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Population dynamics and seasonal polyphenism of *Chilades pandava* butterfly (Lycaenidae) in central India

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Some butterfly species have environmentally induced alternative seasonal forms, which is known as seasonal polyphenism. Many examples of seasonally polyphenic species are known but their population dynamics is poorly understood. Here we present seasonal polyphenism in *Chilades pandava* from central India, documenting patterns of population dynamics of alternative seasonal forms as well as of total population size. We show that relative humidity explained most of the variation in population size, whereas precipitation negatively influenced the proportion of dry season forms in the population. However, dry season forms were more abundant during winter than during summer. This study reveals the multitude of ways in which the Indian monsoon governs aspects of butterfly biology, from population dynamics to wing colouration.

Keywords: Oriental region, phenotypic plasticity, Polyommatini, population biology, tropical butterflies.

SHORT-LIVED butterflies with multiple generations per year usually experience different habitat conditions in successive generations, strongly influenced by seasonal climatic trends. Seasonal changes faced by different generations may include changes in ambient temperature and day-length, differential availability of secure resting places, nectar plants for adults and larval host plants, and a different set of predators and predation risk[1–5]. Typically, butterflies respond to such seasonally varying biotic and abiotic conditions in two ways. The first is to lower reproduction under unfavourable conditions, causing pronounced seasonal population fluctuations even in many tropical species[2,6,7]; or to diapause during unfavourable seasons, a strategy that is especially ubiquitous in temperate areas[8]. A second response is seasonal polyphenism, i.e. the occurrence of environmentally induced seasonal forms that show striking dissimilarity in colouration and wing patterns to each other[9]. Several environmental cues may

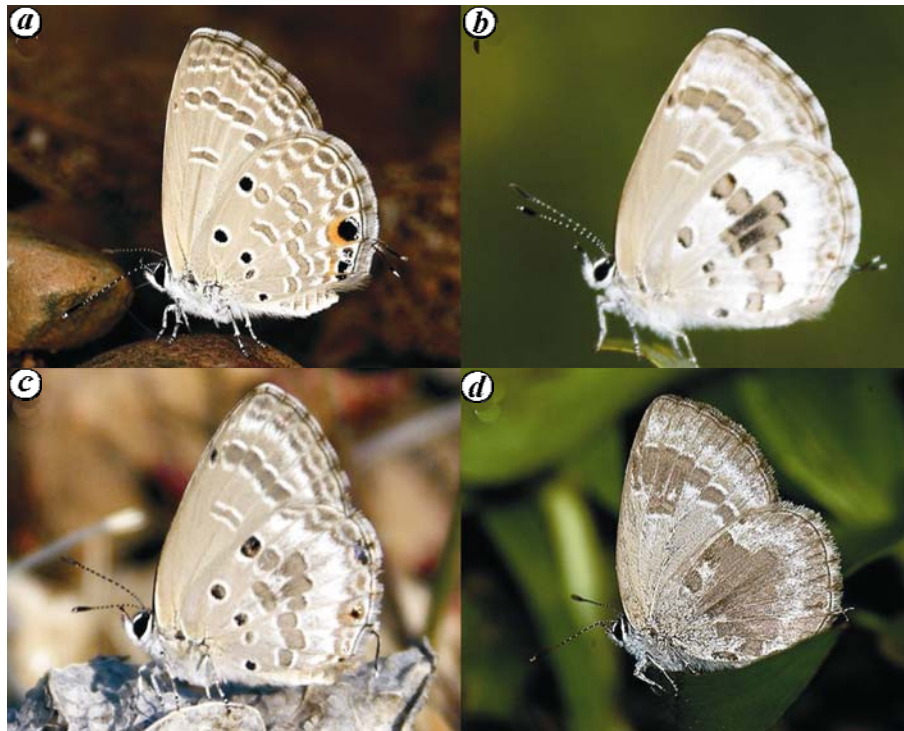*For correspondence. (e-mail: KKunte@cgr.harvard.edu)

Figure 1. Seasonal polyphenism in *Chilades pandava*. *a*, Wet season form. *b*, Typical dry season form (DSF), in which the central area on the hind wing turns dark and the outer areas turn white, the extent and pattern of which are individually variable, as in *c* and *d*.

produce these seasonal forms: photoperiod[10–13], ambient temperature[12–15] and rainfall[15]. The alternative seasonal forms are presumably favoured by the seasonally varying biotic and abiotic selective pressures[4,16], or they may be by-products of phylogenetic and other historical factors[17].

Seasonal polyphenism has been extensively investigated in many Holarctic and African nymphalid and pierid butterflies[11,16,18–22]. Although it is taxonomically widespread[4], seasonal polyphenism has rarely been studied systematically outside Nymphalidae and Pieridae. Here, we report on some population biological aspects of *Chilades pandava* Horsfield, 1829 (Lycaenidae: Lycaeninae: Polyommatini) from central India, a species that responds to seasonally changing environments both in terms of population size and in phenotypically plastic wing colouration. First we present data on seasonal population dynamics of *C. pandava*, and then we analyse environmental factors that govern the occurrence of the seasonal forms. This study is important because it shows in detail how specific seasonal variations in climatic factors govern the population size and wing colour patterns of butterflies. It is also important as a comparative study that provides a phylogenetically independent contrast to previously studied seasonally polyphenic nymphalid and pierid butterflies.

The central Indian populations of *C. pandava* show distinct dry and wet season forms (Figure 1). The wet season form is mostly invariable, with central and submarginal

bands and basal spots forming wing colour pattern elements characteristic of its tribe[23]. On the other hand, the dry season form (DSF) shows considerable individual variation in colouration and pattern, especially in the extent of light colouration and black spots and smears on the wings[23] (Figure 1). Populations and subspecies from the wet southeast Asian and Sri Lankan regions comprise only the wet season form[24].

The study site Ambazari Garden in Nagpur (20°9′N; 79°9′E), central India, is spread over six hectares and contains a mosaic of ornamental flowering plants and native deciduous forest trees. The garden has several *Cycas revoluta* (Cycadaceae) plants (the preferred larval host plant of *C. pandava*), *Acacia* spp. and *Albizzia lebbeck* that are used as alternative larval host plants, and many nectar plants for adults. The climate is marked by three major, widely recognized seasons in central India: hot and dry summer (March–May), south-western monsoon (June–September) and mild winter (November–February; October being the post-monsoon transitory period. Data from October is excluded from Table 1 but included in all other analyses). Weekly data on three climate variables (temperature, percent relative humidity and precipitation; Figure 2 *a*) were obtained from the Department of Meteorology, College of Agriculture, Nagpur, located 3 km from the Ambazari Garden.

The population dynamic data were collected by AT on three 500×10 m transects, each traversed in one hour,

Table 1. Seasonal variation in the population parameters of *C. pandava*

|	Total	Average ± SD (range) per week	Statistical significance
Number of individuals			
Summer	39	3.25 ± 2.49 (0–7)	One-way ANOVA: $F_{2,41} = 22.6$, $P \ll 0.0001$
Monsoon	221	13.81 ± 3.54 (8–21)	
Winter	164	10.25 ± 5.55 (2–18)	
Number of DSF			
Summer	28	2 ± 1.92 (0–6)	2-sample *t*-test: $t = -5.17$, df = 21.6, $P \ll 0.0001$
Monsoon	0	0	
Winter	140	8.75 ± 4.43 (2–16)	
Proportion of DSF			
Summer		0.84 ± 0.319 (0–1)	Welch 2-sample *t*-test: $t = -0.4$, df = 12.45, $P = 0.69$
Monsoon		0	
Winter		0.88 ± 0.094 (0.73–1)	
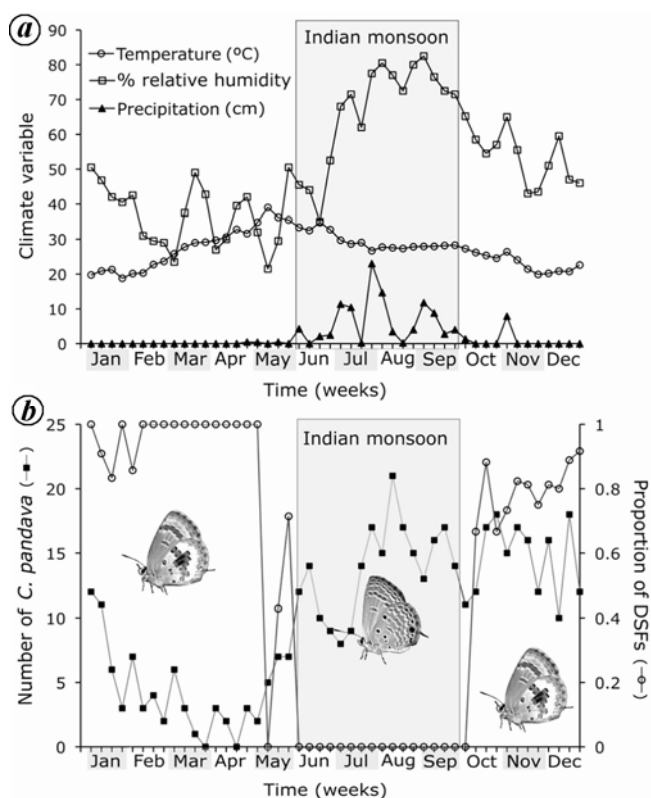
Figure 2. Temporal patterns of (*a*) climatic variables, and (*b*) total number of *C. pandava* and the proportion of DSF in the population. The three butterflies in the lower panel show the seasonal forms that are predominant during the three seasons.

visited once a week between 8:00 and 11:00 h. Each individual *C. pandava* sighted on the transect-belt and its seasonal form were recorded. The population and seasonal polyphenism data were collected from July 2006 to June 2007.

Data from the three transects were pooled to calculate the total number of individuals and the proportion of the DSF in each week. Estimates of population size from periodic censuses of many species are often temporally autocorrelated (i.e. population size at time *t* affects population size at time *t* + *x*), which means that data points are not independent and therefore standard regression analyses are not valid. We tested for population size autocorrelation using the statistical package *R* (ref. 25) and found no significant temporal autocorrelation in the population data (results not shown). Hence, we analysed the data using multiple regression analysis.

To identify the relative importance of the three climatic variables in explaining the variation in population size and composition, we first used a tree model using the package 'tree' in *R*. Tree models produce a bifurcating, tree-like structure by binary recursive partitioning of the data to maximize the amount of variation in data explained at each split (Figure 3). The data partitioning continues until the addition of explanatory variables no longer explains a significant amount of variance at the branch tips. This approach is explained here with an example with reference to Figure 3 *a*. For seasonal variation in the population size, the model first determined that relative humidity was the most important explanatory variable and identified 42.87% humidity as the critical value for the first nodal split of the data. This nodal split alone explained 37.5% of variance in population size of *C. pandava* (30.6% on one branch and 6.9% on the other). It then identified temperature as the second most important explanatory variable with the critical value of 28.47°C, which explained a further 18.8% variance in the dataset (10.9% on one branch and 7.9% on the other). Addition of further climatic variables did not explain additional variance in the dataset. Thus, the best-fit tree in the tree model indicates the relative importance and interactions between explanatory (in this case, climatic) variables that explain most of the variations in the response (population) variables.

The tree model is a useful analytical tool that identifies critical values of explanatory variables and represents data visually, although it does not test statistical signifi-
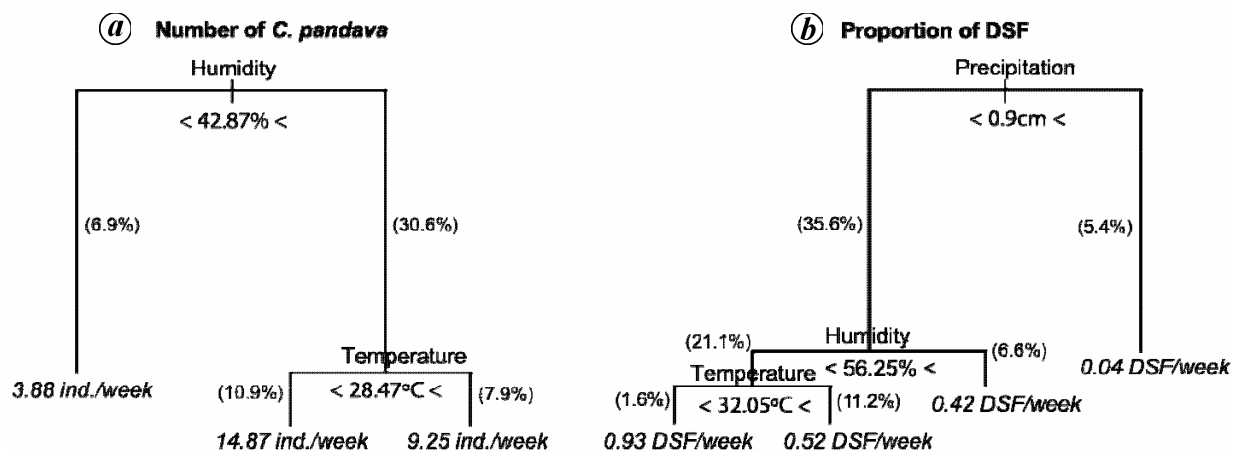
Figure 3. The influence of climatic variables on: (*a*) the number of *C. pandava*, and (*b*) the proportion of DSF in the population. The data were partitioned such that the bifurcating, tree-like structure shows the hierarchical importance of the climatic variables that explain maximum variation in the population parameters. The nodal splits, where critical values of the climatic variables are given, explain the greatest amount of variance between groups. Values in parentheses give the percentage variance explained by the branch. As illustrated by arrow-heads ('<' and '>'), lower values of climatic variables are on the left side and higher values are on the right side of all the nodes. Branch-ends give mean population values for each group or 'branch' of the tree.

cance. To assess statistical significance, we fit a multiple regression model to data on the climatic variables, population size and proportion of the DSF as follows. We used the 'gam' function in the package 'mgcv' in *R* to fit a generalized additive model to the data. We first fit a full model (total population = -1 + s(humidity) + s(precipitation) + s(temperature)), where 's' indicates a smoothed function and '-1' indicates that the model does not include a fixed intercept. We then sequentially removed terms from the full model, evaluating deviance for each new model. A similar procedure was adopted using proportion of DSF as the response variable and specifying binomial error. The final reduced models with the least deviance in the data were: (i) total number of individuals = -1 + humidity + s(temperature, humidity), where s(temperature, humidity) indicates an interaction between the two variables, and the non-smoothed humidity term indicates that it affects the model intercept. These together explained 96% variance in population size; and (ii) proportion of DSF = -1 + s(precipitation) + s(temperature) + s(humidity), which explained 88.5% variance in proportion of the DSF.

During 48 weeks of sampling covering the entire year, we recorded 203 DSF among a total of 482 *C. pandava*. The average number (± standard deviation) of *C. pandava* recorded per week was 10.04 ± 5.83 (range: 0–21), and the average number of DSF was 4.23 ± 5.05 (range: 0–16). The population size and the number and proportion of DSF in the population, however, showed pronounced seasonal fluctuations (Figure 2*b*, Table 1). Population size was highest during the monsoon, whereas the abundance of DSF was greatest during the winter. The proportion of DSF in the population was very high, and comparable, during winter and summer (Table 1 and Fig-

ure 2*b*). The abundance pattern of DSF initially seemed puzzling since we had expected, *a priori*, the abundance of DSF to be greatest during summer, at the height of the dry season. However, the interesting finding that the abundance of DSF was over four times higher during winter months compared to summer months was explained by population size, which was over four times greater in winter compared to summer (Table 1 and Figure 2*b*).

The two panels in Figure 3 illustrate the hierarchical order in which the three climate variables explained most of the variance in population size and the proportion of DSF. Relative humidity critically determined population size (Figure 3*a*): humidity less than 42.87% was associated with the lowest population size (average 3.88 individuals/week), while humidity above 42.87% was associated with higher population size. Temperature interacted with humidity to further affect population size: at high humidity (>42.87%), temperatures less than 28.47°C led to the highest population size (average 14.87 individuals/week), while high humidity combined with high temperature (>28.47°C) was associated with intermediate population size (average 9.25 individuals/week; Figure 3*a*). Note that the Indian monsoon indirectly influenced these patterns: the rains increased relative humidity but lowered the temperature (Figure 2*a*), leading to high population size. The rains affected the proportion of DSF more directly (Figure 3*b*), decreasing it to as low as 0.04 (i.e. 4% of total individuals) when precipitation was greater than 0.9 cm. Lower precipitation (<0.9 cm) and high humidity (>56.25%) negatively affected the proportion of DSF (average 42% of total individuals). On the other hand, DSF was most abundant (93% of total individuals) when all three climatic variables were low (precipitation <0.9 cm, humidity <56.25% and temperature <32.05°C;

Figure 3 b). Thus, the three climatic factors, strongly influenced by the monsoonal rains, explained most of the variations in these two population parameters.

Results of the multiple regression analysis confirmed the impacts of climatic variables on population parameters as identified by the tree model. The multiple regression analysis showed that a smoothed function representing the interaction between humidity and temperature explained most of the weekly variation in the number of *C. pandava* (adjusted $R^2 = 0.725$, $P = 0.0194$). Humidity alone significantly impacted the intercept of the temporal variation in population size ($P < 0.001$). These results indicate that overall population size was determined by relative humidity, but that temporal variation in population size at constant humidity was dependent on the interaction between temperature and humidity. On the other hand, all three climatic variables strongly impacted variation in the proportion of DSF in the population (adjusted $R^2 = 0.939$; $P = 0.0335$ for precipitation, $P < 0.001$ for temperature and $P < 0.001$ for humidity in the interaction term), without any significant interactions between climatic variables.

Seasonal polyphenism provides unusual insights into the evolution of butterfly wing colour patterns, and is useful in investigating the role of natural selection in producing the diversity of life at multiple levels, from genes to phenotypes[26]. Population dynamics similarly offer a window into the seasonal and ecological factors that shape the selection landscape, and show responses of organisms to these factors. In this communication, we were able to study the little-understood population dynamics associated with seasonal polyphenism to examine how *C. pandava* responds to the strongly marked seasonal climatic fluctuations in central India. We showed that the population size and the relative proportion of DSF fluctuated prominently with the seasons. Using multiple regression and tree models we were able to show that the population size and the proportion of DSF in the population were particularly influenced by humidity and rainfall. This is an excellent example of the multiple ways in which the Indian monsoon influences the biology of butterflies in this region, from population dynamics to wing colour patterns.

One remarkable feature of the seasonal polyphenism in *C. pandava* is that its wet season form shows very little wing pattern variation whereas the DSF shows substantial individual variation in the extent and form of various wing pattern elements on the underside[23]. This unequal distribution of wing pattern variation across seasons highlights two important questions: (1) why has seasonal polyphenism evolved in this species, and (2) why is DSF so variable? Several non-exclusive or sometimes complementary hypotheses have been proposed to explain seasonal polyphenism in butterflies: (1) seasonal forms optimize thermoregulation in response to changes in thermal conditions across seasons, (2) predation pressure varies across seasons and the seasonal forms are best suited to match background colouration and thus enable escape from predation in the respective seasons in which they occur, and (3) seasonal polyphenism in some butterflies may have evolved in different selective environments, but persists as a by-product of dispersal and phylogenetic relationships[3,4,17,27,28]. The first two hypotheses are selectionist, while the last one is non-selectionist. The colour pattern changes and variation in the seasonal forms of *C. pandava* is suggestive of the selective processes involved in the first two hypotheses, for the following reasons. The DSF of *C. pandava* shows greater amount of white and other pale colouration[23] (Figure 1), which may help the butterflies to reflect the excessive heat of central Indian summers when the average temperature approaches 40°C and the highest daily temperatures are in the mid-40s. On the other hand, the overall pale colouration and highly reduced amount of orange and black near the tornal hind wing spots may help these butterflies to blend with the pale colouration of dry vegetation. However, it is unclear whether the individual variation observed in the DSF is under selection. Of particular interest is the individual variation in the darkening of the central wing area and whitening of the areas between the central and the submarginal bands on the hind wing of DSF[23] (Figure 1 b–d). It is possible that these individually variable, seemingly unstable wing colour patterns in the DSF of *C. pandava* result not from selective pressures but from stochastic gene expression during wing pattern development, which may be affected by very high summer temperatures of central India. Thus, a combination of thermoregulation, predator escape and temperature-sensitive developmental stochasticity or unstable gene expression is likely to influence seasonal polyphenism and individual variation in *C. pandava*. This form of seasonal and individual variation makes *C. pandava* an attractive species for further studies on seasonal polyphenism. Importantly, it offers a phylogenetic contrast to other seasonally polyphenic species such as *Pieris* and *Bicyclus*, which may be helpful if we want to understand seasonal polyphenism in a wider evolutionary context. Also, it provides a native study system for Indian biologists, who may not have ready access or research facilities to study other established seasonally polyphenic systems. Here we have introduced the seasonal polyphenism and population dynamics of *C. pandava*; we hope that more detailed ecological as well as genetic and experimental developmental work on this species will follow.

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