

Research Article

Short-Term Dynamics Reveals Seasonality in a Subtropical *Heliconius* Butterfly

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Although tropical insect populations are generally regarded as constant and stable over time, some of these tropical populations, including butterflies, may fluctuate according to precipitation and temperature variation, specialized feeding patterns, and density-dependent factors. Heliconiini butterfly populations are generally regarded as stable over time because of the presence of host-plants and absence of diapause. However, peaks of abundance occur in subtropical *Heliconius* populations, and opposite trends concerning stability are found in the literature. Here we further investigate the dynamics of subtropical *Heliconius* butterflies by assessing a population of the species *Heliconius sara apseudes* from southeastern Brazil. We estimated individual apparent survival probability and population growth rate while accounting for the imperfect detectability of individuals using mark-recapture models to evaluate the population dynamics. Adult males presented slightly higher weekly survival estimates than females. Contrary to the common pattern described in the literature for *Heliconius* populations we observed a rapid decline on the adult population by the end of the mating season, possibly leading to local extinction. We discuss the potential drivers for such dynamics.

1. Introduction

The first studies on insect population dynamics were performed to better understand agricultural pests and found that resource availability, parasitoids, and climatic factors were among the most important factors affecting population dynamics [1]. In the tropics insect populations are generally regarded as constant and stable over time mainly because of climate stability [2]. However, changes in local precipitation and temperature may cause tropical insect populations to oscillate mostly because of highly specialized feeding habits, such as those observed for temperate populations, and density-dependent factors [3–5].

Tropical populations of butterflies are also constant over time, where the climatic stability does not directly affect resource availability and density-dependent processes [6–9].

Typically, such populations are regulated by parasitoids, pathogens, and visually oriented predators, besides the difficulty of finding oviposition sites [10–12].

Heliconiini butterflies are generally distributed in small populations and present high longevity [8]. The presence of host-plants year-round and the absence of diapause guaranty reproduction throughout the year, with overlapping generations [6, 8, 13]. Populations of the genus *Heliconius* are often heterogeneous in space, sometimes positively correlating with environmental features, such as riverbanks, floodplains, forests, and disturbed areas. Individuals are generally solitary during the day locating resources and crossing paths daily to feed on the same flowers [14].

Despite the typical constancy over time in *Heliconius* populations, Fleming et al. (2005) found population peaks

of abundance in the late dry and early wet season for *H. charithonia* from a subtropical site in Florida, USA, where fluctuations in this population corresponded to biomass of food plants consumed by larvae. Opposing the results of Fleming et al. (2005), data on *Heliconius* populations from the subtropical region of Southern Hemisphere showed constancy and stability over time [13].

Considering the contrasting evidence found for different subtropical *Heliconius* populations, we surveyed another subtropical *Heliconius* species from the Southern Hemisphere to compare population dynamics. We specifically tested the hypothesis of stability suggested for subtropical Southern Hemisphere *Heliconius*, by providing estimates of individual survival and recapture probabilities, as well as population growth rates for *Heliconius sara apseudes*.

2. Materials and Methods

2.1. Study Site. Our study was conducted in the Quilombo River Valley, southeast Brazil (coordinates 23°51'35"S–46°21'01"W and 23°49'18"S–46°18'37"W). The study area is a road with 8.6 km that encompasses a large forested area, within the Atlantic Forest domain, but highly modified by human activities with mosaics of banana and manioc plantations in small farms.

According to Köppen (updated by [15]) this region is embedded in tropical rain climate and shows two distinct periods in this region, warm/wet (spring-summer) and cold/dry (autumn-winter). The annual mean temperature is 22.0°C and the annual mean total rainfall is 2541 mm, heavily concentrated in the wet season.

2.2. Study Species. *Heliconius sara* is distributed throughout the neotropical region, from southern Mexico to southern Brazil [16–18]. Currently, there are 10 recognized subspecies of *H. sara*, which occur in northwest South and Central America. The only subspecies distributed in the Brazilian Atlantic Forest is *H. s. apseudes* [16, 19–21]. Females of all *H. sara* subspecies lay from 15 to 40 eggs on Passifloraceae leaves [19, 22]. The larvae feed gregariously and pupae also aggregate [8].

2.3. Sampling Protocol. We sampled the adults of the target population for 12 months during 2009 on a weekly basis (one to two times per week), using visual cues and captured them using an entomological net. On each capture, we recorded sex of the individuals and marked them using an alphanumeric code with a black permanent ink marker on the right forewing. After marking, we released the individuals in the same site they were captured.

2.4. Statistical Analysis. We used the Pradel model to obtain maximum likelihood parameter estimates [23]. The parameterization of the Pradel model used provides estimates of apparent survival probability (φ), which is a combination of true survival and site fidelity, recapture probability (p), and the finite rate of population change (λ), where λ shows the rate of change through successive samples (N_{t+1}/N_t) providing information on population stability ($\lambda = 1$), increase

($\lambda > 1$) or decrease ($\lambda < 1$). Model assumptions include a nonzero probability of recapturing all individuals through the study period, no trap response by the individuals, and most importantly, the study area must remain the same size; otherwise estimates of λ may be biased [23, 24]. We present weekly estimates of the parameters of interest adjusting for irregular time intervals when necessary.

We kept a simple parameterization because we anticipated poor support for complex models due to our limited data set. Therefore, we built representing hypotheses about the additive effect of the covariates on the parameters, constraining each parameter to be a logit-linear function of individual and/or temporal covariates. We modeled survival as a function of sex (sex) because we suspected activity differences between adult males and females, and also as a constant parameter denoted by a period (.). Recapture probability was modeled as an additive function of maximum temperature (temp) and effort (effort) because sampling effort varied over weeks, and sex. Population growth was modeled as a function of time (t), and also as a function of sex to check for different patterns of decline in adult males and females.

We selected and ranked models using the Akaike Information Criterion [25] adjusted for small sample sizes (AICc, Burnham and Anderson, 2002). We then model-averaged the parameters in order to include uncertainty in model selection [26] and reported parameter estimates with the 95% unconditional variance confidence intervals. All routines were performed in Program MARK [27].

3. Results and Discussion

3.1. Results. We marked 378 males and 120 females and recaptured 106 (28.04%) and 32 (26.67%) at least once, respectively. The adults were found from late April (dry season) to early October (early wet season). No adult butterfly was detected before April and after October, and we present estimates for the 14-week period only.

Sex correlated with apparent survival in our best candidate models. Effort, temperature, and sex had similar impacts on recapture probability, and the additive effect of sex and time was important for the population change (λ ; Table 1). Weekly apparent survival estimates differed between sexes ($\beta_{\text{sex}} = 0.50$, CI 0.03–0.98, top model, Table 1). Males (0.66, CI 0.57–0.73) presented higher survival estimates than females (0.57, CI 0.43–0.70).

Estimates of weekly recapture probability varied from 0.15 to 0.20, and recapture was mostly constant over the study (Figure 1). Although sampling effort and maximum temperature had slightly positive effects on recapture probability, no significant influence was observed ($\beta_{\text{effort}} = 0.27$, CI –0.25–0.80 and $\beta_{\text{temp}} = 0.06$, CI –0.06–0.18). The same occurred with sex, where females presented a slightly higher recapture probability, but not statistically different from males ($\beta_{\text{sex}} = 0.36$, CI –0.25–0.98).

Although models with sex ranked higher for the finite population growth rate, males and females presented almost the same pattern of growth, with males having slightly higher rate ($\beta_{\text{sex}} = 0.06$, CI 0.007–0.11; Figure 2). The population

TABLE 1: Model selection results for apparent survival probability (φ), recapture probability (p), and the finite growth rate (λ). AICc = Akaike's information criteria with small sample size correction, $\Delta AICc$ = difference between top model and the current model, w_i = AICc weights, k = number of parameters, deviance = difference of the current model and the saturated model. For covariate notation, see text.

Model	AICc	$\Delta AICc$	w_i	k	Deviance
φ (sex) p (effort) λ (sex + t)	2324.96	0.00	0.17	43	2229.60
φ (sex) p (temp) λ (sex + t)	2325.11	0.15	0.16	43	2229.74
φ (sex) p (sex) λ (sex + t)	2325.68	0.71	0.12	43	2230.31
φ (\cdot) p (sex) λ (sex + t)	2326.72	1.75	0.07	42	2233.80
φ (\cdot) p (effort) λ (sex + t)	2326.91	1.95	0.06	42	2233.99
φ (sex) p (effort) λ (t)	2327.07	2.10	0.06	42	2234.15
φ (sex) p (temp) λ (t)	2326.15	2.19	0.06	42	2234.23
φ (\cdot) p (effort) λ (t)	2326.20	2.23	0.06	41	2236.71
φ (\cdot) p (temp) λ (sex + t)	2327.51	2.55	0.05	42	2234.59
φ (\cdot) p (sex) λ (t)	2327.52	2.56	0.05	41	2237.04
φ (\cdot) p (temp) λ (t)	2327.69	2.73	0.04	41	2233.21
φ (sex) p (sex) λ (t)	2327.92	2.96	0.04	42	2225.00
φ (sex) p (sex + temp + effort) λ (sex + t)	2329.56	4.59	0.02	45	2229.26
φ (\cdot) p (sex + temp + effort) λ (sex + t)	2330.16	5.19	0.01	44	2232.33
φ (\cdot) p (sex + temp + effort) λ (t)	2330.80	5.83	0.01	43	2235.43
φ (sex) p (sex + temp + effort) λ (t)	2331.73	6.76	0.01	44	2233.90

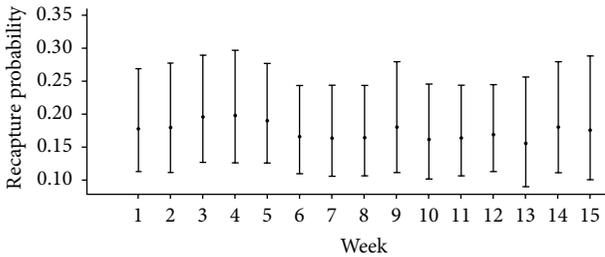


FIGURE 1: Model averaged weekly recapture probability for *H. sara apseudes* adults during the study period where individuals were active.

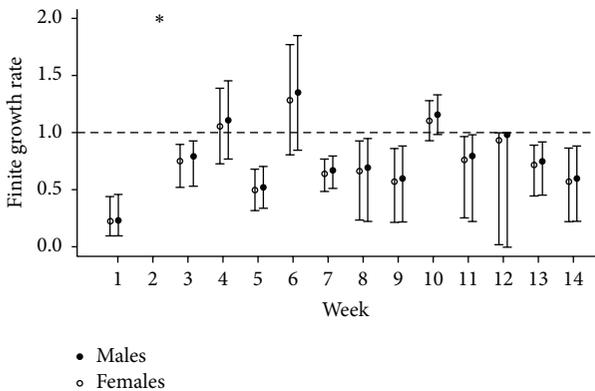


FIGURE 2: Finite growth rate of adult males and females *H. sara apseudes* during the period where the population was active (15 weeks). The grey dotted line represents a stable population ($\lambda = 1$). The asterisks on interval 2 indicate the abrupt increase (see text) that we chose not to plot in order to avoid distortions of values close to 1. Estimates and 95% confidence intervals are shown.

presented an abrupt increase in interval 2 (late April), where a high growth rate was detected increasing the size of the population by six times, for males ($\lambda = 12.30$, CI 3.60–21.4) and for females ($\lambda = 12.02$, CI 3.65–20.40). This was the only statistically significant increase in the population, since the lower boundary of the confidence interval was higher than 1. Most of the remaining periods were characterized by declines and also some stable periods (where confidence intervals included 1; Figure 2).

3.2. Discussion. Our data demonstrates that males have a slightly higher probability of apparent survival than females. Ehrlich et al. 1984 [28] found a significantly greater number of males than females in a population of *Euphydryas editha* (Nymphalidae), relating this trend to either a possible female dispersion or a higher female mortality than males. It would be challenging to isolate dispersion from differential survival if detection probability is not considered during the sampling protocol. By accounting for the imperfect detectability of the individuals, we were able to split survival probability that was slightly higher for males, from the detection process of males and females, which was not different between sexes. If female dispersion was effective we would expect a lower female detection probability, which was not the case. The higher female mortality may be linked to oviposition sites, since the *Heliconius* host-plant, Passifloraceae, is found within the forest where more predators are present, including birds, small mammals, and spiders [10, 11].

Our results suggest seasonality in the adult population with a single substantial input of individuals in the early dry season (late April). No other significant input was found in the population despite the considerable uncertainty around the estimates (Figure 2). In *Heliconius sara*, eggs, larvae,

and pupae are gregarious [8, 22] and emerge almost at the same time, because the development time is similar for the individuals. The only difference in this species is that males fly before females and compete for mating sites, since pupal mating is described for this species [29]. Although male population presented a slightly higher growth rate than female population, no biological difference was observed since the estimate for the intercept was close to zero, meaning that losses occur for both males and females, showing the total decline for the population.

We observed a gradual reduction in the number of males and females in the population, especially in the last time intervals, until individuals were no longer detected in the onset of the wet season (October). Although the current available information for tropical populations of *Heliconius* regards such group as having constancy and overlapping generations over time [6, 8] recent evidence on population dynamics of other *Heliconius* species contradicts such trend, such as that observed for *H. ethilla* near our study site (TSS, personal observation) and the current study. This fact may suggest a depletion of host and flower resources over a period of the year [30]. A similar pattern was found for the subtropical population of *H. charitonia* from North America, characterized by a seasonal peak from the end of the wet season and the onset of dry season [31]. The population of *H. charitonia* never disappeared completely and its seasonality was related to the availability of host-plant [31].

In the face of such results, a question remains: what happens to the population of *H. s. apseudes* between October and April, when no adult individual was detected? Diapause and host-plant dynamics may be important in explaining why we were unable to observe adult individuals after October. Fertilized females lay eggs during the cold and dry period (July–October) where climatic conditions are harsh and the availability and quality of host-plant is low. Evidence points to differences in quality between *Heliconius* host species (Passifloraceae) [32]. During the winter host-plants are almost totally defoliated and the tender meristem tissues are important for larval performance [33]. Such characteristics may favor a temporary delay in egg development until more favorable conditions are present, evidencing a potential diapause in the egg stage. As the temperature and humidity increases, host-plant availability increases as well, and hatchling larvae will feed on plants in full vegetative growth. Although diapause has never been documented before in *Heliconius* species [8], other butterfly species from the same locality pass through diapause stages including close relatives such as *Actinote carycina* (Nymphalidae) [34], or significant decreases in the developmental rate (e.g., *Tegosa claudina*) [35] during the dry period.

The *Heliconius* population studied may become extinct in the late dry season and may be recolonized by neighboring populations in late wet season (summer/early autumn) when conditions are favorable again. Individuals from a colonizing population mate and give rise to a new population between April and October. In another locality within its distribution, about 200 km from the target population, *H. sara apseudes* is a migrant [36]. On the other hand, tropical subspecies of *H. sara*, especially from the Amazon, are considered

resident, with constant populations throughout the year without extinction and recolonization dynamics [8, 29].

One last hypothesis to explain the disappearance of the population lies on the formation of a pocket population within the forest in the same locality of this studied population between November and March. A pocket population is an elusive and small population with low detectability occurring in climatically stable localities into the forest [37]. When the availability of host-plant increases, the population explodes and colonizes other localities during the reproductive season (April to October). Pocket populations have never been described for *Heliconius* but have been documented in Ithomiinae butterflies [17], which inhabit areas with adverse conditions [38].

In this study, we showed seasonality for *Heliconius sara apseudes* population in the subtropical Southern Hemisphere. Our results demonstrate the need for new studies in neotropical butterflies to test the hypotheses here raised and further advance the knowledge on butterfly population dynamics and vital rates.

Conflict of Interests

The authors declare that there is no conflict of interests regarding the publication of this paper.

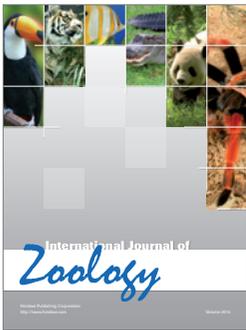
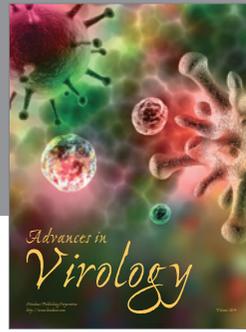
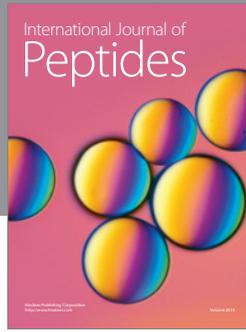
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