{(s)}$) is treated as an approximately normal random variable, yielding the following 95% confidence interval, ($n_i^{(s)} + \hat{f}_{0,i}^{(s)}/C,\; n_i^{(s)} + \hat{f}_{0,i}^{(s)}C$), where

$$C = \exp\left(1.96\left[\ln\left(1+\frac{var\,(\hat{N}_i^{(s)})}{(\hat{f}_{0,1}^{(s)})^2}\right)\right]^{1/2}\right).$$

Statistical Analyses

We used one- and two-way ANOVAs to test for the effects of sex and season on individual and population variables and Pearson correlation analyses to assess relationships between rainfall and butterfly population variables and *Passiflora* biomass. Analyses were conducted with Statmost ver. 3.5 (Dataxiom Software, Inc., Los Angeles, CA) and Systat ver. 10 (SPSS, Inc., Chicago, IL). For population and weekly count data, we tested for effects of season using repeated measures (rm) ANOVAs with Type III sums of squares (Zar, 1999) using SPSS ver. 10.1.0 (SPSS 2000, SPSS, Inc., Chicago, IL). We used the Greenhouse-Geisser correction to adjust degrees of freedom whenever inequality of sphericity was rejected by Mauchly's test. We used the "Standard Tests" module in EcoSim (Gotelli & Entsminger 2003) to assess the relationship between weekly adult population size and *Passiflora* biomass. Unless otherwise noted, means ± 1 SE are reported throughout this paper.

RESULTS

Capture Statistics

In the 2 yrs, we marked a total of 1,476 adults, including 929 males (62.9%) and 547 females, and recorded a total of 2,729 captures and recaptures. Capture statistics, including the number of captures per individual and the number of weeks between first and last capture for each individual by sex and season, are summarized in Fig. 1A,B. A two-way ANOVA indicated that number of captures per individual varied by sex and season (sex: $F_{1,1470} = 7.43$, $P = 0.007$; season: $F_{4,1470} = 23.55$, $P < 0.0001$; the interaction was also significant: $F_{4,1470} = 4.79$, $P = 0.001$). Males were generally captured more times than females (grand means were 2.08 ± 0.06 and 1.82 ± 0.08 captures, respectively), and number of captures per individual in the 1996-97 dry season was about 50% higher than in other seasons (Fig. 1A). A two-way ANOVA revealed that the number of weeks between first and last capture also differed by sex and season (sex: $F_{1,1471} = 8.64$, $P = 0.003$; season: $F_{4,1471} = 20.91$, $P < 0.0001$; the interaction was not significant ($P = 0.23$)). Males were generally captured over a longer time period than females (grand means were 2.05 ± 0.05 and 1.81 ± 0.07 weeks, respectively), and individuals had longer capture periods in the first three seasons of this study than in the last two (Fig. 1B). Reanalysis of these data after data from the short dry season in late 1997 were eliminated produced similar results.

The Population Model

The G^2 goodness-of-fit statistic for general model $(S_i^{(s)}, p_i^{(s)}, \gamma_i^{(s)})$ was 692.83 and was larger than all 100 of the G^2s resulting from the bootstrap simulations. Because of the lack of fit of the general model to the capture-recapture data, we computed the quasi-likelihood variance inflation factor as described above to obtain $\hat{c} = 1.21$. Models with the lowest QAICc values were those with parameters constant over time and with no difference between survival of unmarked and marked butterflies ($\gamma = 1$) (Table 1). There was very little basis for selecting among the first few models, as indicated by the small ΔQAICcs. Daily survival estimates based on model $(S^{(s)}, p^{(s)}, \gamma = 1)$ were 0.944 ± 0.0021 for males and 0.939 ± 0.0032 for females. Estimated capture probabilities under this model were 0.479 ± 0.0163 for males and 0.447 ± 0.0231 for females. Parameter estimates for males and females were very similar, providing little evidence for sex-specific differences in capture probabilities. In fact, the very simplest model $(S, p, \gamma = 1)$ with single survival and capture parameters that were constant over time and sex was among the most reasonable models for this data set. From this, we conclude that survival rates and capture probabilities likely did not vary with season or sex.

Adult Population Size and Sexual and Body Size Composition

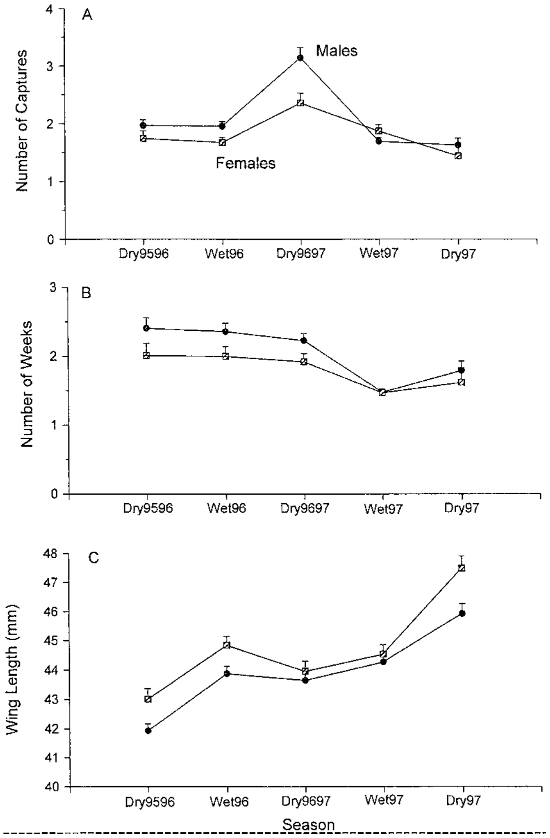

Fig. 1. Summary of the capture statistics for adults of *Heliconius charithonia*. A. Number of captures and recaptures per individual. B. Number of weeks between first and last capture records. C. Size of adults. Data are means ± 1 SE. Sample sizes range from 29-330.

Estimates of the number of adults foraging in or passing through the garden each week averaged 58.9 ± 2.9 and ranged from a minimum of 9 (in August 1997) to a maximum of about 115 (in April 1997) (Fig. 2). In 1996 the population ranged between 20 and 70 individuals except for peaks of 85-100 individuals in the middle of the wet season (September) and early in the 1996-97 dry season (December). In 1997, the population steadily increased during the dry season and averaged over 80 individuals through July before declining rapidly. We removed most of the *Passiflora* in the garden after the decline began, and numbers slowly increased after 1 August 1997.

Size of the adult population fluctuated in parallel with changes in the biomass of *Passiflora* in the study area (Fig. 2). A simulation comprising 1,000 iterations indicated that the correlation between adult population size (Y) and *Passiflora* biomass (X) was significant ($r_{\text{observed}} = 0.69$; $r_{\text{simulated}} = 0.00$, $P = 0.00$). One-way rm ANOVAs indicated that seasonal differences in weekly size of the butterfly population and *Passiflora* biomass were significant (adult population size: Greenhouse-

TABLE 1. MODEL SELECTION INFORMATION FOR MODELS FIT TO ZEBRA LONGWING BUTTERFLY CAPTURE-RECAPTURE DATA. QAICC IS CORRECTED QUASI-LIKELIHOOD AKAIKE'S INFORMATION CRITERIA.

Model[a]	No. parameters estimated	Log-likelihood	ΔQAICc
$S^{(s)}, p, \gamma = 1$	3	-1366.9	0.0
$S^{(s)}, p^{(s)}, \gamma = 1$	4	-1366.3	0.5
$S, p^{(s)}, \gamma = 1$	3	-1367.5	0.9
$S, p, \gamma = 1$	2	-1369.1	1.4
S, p, γ	3	-1368.6	3.4
$S^{(s)}, p^{(s)}, \gamma^{(s)}$	6	-1365.8	4.5
$S, p_i, \gamma = 1$	97	-1258.7	17.1
$S^{(s)}, p_i(s), \gamma = 1$	194	-1177.4	99.2

[a] Abbreviations: S = probability that a marked butterfly survives from sampling time i to $i + 1$, p = probability that a butterfly that is in the population at time i is captured at i, and γ = the ratio of survival probabilities (from i to $i + 1$) of unmarked to marked butterflies, s = sex.

Geisser-corrected $F_{1.6, 26.4} = 5.90$, $P = 0.012$; *Passiflora* biomass: Greenhouse-Geisser-corrected $F_{1.5,28.6} = 13.54$, $P < 0.001$; data from the abbreviated 1997 dry season not included in these analyses). The adult butterfly population averaged 36% larger in 1997 than in 1996, and *Passiflora* biomass was 48% lower during the 1995-96 dry season than in the next three seasons (Fig. 3A).

Neither size of the adult butterfly population nor *Passiflora* biomass appeared to respond to rainfall seasonality. Correlations between weekly estimates of both adult population size and pas-

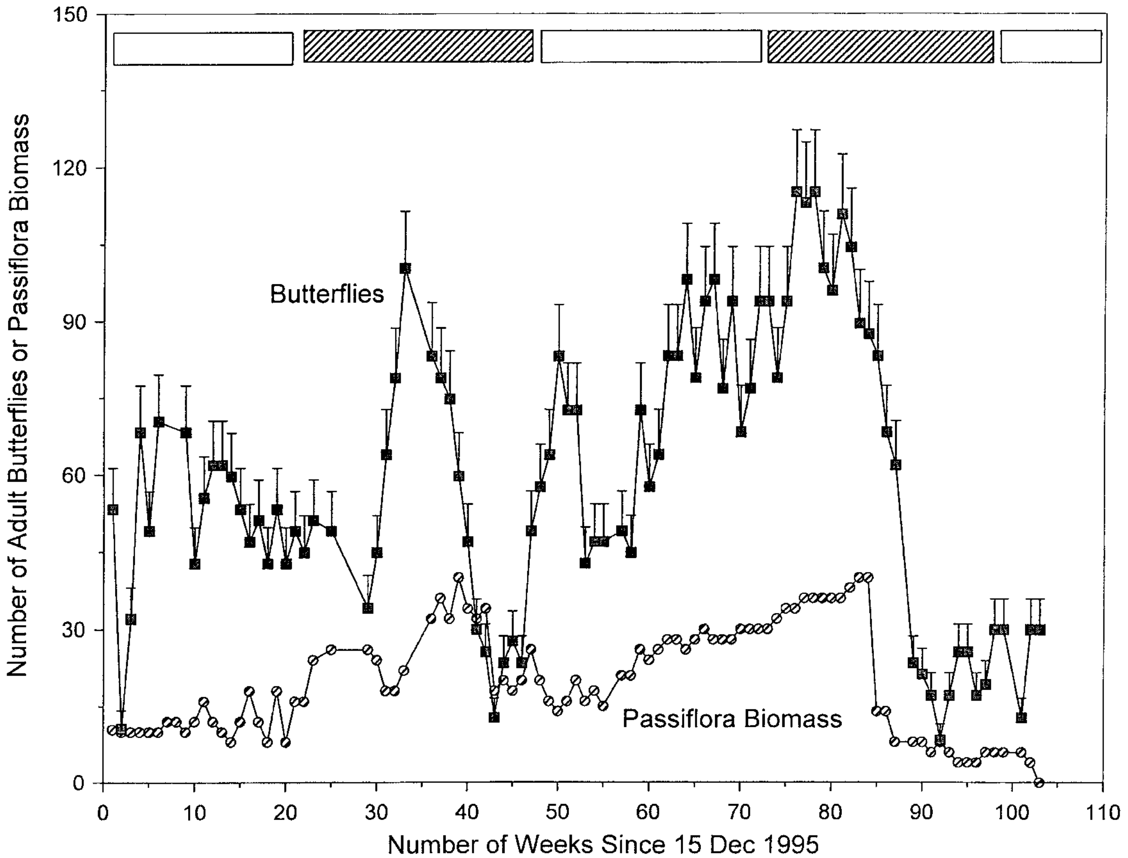

Fig. 2. Weekly estimates of the adult population size (+ 1 SE) of *Heliconius charithonia* and the biomass (in m^2) of the larval host plant *Passiflora incense* from 15 December 1995 to 15 December 1997. The upper rectangles indicate dry seasons (open) and wet seasons (hatched).

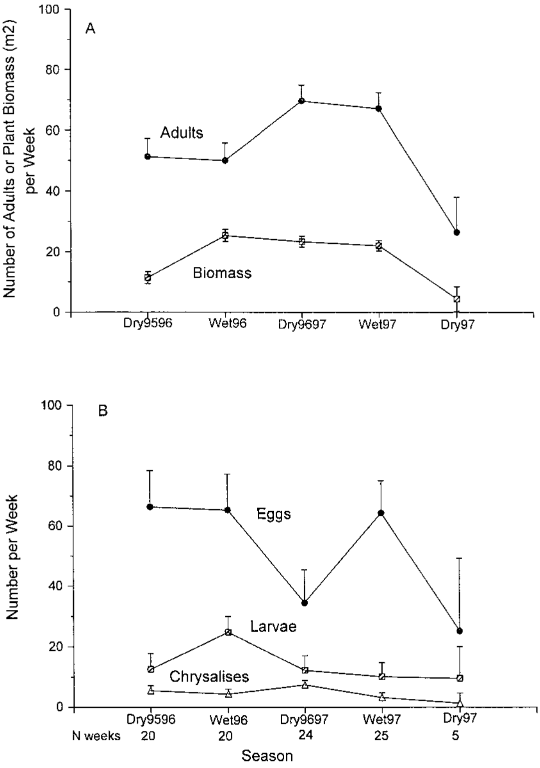

Fig. 3. Seasonal summaries of (A) weekly estimates of the adult butterfly population size and biomass of its larval host plant, *Passiflora incense*, and (B) weekly numbers of butterfly eggs, larvae, and chrysalises. Data are means + 1 SE. Sample sizes are indicated as N weeks.

sion vine biomass and rainfall were nonsignificant (Bonferroni-corrected *P*s ≥ 0.28). Similar results were obtained when rainfall records were lagged by one and two weeks (*P*s ≥ 0.26).

Between 4 July 1996 and 24 March 1997, an average of 20.3 ± 2.6 (range = 0-46; n = 25 counts) adults night-roosted in the garden. The number of night-roosting adults was positively correlated with adult population size (Pearson's $r = 0.75$, $df = 23$, $P < 0.001$). At times, most of the adults foraging in the garden night-roosted there.

In most weeks the adult sex ratio was male-biased and averaged 65.6 ± 1.2% males overall (n = 94 weeks). A one-way rm ANOVA indicated that sex ratio varied among seasons ($F_{3,57} = 2.95$, $P = 0.04$; arcsine squareroot-transformed data and the short 1997 dry season not included). Sex ratio was higher in the dry season of 1996-97 (71.7 ± 2.1% males) than in the wet season of 1997 (60.3 ± 2.7% males). Thirty of 72 adults (41.7%) that we sexed at eclosure in the garden were males. Sex ratios of marked and eclosed adults differed significantly ($\chi^2 = 12.3$, $df = 1$, $P < 0.001$).

A two-way ANOVA indicated that the size (wing length) of adults varied by sex and season (sex: $F_{1,1445} = 12.50$, $P < 0.001$; season: $F_{4,1445} = 24.49$, $P < 0.001$). Except in the wet season of 1997, females were larger than males, and butterflies of both sexes were about 10% larger in late 1997 than in early 1996 (Fig. 1C).

Adult Survivorship and Wing Wear

Turnover rate of adults in this population was relatively high. Most adults were recaptured for periods of less than three weeks (Fig. 1B), and maximum capture periods were 9-10 weeks in both sexes. Most adults (86%, $n = 1{,}504$) were recently eclosed (condition score 0) at first capture; individuals occurring in condition score categories 0 or 1 accounted for 98% of all first captures. In 1996, we tallied the wing wear condition of 57 and 30 recently eclosed males and females, respectively, that were captured ≥3 times. Rate of wing wear was high in both sexes. Most individuals had worn to very worn wings 6-8 weeks after first capture.

Results of the mark-recapture analysis also indicated that adult turnover rate was high. Adult males and females had daily survival probabilities of about 0.94, which represents a weekly survival probability of about 0.65. At this rate, adults had a probability of 0.031 and 0.013 of being alive eight and ten weeks after eclosion, respectively.

Egg and Larval Surveys

Eggs and larvae were found in most weeks, indicating that reproduction occurs year-round in south Florida (Fig. 4). The number of eggs counted each week averaged 55.3 ± 5.6 (range: 0-326) and exhibited no significant seasonal variation (one-way rm ANOVA: $F_{3,57} = 2.36$, $P = 0.08$; only the first four seasons included in this analysis) (Fig. 3B). The number of zebra longwing butterfly larvae (of all sizes) counted per week averaged 14.3 ± 2.4 (range: 0-167) and also exhibited no significant seasonal variation (Greenhouse-Geisser-corrected one-way rm ANOVA: $F_{1.7,\,31.7} = 1.55$, $P = 0.23$) (Fig. 3B). Finally, number of zebra longwing butterfly chrysalises counted per week averaged 5.0 ± 0.78 (range: 0-38) and did not vary seasonally (Greenhouse-Geisser-corrected one-way rm ANOVA: $F_{1.6,30.2} = 1.90$, $P = 0.17$) (Fig. 3B).

Only the number of eggs per week was significantly correlated with estimated adult population size (Pearson's $r = 0.32$, $df = 90$, Bonferroni-corrected $P = 0.037$). Total number of *H. charithonia* larvae per week but not chrysalises was significantly correlated with number of eggs (Pearson's $r = 0.36$, $df = 92$, Bonferroni-corrected $P = 0.011$). When we applied a 3-week time lag (the average egg-to-chrysalis duration) to the egg data, however, number of chrysalises was significantly correlated with number of eggs (Pearson's $r = 0.25$, $df = 89$, Bonferroni-corrected $P = 0.018$). Finally,

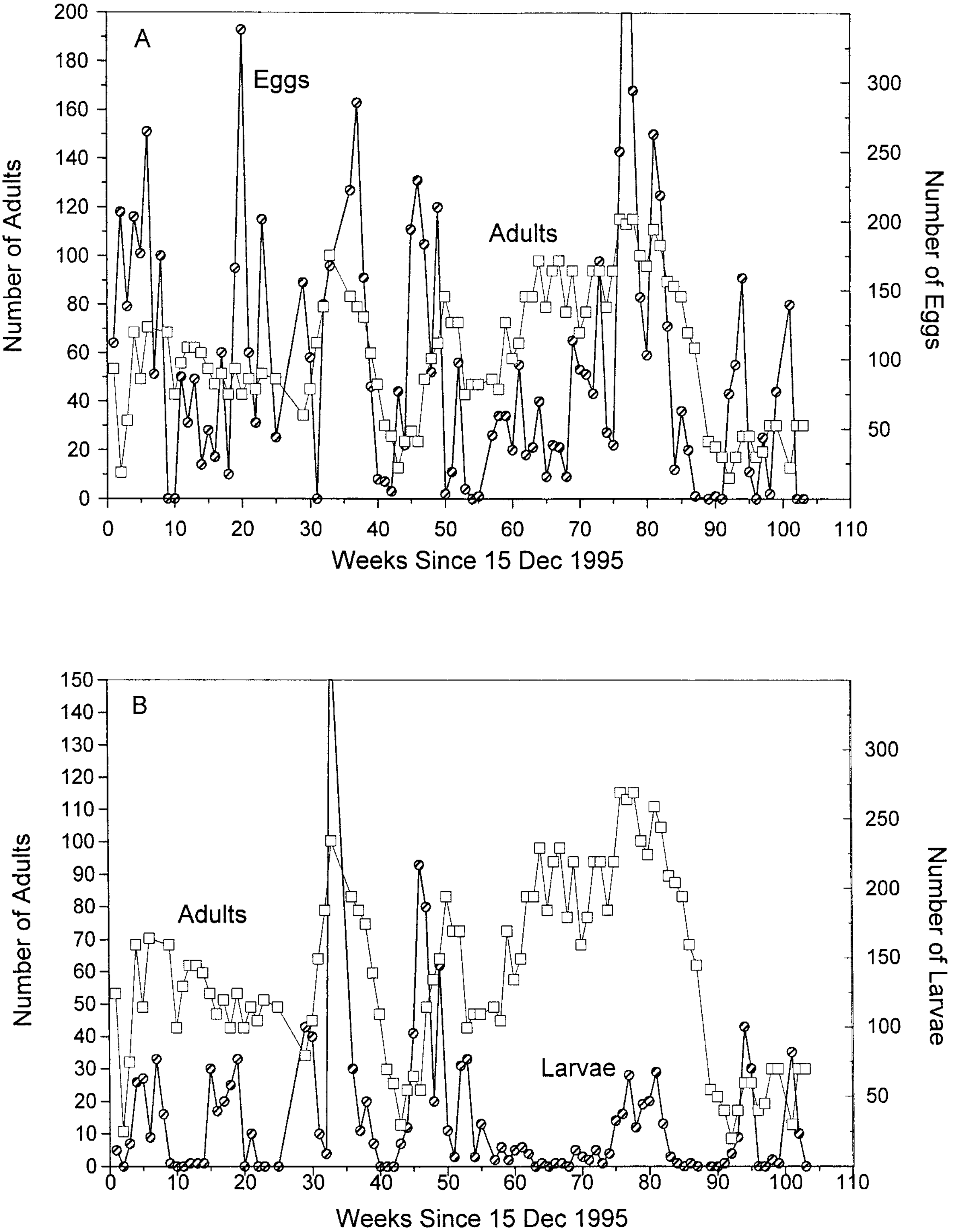

Fig. 4. Weekly counts of eggs (A) and larvae (B) of *Heliconius charithonia* between 15 December 1995 and 15 December 1997. Estimated weekly adult population size is included in each panel.

weekly numbers of eggs, larvae, and chrysalises were not correlated with weekly *Passiflora* biomass (Bonferroni-corrected *P*s ≥ 0.18).

Two species of heliconiid larvae co-occurred on the *Passiflora* vines between weeks 30 and 85 (from July 1996 to August 1997). During this period, number of zebra longwing butterfly larvae averaged 17.0 ± 3.9 per week (range: 0-167), and number of gulf fritillary larvae averaged 10.7 ± 1.9 (range: 0-55); these means do not differ significantly (paired t-test, $t = 1.56$, $df = 52$, $P = 0.12$). Numbers of these two larvae were not correlated (Pearson's $r = 0.17$, $df = 51$, $P = 0.21$), and hence the larvae did not appear to be interacting in an antagonistic (i.e., competitive or predator-prey) fashion.

Egg Parasitism

Egg survival was low (about 14% based on ratios of eggs to small larvae over all seasons), and a major reason for this was parasitism by an unidentified trichogrammatid wasp. We determined percent parasitism of zebra longwing butterfly eggs by this wasp on 22 occasions between 6 October 1996 (week 43) and 25 November 1997 (week 101). Percent parasitism averaged 53.0 ± 5.0% (range: 0-100%). Parasitized eggs produced an average of 6.6 ± 0.6 wasps (n = 34; range: 1-14). There appeared to be no seasonal pattern to wasp parasitism.

Rates of Population Increase and Decrease

Changes in population size result from the interaction of four factors: births, deaths, immigration, and emigration. To what extent are the population increases and decreases we documented in this study (Fig. 2) the result of demographic (i.e., births, deaths) rather than behavioral (i.e., immigration, emigration) factors? To answer this question, we analyzed events occurring during three increase episodes (weeks 29-33, 46-50, and 58-64; Fig. 2) and three decrease episodes (weeks 33-43, 50-53, and 81-92). For the increase episodes, we determined the relative contribution of "births" (i.e., eclosion of new adults) to the overall population increase by comparing the number of chrysalises produced during each episode to the estimated number of individuals added to the population. To avoid re-counting the same chrysalises, we counted only "new" (= unmarked) chrysalises that we found beginning and ending one week before the increase period began and ended. For the decrease episodes, we compared the number of individuals that were "lost" from the population with the number of expected losses based on a weekly survival rate of 0.65.

Results of these calculations (Table 2) indicated that local births and deaths likely accounted for most of the changes in population size during these episodes. Eclosion of new adults accounted for about 90% of the population increases, and expected adult deaths accounted for virtually 100% of the population decreases. Absolute values of increase (≈13.5 adults/wk) and decrease (≈10.5 adults/wk) were similar during these six episodes (Fig. 2).

DISCUSSION

Our results indicate that the size of a suburban, subtropical population of *H. charithonia* ranged from about 10-115 adults during a two-year period. Weekly variation in adult population size was moderate (coefficient of variation = 0.47), and changes in the size of this population closely mirrored changes in the biomass of the larval host plant *Passiflora incense*. Neither adult population size nor passion vine biomass appeared to be influenced by weekly rainfall. Reproduction occurred year-round, and although the sex ratio at eclosion was female-

TABLE 2. ESTIMATES OF THE CONTRIBUTION OF LOCAL BIRTHS AND DEATHS TO POPULATION INCREASES AND DECREASES, RESPECTIVELY, IN THE ZEBRA LONGWING BUTTERFLY.

A. Population increases

Weeks (n)	Δn	n Chrysalises	n Chrysal./Δn
29-33 (4)	+66.2	57	0.86
46-50 (4)	+59.7	96	1.61 ≈ 1.00
58-64 (6)	+53.3	39	0.73
		Mean	≈0.90

B. Population decreases

Weeks (n)	Δn	Expected Δn[a]	Expected/observed
33-43 (10)	-87.5	-85.5	0.98
50-53 (3)	-40.5	-60.4	1.49
81-92 (11)	-102.4	-107.8	1.02
		Mean	≈1.00

[a] Calculated as $n_1 - (n_1 * 0.65^n)$, where n_1 is the number of individuals in week 1 of the episode, 0.65 is the weekly adult survival rate, and n is number of weeks in the episode.

biased, sex ratio of the adult population was strongly male-biased. Rates of wing wear in adults were high, and maximum adult longevity was 9-10 weeks. Given that the egg-to-adult period lasts 30 days in this species in the subtropics (Quintero 1988), maximum lifespan of *H. charithonia* in south Florida is 13-14 weeks (91-98 days). Most adults, however, live less than one month, so average lifespan is less than eight weeks (<56 days).

The best predictor of adult population size in this study was biomass of the larval host plant, *Passiflora incense*. It appeared that both males and females were tracking biomass of this plant, but for different reasons. Females track passion vine biomass in searching for oviposition sites, whereas males track this biomass looking for female chrysalises (mates). Of the two sexes, males appeared to be more sedentary, as indicated by their higher number of recaptures and the longer time between first and last capture. Many males virtually 'camped out' in the garden waiting for female chrysalises to become sexually receptive. Receptive females were quickly 'swarmed' by several males, one of which ultimately mated with her (THF, pers. obs.). Females, in contrast, appeared to be "trap-lining" and passed through our study site en route to other oviposition or feeding sites. While in the garden, they laid one or more eggs on new growth on several stems.

The shift from a female-biased sex ratio at eclosion to a male-biased sex ratio in the local population suggests that adult females are more mobile than males. As in most birds (Greenwood 1980), females appear to be the dispersing sex in *H. charithonia*. Many males apparently stay near their natal sites to search for mates whereas females disperse some distance away from their natal sites before establishing a home range. Because of high female mobility, however, males are not likely to mate with close relatives, and rates of inbreeding are likely to be low. This mobility also likely results in substantial gene flow among zebra longwing butterfly subpopulations.

In support of these predictions, Kronforst & Fleming (2001) reported very low levels of inbreeding (Wright's fixation index $F_{is} = -0.027$, a slight excess of heterozygotes) and low population genetic subdivision (Wright's fixation index $F_{st} = 0.003$) in *H. charithonia* over a wide area in Miami-Dade County. These results call into question the suggestion (e.g., Haag et al. 1993) that *Heliconius* populations have an island-like structure and are highly inbred.

Although the dynamics of all populations are influenced by abiotic and biotic factors, biotic factors are likely to most strongly influence the population dynamics of *H. charithonia* in south Florida. This conclusion is based on the absence of a correlation between rainfall and adult population size and *Passiflora* biomass as well as the absence of a strong seasonal effect on numbers of eggs, larvae, chrysalises, and rates of egg parasitism. Butterfly reproduction, egg parasitism, and *Passiflora* growth occurred year-round and were not strongly seasonal. *H. charithonia* in south Florida is clearly behaving like a tropical butterfly.

Two biotic factors, host plant biomass, especially the availability of growing shoot tips, and egg parasitism, appeared to affect the dynamics of this population. Although numbers of eggs and larvae showed no strong seasonal trends, their numbers were highly variable from week to week. Coefficients of variation of weekly number of eggs, total larvae, and chrysalises, respectively, were 0.99, 1.64, and 1.52 compared to a value of 0.47 for number of adults. Variation in egg number, in part, reflected variation in the availability of fresh growing tips which was determined, in turn, by caterpillar herbivory. At times, herbivory eliminated the growing tips from most stems, which resulted in few eggs being laid. Egg parasitism by trichogrammatid wasps also eliminated an average of 50% of potential *Heliconius* larvae. Parasitism was especially high during weeks 61-69 (early February-mid-April 1997) when it averaged 75%. During that period, few larvae were produced, and *Passiflora* biomass began to steadily increase. Despite low larval numbers during this period, adult butterfly numbers were high. This was the only time during the study that immigration, rather than in situ recruitment, appeared to be responsible for high adult population numbers.

Many aspects of the population biology of *H. charithonia* in south Florida are similar to those of tropical *Heliconius* populations. Similarities include low, relatively stable population densities, biased adult sex ratios, year-round reproduction, and the importance of larval host plants in determining the distributions and densities of adult butterflies (e.g., Ehrlich & Gilbert 1973; Cook et al. 1976; Quintero 1988; Gilbert 1991; Ramos & Freitas 1999). Coefficients of variation of population size of *H. charithonia* in Costa Rica and Puerto Rico ranged from 0.34 to 1.05 (based on data in Cook et al. 1976; Quintero 1988) compared with 0.47 in this study; CV of mean population size in *Heliconius erato* in southern Brazil was 0.73 (Ramos & Freitas 1999). As in this study, Quintero (1988) found no correlation between population size and rainfall in Puerto Rico. Under normal conditions, the population density of *H. charithonia* in urban Miami is low, on the order of a few individuals per hectare in forested areas (Kronforst & Fleming 2001). This low density undoubtedly reflects the low density and biomass of *Passiflora* in these areas. Average lifespan was also similar in populations of *H. charithonia* in south Florida, Puerto Rico, and Costa Rica. Compared with *H. ethilla* the maximum lifespan of which in Trinidad is about 180 days and *H. erato* in southern Brazil with a maximum lifespan of about 150 days, *H. charithonia* is a short-lived butterfly. Maximum longevities are 90-116 days, and average adult lifespans are less than one month after eclosion.

In conclusion, populations trends in *H. charithonia* in south Florida do not appear to differ qualitatively or quantitatively from those at lower latitudes. The mild climate of subtropical Miami permits this butterfly to act as though it is still in the tropics. These results contrast with those reported for butterflies in England, where marginal populations of some species fluctuate much more strongly than central populations (Thomas et al. 1994; Shreeve et al. 1996). Studies of the population dynamics of *H. charithonia* closer to its northern geographic limits (e.g., in northern Florida) are needed to determine whether population sizes are more variable and more strongly influenced by abiotic factors than in south Florida. Such studies in *H. erato* in subtropical Brazil indicate that climate-related (either cold temperatures or drought) extinctions can occur in *Heliconius* butterflies at the southern limits of their distribution (Saalfed & Araujo 1981).

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