The effects of methodological limitations in the study of butterfly behavior and demography: a daily study of *Vanessa atalanta* (Lepidoptera: Nymphalidae) for 22 years

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Abstract: Normally, butterfly behavior and population size are studied intensively for brief periods or occasionally for long periods, not in detail for long periods, producing an incomplete view in both cases. How time limitation affects studies has been unknown for a long time. This paper analyses this problem based on an intensive long term study of *Vanessa atalanta* (L.) that covered nearly 8000 days, most of them consecutive, for 22 years (April 15, 1977-April 14, 1999), in a subtropical habitat near Orlando, Florida. There is no evidence that ethological studies are affected by their normally brief duration (one year or less), but the analysis of yearly values hid the associations of number of individuals and arrival time with climate. In small areas, isolated population counts lasting less than two weeks are not reliable, according to this study. We found no difference in number of visitors for El Niño years. The daily number of visitors was inversely correlated with temperature and precipitation, but arrival time of the first visitor was positively correlated with both. The number of visitors reaches a peak near the end of Winter. The activity period span is greater than in more seasonal climates. Individuals were active even at 10° C and with 9 mIs winds. Individuals with fresh wing condition were most common from January to June. There were 82 atypical cases of individuals arriving before 12:00 hr. Aerial interactions were seen whenever there was more than one individual in the site *(i.e.* 41 % of days, N=7634 total days). Only once in these 22 years was predation seen.

Key words: Long term study, population size, daily visitation pattem, Lepidoptera, weather, El Niño, phenology. behavior, methodology.

For economic and logistic reasons, butterfly biology normally is studied by observing a population intensively for short periods (which is satisfactory to solve ethological problems, *e.g.* Monge-Nájera *et al.* 1998), or through isolated observations over a long time *(e.g.* Stekolnikov's 1992 study that spanned more than half a century). The effort closest to a long term intensive study may be the British monitoring system (Pollard *et al.* 1997), but it also has important methodological limitations (Nielsen and Monge-Najera 1991). In general, we ignore how the lack of long term intensive studies effects our view of butterfly ecology.

The current view of butterfly population ecology is summarized in the following paragraphs.

Density dependent factors *(e.g.* **hostplants):**The importance of specific hostplant species, individuals and even plant parts for population size, distribution and genetic variability is controversial (Thompson 1988, Daily *et at.* 1991 Goulson *et at.* 1997) but there is agreement that food abundance is associated with population increases *(e.g.* Wickman *et at.* 1990)

Density independent factors: In tropical areas of varying altitude, warmer and moister periods are associated with butterfly population increases, while in temperate areas, warm weather normally produces premature emergence, additional generations, increased breeding success and larger adult populations (Pollard *et at.* 1997, Wickman *et at.* 1990, Steiner 1991).

How butterflies reduce the effect of ecological factors: Butterflies can control density dependent and density independent factors in two ways: (1) locally by behavioral and physiological mechanisms, and (2) *ex situ* by migration. Behavioral mechanisms include activity pattern coordination with the hostplant's reactions to climate, while physiological adaptations even involve larval monitoring of day-length to control development (Young 1983, Kunte 1997, Nylin 1997).

Migration: Butterfly travelling varies from small changes in microhabitat distribution to long range migration. Migration seems to be genetically determined and relates with lifespan (Baker 1984, Ehrlich 1984). Solar radiation, temperature and wind may (Calvert *et al.* 1992, Monge-Nájera *et at.* 1998) or may not (Frey *et at.* 1992) help predict the micro- habitats where populations concentrate. It seems clear that topography (and the microclimate pattern that topography creates) affect both butterfly population size and biodiversity (Gutiérrez 1997).

Mid-range movements: Mid-range movements are associated with isolated habitat patches that predispose a species to the shifting mosaic metapopulation model (Harrison *et al.* 1998), with relatively

frequent local extinctions and re-establishments. Stepping-stone gene flow is important at least in some metapopulations (Neve *et at.* 1997, Peterson 1997, Singer and Thomas 1997).

Long-range migrations: Long-range migrations are known in tropical and temperate butterflies, among them the Red Admiral, *Vanessa atalanta* L., a species that appears to fit the requirements for survival in urban areas (Swanson 1979, Kitahara and Fujii 1997, Srygley *et at.* 1997, Thomas 1984). It is a widespread nymphalid found in the American continent from central Canada to Guatemala, often in clearings (Bitzer and Shaw 1979, Tuberville *et at.* 1996).

This paper reports on an intensive (daily) long term study (22 years) of a *V atalanta* population in a subtropical habitat with emphasis on the association of number of individuals and arrival time with climate.

MATERIALS AND METHODS

Individual butterfly visitation records (and a qualitative microclimatic classification) were made daily by the senior author in an urban clearing devoid of hostplants in Winter Park, near Orlando, Florida, USA (28°34'57" N, 81°20'04" W) for 22 years (April 15, 1977- April14, 1999: 8035 days). Details of the site and the unusual conditions that allowed daily observations for such a long period appear in Swanson (1998).

Climatic data are from monthly means provided by government databases available in the Internet (http://water.dnr.state.sc.us/climate/May 1999). Besides the inferential statistics presented here, graphs of daily changes in number of visiting butterflies and their arrival time (available in the on-line edition of this journal) were analyzed visually for non-linear associations (Kozlov *et at.* 1997) but none were found. Non-parametric statistics were used to avoid potential conflict with the less realistic requirements of parametric tests. "Visitation" and "number of daily visitors" are defined as total number of occupants and intruders arriving each day.

RESULTS

Natural history: Individuals were active even at 100 C and with 9 m/s winds. Individuals with wings in fresh condition were most common in the first half of year (January-June) when they represented roughly three quarters of the population. Smaller individuals (general impression: no measurements were taken) were seen from late December to late March. There were 82 atypical cases of individuals arriving before 1200 hr (not included in the graphs). Aerial interactions were seen whenever there was more than one individual in the site *(i.e.* 41 % of days, N=7634 total days, Fig. 1).

A total of 4 794 visits were recorded, with an overall attendance rate of 59.5 %. During the 2 hr afternoon visit period there were frequently 1-3 individuals in the site, two times there were eight and once (March 15, 1982) there were ten. Only once in these 22 years was predation seen: an individual that flew with difficulty was captured by a bird *(Cardinalis cardinalis).* Some specimens had missing legs or lacked parts of wings, antennae or proboscis.

Visitation pattern: There are no host- plants on the site. The population is composed of visitors that perch and participate in aerial interactions *sensu* Bitzer and Shaw (1979). The number of visitors begins to increase in autumn, reaches a peak near the end of winter and decreases almost constantly during the spring and summer (Fig. 2a, 2b). Generally, there are two visitation patterns. Pattern I (1977 to *1985):* a marked curve with zero population around October, *e.g.* Fig. 2a). Pattern 11(1986- 1996): a flatter curve with 1-5 months without visitors, *e.g.* Fig. 2b. Arrival time of first individual to enter the area had the same pattern during the study period, with a soft increase from January through June and a soft decline until December (Julian dates, Figs. 2b and 2 d).

The mean daily number of visitors a particular month was inversely correlated with mean monthly temperature (Spearman Rank Correlation, SRC: r =-0.43, p< 0.01, n=261 months; mean monthly values for number of visitors and climatic factors were used in this and following tests) and precipitation (SRC: r = -0.34, p< 0.01, N=261) (Fig. 3A,C). There were occasional absences of 1-14 days that represented gaps in the general trend mostly during stormy weather (Fig. 2 A-D, a few represent the rare instances in which observer was absent). Arrival time of the first visitor was positively correlated with mean monthly temperature (SRC: r = 0.84, p< 0.01, N=238) and with mean monthly precipitation (SRC: r = 0.49, p< 0.01, N=231) (Fig. 3B,D). Total daily number of individuals arriving at the site was associated with a subjective classification of climate (Kruskal-Wallis ANOVA, p<0.0001, N=5658 days; mean ranks: 4229 windy, 3152 good climate, 2614 cold, 743 overcast or rainy) but not with arrival time (KruskalWallis ANOVA 1.7, p=O.63, N=4 681 days).

Yearly mean values were not correlated (SRC values: visitors versus temperature -0.17, visitors versus precipitation -0.40; arrival time versus temperature 0.17, arrival time versus precipitation 0.02; in all cases N=22 years and p>O.O5). (Fig. 4) There was no significant difference in number of visitors

between El Niflo (mean 1.13 visitors/day, standard deviation SD 0.21, range 0.90-1.50, N=ll, years 1977, 1978, 1982, 1983, 1986, 1987 and 1991-1995) and non-El Niño years (mean 1.25, SD 0.28, range 0.80-1.70 visitors/day).
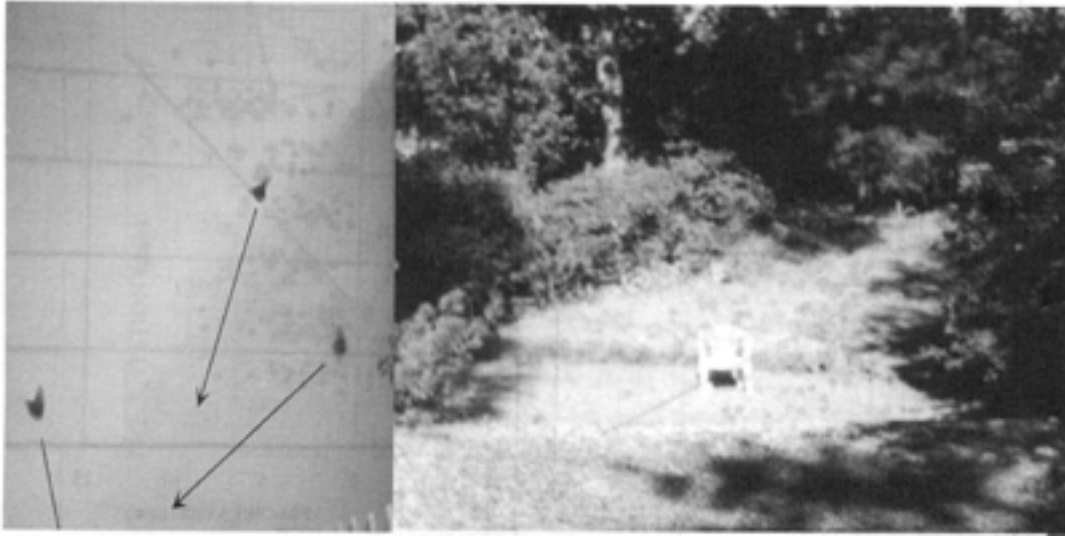

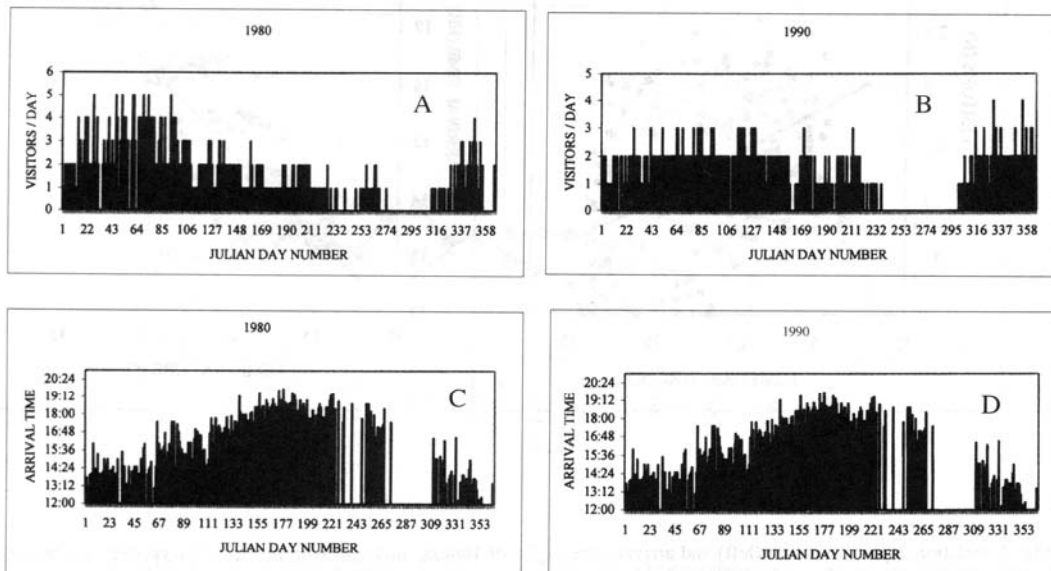Fig. 1 Aerial interaction of *Vanessa atalanta* and study site (from a video)

Fig. 2. Two tipical visitation and first daily arrival time patterns throughout the year for *Vanessa atalanta* in a subtropical habitat in Florida. Visitation is shown as number of visitors per day and arrival time of first visitor is given in hours. A., C. visitation rate daily arrival times for 1980. B., D. visitation rate and initial daile arrival times for 1990.
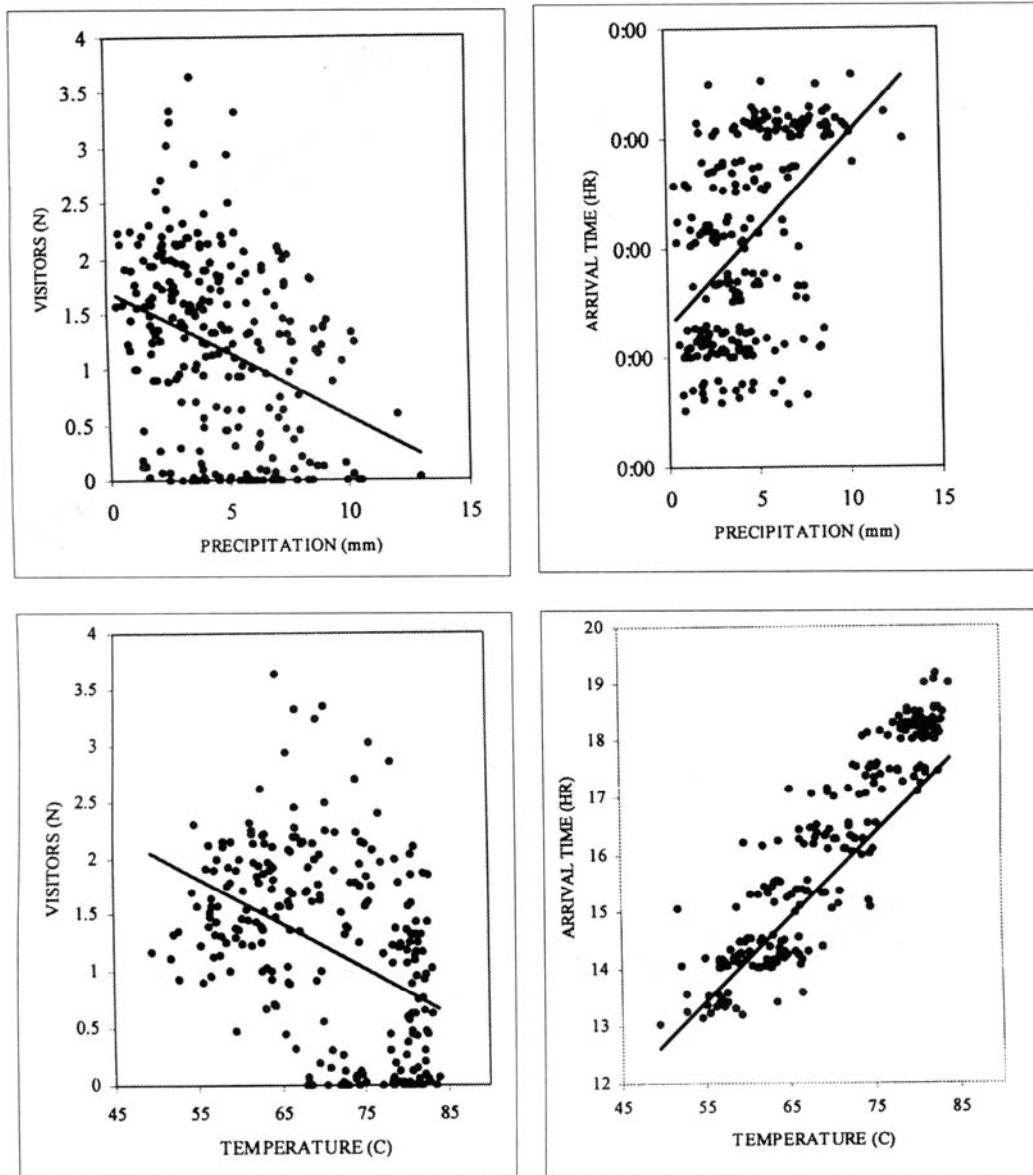
Fig. 3. Relationship of visitation (left) and arrival time (right) of *Vanessa atalanta* with precipitation (above) and temperature in a subtropical habitat (statistical values in text).
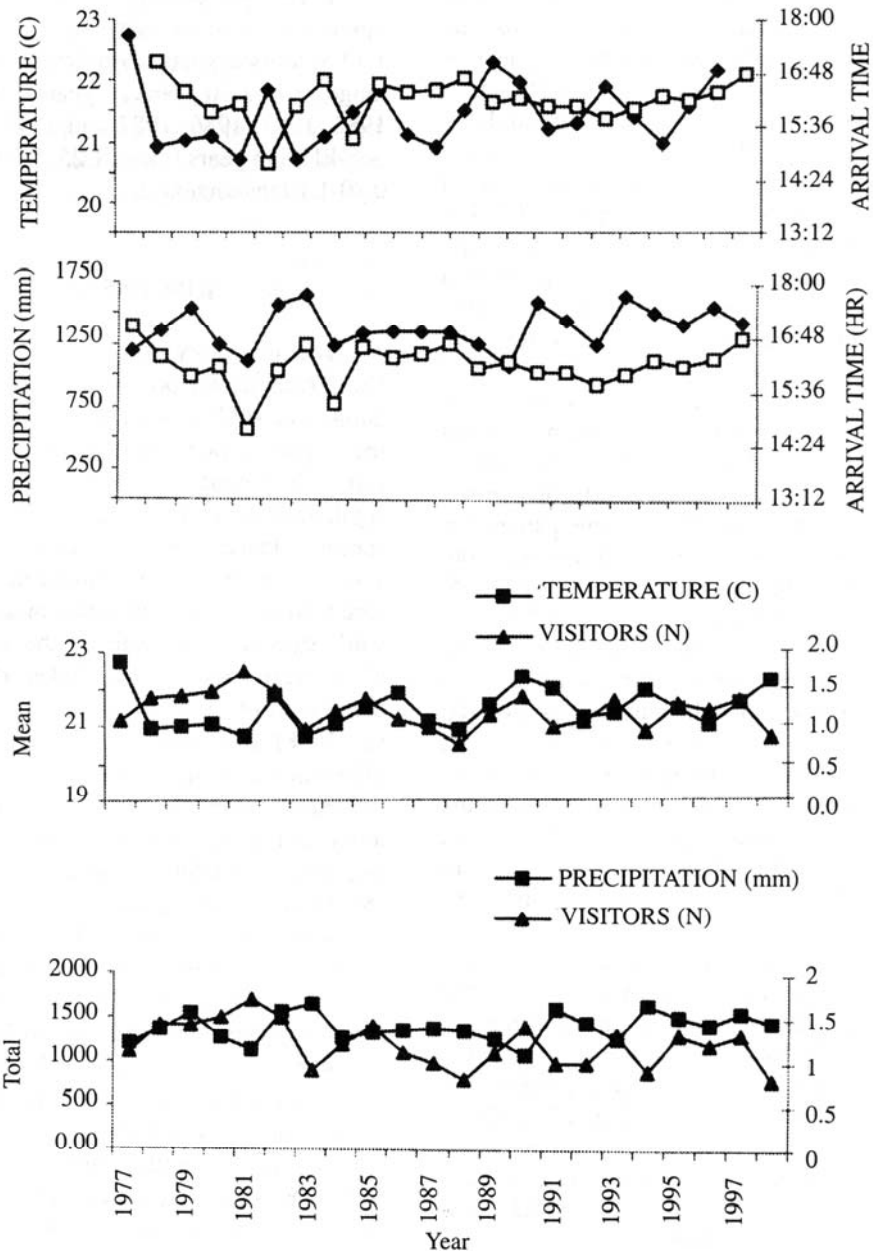
Fig. 4. Yearly arrival time and visitation patterns of *Vanessa atalanta* versus temperature and precipitation in a subtropical habitat (statistical values in text)

DISCUSSION

The migratory routes of *V atalanta* in North America are poorly known, but a greater number of studies in Europe have shown that the migratory population follows temperature layers (Benvenuti *et al.* 1996), is subjected to significant wind drift and travels with other species (Hansen 1997); has time-compensated sun orientation, migrates thousands of kilometers, feeds in winter and sometimes reproduces while traveling northward in the warmer part of the year, around June (Baker 1972, 1984, Stefanescu *et al.* 1996, Hansen 1997, Palmqvist 1998). It is now clear that migrations are bidirectional (Benvenuti *et al.* 1996) but how the travel information is passed among butterfly generations in general is not known (Pasteur 1984) and future studies of *V atalanta* should stress this aspect.

In this study, seasonal changes in the number of visitors, with fewer visitors in the moister and warmer months and predominance of fresh individuals from January to June suggest that *V atalanta* overwinters in Florida and migrates to northerly regions when high summer temperatures affect Florida (R. Bitzer 2000, pers. comm.). A similar migration from Africa to Europe is known (Larsen 1993). This

would fit with the smaller individuals seen from late December to late March: fresher individuals may emerge in Florida as the offspring of the larger butterflies first seen in late October - early November. These larger individuals could have migrated from more northerly regions earlier in the fall, according to the parallel migration pattern of *V atalanta* in Europe described by Larsen (1993) and Benvenuti *et al.* (1996)(R. Bitzer 2000, pers. comm.). For *V. atalanta* temperature is a more important limiting factor than host plant availability (BryantSimon *et al.* 1997, Maier and Shreeve 1995).

The activity period span in Florida is greater than in the more seasonal climate of Iowa, where *V atalanta* is active from April to October (Bitzer and Shaw 1979, 1995). The greater number of visitors on windy days suggests that the site was selected because it was surrounded by vegetation and buildings (see Swanson 1998).

The El Niño Migration Model predicts that overpopulation increases butterfly migra tion to outbreak level during El Niño years (Larsen 1984, Myres 1985). We found no difference in number of visitors for El Niño years, apparently because *V atalanta* is a regular rather than an outbreak migrator.

The limited temperature range that characterizes sites where *V atalanta* occurs (Bryant-Simon *et at.* 1997, Maier and Shreeve 1995) and butterflies' inability to fly under heavy rain can explain why individuals arrive at their perching spots later in the hot, rainy months. *V atalanta* males establish courtship territories 2-4 hours before sunset (Wiltshire 1997, Bitzer and Shaw 1979, 1995) and use neural motion detectors adapted to great speed (O'Carroll *er al.* 1996) in aerial interactions (Bitzer and Shaw 1979). Territories have distinct characteristics (sunlit clearings and ridge tops) and are used by different individuals over the years (Bitzer and Shaw 1979, Wiltshire 1997). Despite its methodological difference with previous studies, this study produced the same conclusions about territorial behavior, and also agrees with the ecological model of perching behavior which proposes that perching is associated with relatively high temperature, lekking and long life (Wickman l992a,b, van Dyck *et al.* 1997a,b, van Dyck and Matthysen 1998. No data are available regarding the wing color and body proportion elements of the model).

If our results can be generalized (and that will be unknown until more long term intensive studies become available) behavioral studies of butterflies do not suffer from the general impossibility of daily observation for long periods, but at least for small areas, occasional population counts covering less than two weeks are unreliable: even total absence of individuals for such periods can simply represent gaps in the general trend. Furthermore, the analysis of yearly values hid the associations of number of individuals and arrival time with climate that were found when a smaller scale was used. Long term studies based on yearly samplings should be re-evaluated for this aspect.

ACKNOWLEDGMENTS

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