Biological Journal of the Linnean Society (1999), *66:* 345–356. With 4 figures
Article ID: bijl.1998.0268, available online at http://www.idealibrary.com on IDEAL

Seasonal polyphenism in *Bicyclus* (Lepidoptera: Satyridae) butterflies: different climates need different cues

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Received 17 February 1998; accepted for publication 2 July 1998

A comparison is made between northern and southern hemisphere populations of *Bicyclus* butterflies in Africa regarding their responses in wing pattern polyphenism to seasonal change in rainfall and temperature. In southern habitats where temperature and rainfall are often positively correlated, a high temperature during the larval period induces conspicuous wet season forms whereas a fall in temperature elicits cryptic dry season forms. In northern habitats, however, where temperature and rainfall usually are negatively correlated, a rise in temperature should not induce a wet season form because such a rise is correlated with the onset of the dry season. Here, wing pattern plasticity, as measured using museum material, was regressed on mean monthly values for rainfall and temperature. Rainfall appeared to be a frequent determinant of wing pattern plasticity whereas temperature was much less often a significant independent variate. We conclude that the wing pattern may only respond to seasonal change in temperature if rainfall and temperature are positively correlated; in other situations rainfall remains the only significant determinant for wing pattern plasticity.

ADDITIONAL KEY WORDS:—wing pattern – phenotype plasticity – climate variation – reaction norm.

CONTENTS

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INTRODUCTION

Response to seasonality is an important aspect of life-history characteristics (Tauber *et al.*, 1986). Many species may enter diapause, others migrate and again others are able to develop seasonal forms. It is essential that the response to seasonal, hence predictable, environmental variation is fine-tuned. Closely related species belonging to the same taxonomic group or even populations belonging to a species, may be distributed over geographic areas with different seasonal environments. Different species sharing similar genomes should be able to respond to sometimes strikingly different environments. In this study we compare the responses of such groups.

African *Bicyclus* species are an excellent example with which to tackle this question: about 70 species occur south of the Sahara in a great variety of rain forest, savannah and mountain habitats. Therefore, many species experience a variety of aseasonal to seasonal environments due to their large distribution areas (Condamin, 1973). *Bicyclus* butterflies respond to seasonal change by producing different wing patterns: wet season butterflies have brown wings with conspicuous eyespots and bands whereas dry season butterflies have dull, cryptic wing patterns which match a background of dead, brown vegetation. Such a change in wing pattern may be understood as involving eyespots as a mechanism for active wet season butterflies to deflect attacks by small vertebrate predators and to ensure that inert dry season butterflies are less apparent (see Roskam & Brakefield, 1996, and references therein).

Responses of wing pattern elements such as eyespots to environmental change can be represented by population reaction norms: a graphic representation of the set of phenotypes produced by a mean population genotype through its environmental range (Schmalhausen, 1949). Windig (1992) found that development time but not temperature may be the real predictor for the seasonal forms. Indeed, if lines of *B. anynana* are selected for development time, slow cohorts generate butterflies with smaller eyespots than the fast cohorts at the same temperature (P.M. Brakefield and F. Kesbeke, unpublished data).

Most of our research on interactions between habitat and wing pattern to date has concerned butterflies originating from localities in Malawi (Brakefield & Reitsma, 1991; Windig *et al.*, 1994). A rise in temperature predicts the onset of the rain season, not only in south-eastern but also in south-western African habitats (Fig. 1). Significant correlations, however, are absent from inland localities in a zone from 15 to 28°E. In localities with significant temperature/rainfall (t/r) correlations the sign of the correlations switches at the equator resulting in different climatic regimes. Douala (4.00°N, 9.44°E) and Tsibinda (2.19°S, 28.45°E) for example are both situated close to the equator but have dramatically different coefficients of correlation, $r = -0.92$ and $+0.83$, respectively (data from RNMI, 1996). This means that there must be a different use of environmental cues by species of *Bicyclus* in northern seasonal habitats to match their seasonal forms with the seasonality of the climate. This study is intended to examine this paradox by comparing the covariation of wing pattern elements and climatic conditions from seasonal localities characterized by positive (P, southern latitudes) and negative (N, northern latitudes) temperature/rainfall correlations. This paper examines how:

(1) population reaction norms differ between butterflies from localities with different t/r correlations; and

(2) the patterns of covariation of wing pattern elements with climatic factors differ in localities with positive and negative t/r correlations.

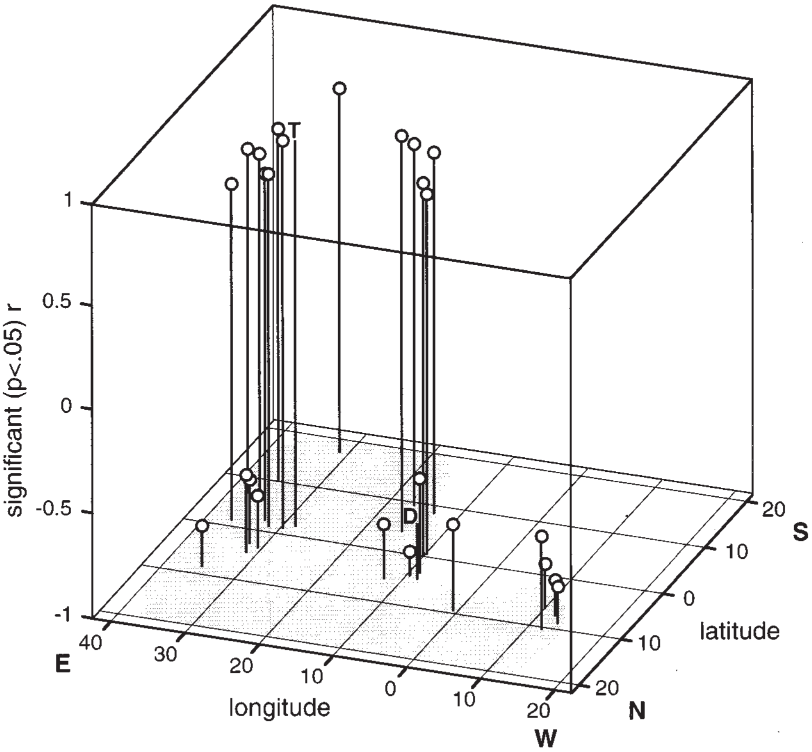

Figure 1. Correlation between 30-year mean monthly temperature and rainfall records. Only significant ($P<0.05$) correlations are included. The stippled area represents the central part of Africa, as seen from a *northern* viewpoint (in a conventional representation many negative correlations would disappear as overstrikes behind positive ones). D, Douala; T, Tsibinda.

We finally discuss seasonal factors to which butterflies may respond in localities with negative t/r correlations.

MATERIAL AND METHODS

Wing plasticity and climate

Six measurements of plastic pattern elements of the ventral wing surface (wing size, distance vein 'junction' Cu1a to distal band, width of the black ring of both forewing ventral anterior 'fv2' and posterior 'fv5' eyespots, and this same measurement for hindwing 'hv2' and 'hv5' eyespots, see for further description Roskam & Brakefield, 1996) were taken from about 1500 butterflies in two museum collections: British Natural History Museum (London) and Zoologische Staatssammlung (Munich). Measurements were made with a stereomicroscope fitted with micrometer eyepiece at 10 × or 40 × magnification.

Because the climatic conditions experienced during the fourth and fifth larval stages are critical to generate either dry or wet season forms (Kooi *et al.*, 1994, reported for *B. anynana*), wing pattern measurements were matched with 30-year (1930–1960) monthly means for temperature and rainfall in the month preceding

the month of collection of the specimens. The climatic data were provided by weather stations which are situated as close as possible in distance and altitude to the collection site (RNMI, 1996). We distinguished three types of areas:
(N), with a significant ($P<0.05$) negative t/r correlation;
(P), with a significant positive t/r correlation;
(Z), with a t/r correlation not significantly deviating from zero.

Norms of reaction and multiple regression coefficients

To obtain information about the plasticity responses, phenotypic variations of the anterior eyespot on the ventral surface of the hindwing (hv2) are presented for three species, namely, *B. sanaos* from N-habitats in West Africa, *B. kenia* occurring in mountain P-habitats in East Africa, and *B. evadne* collected in Z-habitats in West Africa. These species were selected because they were represented by relatively large numbers of specimens in different types of geographic areas. Populations of *B. safitza* from these three areas were also compared because of the closer genetic similarity of conspecific populations and thus the potential to examine how natural selection may have shaped their plasticity under different climatic regimes.

In order to detect whether general patterns emerge, the width of eyespot hv2 was regressed on the 30-year monthly values of temperature and rainfall and their interaction term, temperature*rainfall. The *P*-values in this multiple regression model were used in order to determine the impact of these variables (Rice, 1988). If the interaction term was not significant ($P=\alpha<0.05$) this term was excluded from the model and the *P*-values were calculated anew. Because a possible interdependence might exist between the two environmental variables we applied an improved Bonferroni correction in which the highest significant *P*-value should not exceed $\alpha=0.05$ and the following *P*-values should be lower than $\alpha/2..3$ (Haccou & Meelis, 1994; Hochberg, 1988; Simes, 1986). *P*-values were calculated for the *Bicyclus*-species present in the collections we have used. We restricted ourselves to a single eyespot measurement because the sample size was in general too small for using a concatenation of more plastic wing characters (e.g. scores from a PCA-ordination). Each species was divided into subgroups according to the t/r correlation type of the localities where specimens were collected. No further subdivision according to sex was made because sexual differences among the selected characters were small and most sample-sizes did not allow further subdivision.

Finally, all six plastic wing characters were simultaneously analysed using principal component analysis (PCA) to describe how patterns of covariation differ between cohorts from regimes of opposite t/r correlation. A standardized matrix of these characters, combined with mean monthly temperature and rainfall data, was subdivided into two cohorts of specimens: those from positive (P), and from negative (N) t/r correlation localities. Only those species which showed discrete seasonal forms in our museum material were used. From these species, only specimens were analysed which were collected at seasonal localities having dry periods with a mean monthly rainfall of less than 5 mm during at least two consecutive months. Sample sizes were 43 specimens collected in P-localities and 48 specimens from N-localities. Scores on pc-axes 1–3 were finally used as dependent variables to calculate multiple regression coefficients for subgroups coming from such seasonal areas.

RESULTS

Species in different t/r correlation areas

B. sanaos is a species from rainforest habitats but is occasionally able to generate dry season forms (Condamin, 1973). In equatorial rainforest habitats, rainfall fluctuates dramatically with the seasons whereas temperature varies very little. Only minor differences in eyespot diameter have been found in our N-areas over the year, 27% of which could be attributed to the independent variables rainfall and temperature (Fig. 2a, Table 1). Temperature alone contributed to eyespot variation in *B. evadne* (Fig. 2b, Table 1) which originated from Z-areas (without significant t/r correlation). In this rainforest species dry season forms are unknown. Temperature as well as rainfall affected eyespot size of *B. kenia* in P-areas. This species is restricted to montane forests in Kenya, Tanzania and Uganda (Fig. 2c, Table 1). Since all collections were made above 1500 m, it was not possible to include the range in altitude as an additional variable in the regression model. Condamin (1973) does not report dry season forms for *B. kenia*, but specimens with punctiform eyespots are common. Low temperature (±18°C), which is frequent at high altitude, may primarily be responsible for the induction of small eyespots.

B. safitza is a common species in savannah-rainforest ecotones south of the Sahara. Seasonal polyphenism is well developed (Windig *et al.*, 1994; Roskam & Brakefield, 1996). The change in eyespot diameter followed the change in rainfall in P-areas. Eyespot regression on temperature and rainfall are both significant in Z-areas and were significant for temperature and temperature/rainfall interaction in N-areas. It is remarkable that, at least in the latter category and for the months when material was available, the shapes of the curves for eyespot diameter and temperature are quite similar (Fig. 2d–f, Table 1).

Multiple regression coefficients

Out of the total of 77 species of *Bicyclus* listed in Condamin (1973), sufficiently large samples could be obtained for 46 species (Table 1). For an overall picture of effects on eyespot variation the species were pooled together and the significant contribution of rainfall and temperature was calculated (row 'total' in Table 1: e.g. in column 'temperature, P' 5/16 = 0.31 cases were significant; in column 'R-SQ, P' in 12/16 = 0.75 cases the independent variables explained more than 50% of eyespot variation). The interaction factor 'temp*rain' was significant for only a quarter (P- and N-areas) to 7% (Z-areas) of the cases. The column 'rainfall' resulted in a twice as many significant values for eyespot diameter than the column 'temperature'. This indicates that rainfall is clearly more relevant as an independent variable than temperature. Temperature contributed significantly in only one case, *B. evadne* (N-area), whereas rainfall contributed in many cases (e.g. *B. funebris*, all cohorts). Furthermore, the amount of explained variation (R-SQ) was highest in P-areas and lowest in Z-areas. This means that if a significant correlation, whether positive or negative, between rainfall and temperature exists, this results in high percentages of explained variation.

Distinct patterns in differences between species were not obvious. Six species were

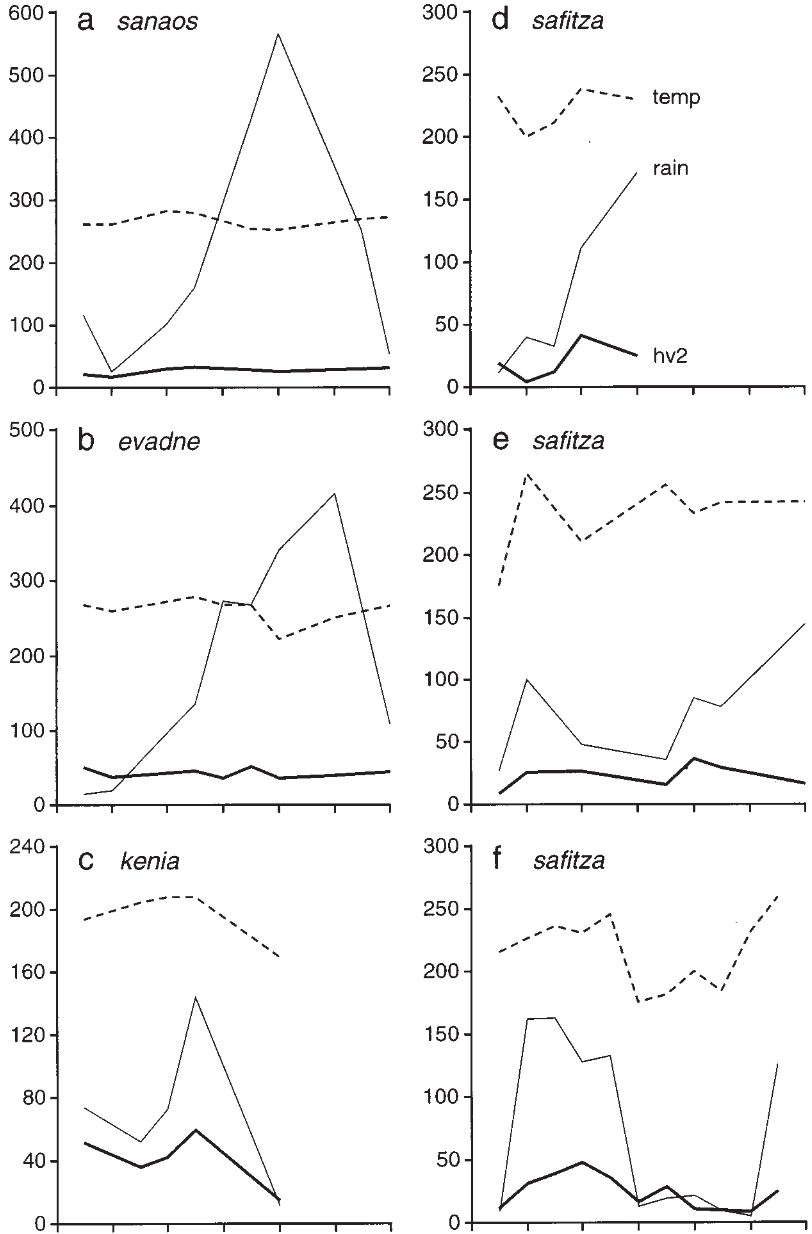

Figure 2. Representative patterns of phenotypic variation found in the field. All values are means for variables in the respective months. (a, d) areas with negative temperature-rainfall correlation; (b, e) ditto, no correlation; (c, f) ditto, positive correlation. X-axis, months of the year; y-axis, rainfall (mm), temperature (°C*10), diameter of eyespot hv2 (units of measurement).

collected in all habitat types. The effect of rainfall was significant in all habitat types for *B. funebris*, and *B. safitza* but was not so for *B. sebetus*. Rainfall reached significant values for a part only of the populations of *B. dorothea*, *B. smithi* and *B. vulgaris*.

Table 1. Multiple regression of eyespot ‘hv2’ diameter on temperature and rainfall. Species are partitioned in cohorts from positive (P), negative (N) and zero (Z) temperature-rainfall (t/r) correlation localities. If interaction term temp*rain was not significant (ns) at 95% confidence level, it was removed from further regression analysis for the respective species. *P*-values labelled with an asterisk (*) given for independent factors are significant at 95% confidence level after correction for improved Bonferroni (Hochberg, 1988; Rice, 1988; Simes, 1986). R-SQ, proportion of variation in eyespot size explained by temperature and rainfall. All species were present in the samples with dry season forms, excepted the ones labelled with a double asterisk (**). For explanation of row ‘total’, see text

Species	No. specimens			Temperature			Rainfall			temp*rain			R-SQ (adj.)		
	P	N	Z	P	N	Z	P	N	Z	P	N	Z	P	N	Z
angulosus (Butler)	26	14	–	0.50	0.07	–	0.00*	0.35	–	(0.73)	(0.38)	–	0.61	0.51	–
anynana (Butler)	53	–	–	0.00*	–	–	0.00*	–	–	0.00*	–	–	0.57	–	–
auricrudus (Butler)	–	13	45	–	0.07	0.00*	–	0.90	0.04*	–	(0.28)	(0.09)	–	0.35	0.27
buea (Strand)	–	–	27	–	–	0.76	–	–	0.06	–	–	(0.20)	–	–	0.07
campinus (Aurivillius)	49	–	19	0.66	–	0.64	0.00*	–	0.04*	0.01*	–	(0.91)	0.62	–	0.18
campus (Karsch)	–	13	7	–	0.00*	0.86	–	0.02*	0.81	–	(0.13)	(0.95)	–	0.94	0.00
condamini van Son	–	–	14	–	–	0.46	–	–	0.02*	–	–	(0.49)	–	–	0.29
cooksoni (Druce)	15	–	–	0.67	–	–	0.03*	–	–	(0.13)	–	–	0.65	–	–
cottrelli (van Son)	26	–	–	0.03*	–	–	0.00*	–	–	(0.93)	–	–	0.61	–	–
danckelmani (Rogenhofer)	19	–	–	0.22	–	–	0.00*	–	–	(0.71)	–	–	0.53	–	–
dentatus (Sharpe)	–	–	25	–	–	0.09	–	–	0.80	–	–	(0.65)	–	–	0.06
dorothea (Cramer)	11	24	56	0.71	0.14	0.44	0.36	0.00*	0.00*	(0.53)	(0.37)	(0.25)	0.00	0.80	0.21
dubius (Aurivillius) **	–	–	19	–	–	0.73	–	–	0.60	–	–	(0.27)	–	–	0.00
ena (Hewitson)	39	–		0.37	–	–	0.00*	–	–	0.04*	–	–	0.71	–	–
evadne (Cramer) **	–	–	21	–	–	0.00*	–	–	0.30	–	–	(0.10)	–	–	0.35
funebris (Guérin–Méneville)	8	25	23	0.46	0.07	0.18	0.01*	0.00*	0.00*	(0.16)	(0.17)	(0.96)	0.80	0.61	0.55
golo (Aurivillius)	–	14	13	–	0.00*	0.21	–	0.01*	0.04*	–	0.01*	(0.88)	–	0.85	0.37
graueri (Rebel)	–	20	18	–	0.35	0.75	–	0.02*	0.00*	–	(0.27)	(0.50)	–	0.20	0.45
hewitsoni (Doumet)	–	–	25	–	–	0.13	–	–	0.01*	–	–	0.01*	–	–	0.54
iccius (Hewitson)	–	10	–	–	0.01*	–	–	0.00*	–	–	(0.70)	–	–	0.70	–
ignobilis (Butler)	–	–	37	–	–	0.95	–	–	0.36	–	–	(0.47)	–	–	0.00
istaris (Plötz)	–	–	11	–	–	0.40	–	–	0.18	–	–	(0.69)	–	–	0.20
italus (Hewitson)	–	–	18	–	–	0.18	–	–	0.04*	–	–	(0.42)	–	–	0.21
jeffereyi Fox	–	–	19	–	–	0.44	–	–	0.03*	–	–	(0.08)	–	–	0.38
kenia (Rogenhofer)	22	–	–	0.02*	–	–	0.01*	–	–	(0.41)	–	–	0.57	–	–
mandanes (Hewitson)	–	14	40	–	0.09	0.76	–	0.01*	0.00*	–	(0.67)	(0.52)	–	0.37	0.17
matuta (Karsch)	–	–	17	–	–	0.72	–	–	0.12	–	–	(0.69)	–	–	0.27
medontias (Hewitson)	–	–	12	–	–	0.00*	–	–	0.00*	–	–	0.00*	–	–	0.73
mesogenus (Karsch)	–	–	27	–	–	0.38	–	–	0.00*	–	–	(0.60)	–	–	0.76

continued

TABLE 1. *continued*

Species	No. specimens			Temperature			Rainfall			temp*rain			R-SQ (adj.)		
	P	N	Z	P	N	Z	P	N	Z	P	N	Z	P	N	Z
milyas (Hewitson)	–	25	–	–	0.14	–	–	0.02*	–	–	0.05*	–	–	0.52	–
mollitia (Karsch)	–	16	22	–	0.90	0.01*	–	0.01*	0.01*	–	(0.05)	–	–	0.37	0.38
procorus (Karsch)	–	13	–	–	0.01*	–	–	0.02*	–	–	0.05*	–	–	0.81	–
safitza (Hewitson)	55	13	20	0.42	0.08	0.01*	0.00*	0.02*	0.00*	(0.34)	0.02*	(0.66)	0.55	0.82	0.67
sambulos (Hewitson)	–	14	29	–	0.02*	0.00*	–	0.03	0.02*	–	0.02*	(0.40)	–	0.81	0.69
sanaos (Hewitson)	–	21	–	–	0.01*	–	–	0.01*	–	–	(0.15)	–	–	0.27	–
sandace (Hewitson)	–	17	22	–	0.34	0.00*	–	0.12	0.00*	–	(0.56)	(0.14)	–	0.16	0.69
saussurei (Dewitz)	–	–	11	–	–	0.11	–	–	0.28	–	–	(0.99)	–	0.00	0.15
sebetus (Hewitson)	13	13	17	0.61	0.95	0.11	0.34	0.38	0.24	(0.37)	(0.42)	(0.91)	0.00	0.00	0.30
simulacris Kielland	18	–	7	0.90	–	0.06	0.00*	–	0.00*	(0.77)	–	(0.37)	0.42	–	0.87
smithi (Aurivillius)	24	34	10	0.00*	0.48	0.52	0.00*	0.82	0.04*	0.00*	(0.27)	(0.08)	0.58	0.00	0.24
sophrosyne (Plötz)	–	15	10	–	0.01*	0.26	–	0.01*	0.03*	–	0.01*	(0.60)	–	0.88	0.48
uniformis (Bethune-Baker)	–	13	7	–	0.00*	0.48	–	0.00*	0.79	–	0.00*	(0.37)	–	0.82	0.00
vansoni Condamin	37	–	–	0.03*	–	–	0.02*	–	–	(0.50)	–	–	0.42	–	–
vulgaris (Butler)	16	17	31	0.63	0.43	0.04*	0.00*	0.24	0.00*	(0.25)	(0.29)	(0.96)	0.82	0.00	0.45
xeneas (Hewitson) **	–	17	–	–	0.07	–	–	0.32	–	–	(0.39)	–	–	0.16	–
xeneoides Condamin **		19	–	–	0.68	–	–	0.20	–	–	(0.87)	–	–	0.00	–
Total				0.31	0.38	0.23	0.88	0.58	0.68	0.25	0.25	0.07			

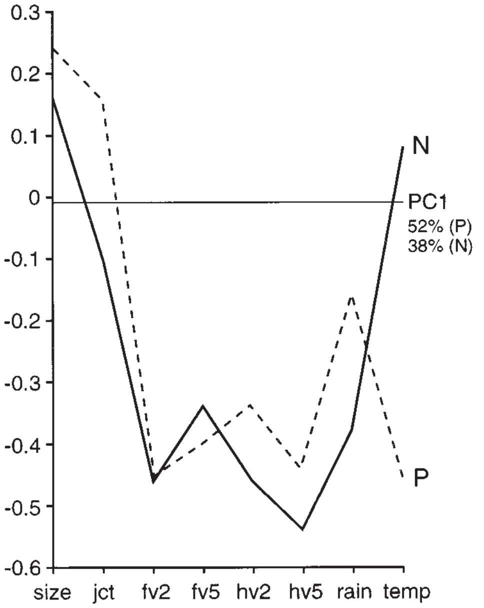

Figure 3. Comparison between transformation vectors of two PCAs for cohorts with significant positive (P) and negative (N) temperature/rainfall correlations. Projection of transformation vectors for six plastic wing characters, temperature and rainfall along pc-axis 1, with 52% loading for the P-cohort and 38% loading for the negative cohort.

Multivariate patterns in opposite t/r correlation areas

A comparison between PCAs for the P- and N-cohorts, respectively, is presented in Figure 3. The transformation vectors for temperature and rainfall have for the P-cohort, as for such vectors for the eyespots, a high loading along pc-axis 1. For the N-cohort, however, the transformation vector for rainfall still covaries with the vectors for the eyespots, but the vector for temperature has a negative loading and does not covary with any other characters.

We ran a further PCA over all 91 specimens (the cohorts P and N together) excluding temperature and rainfall. In this PCA all four eyespot diameters had high loadings along pc-axis 1, whereas variation in wing size and the band character 'jct' spanned pc-axis 2. Figure 4 presents a plot of the 95% confidence ellipses of the scores on pc-axis 1 against temperature. The dependence on temperature is obvious for cohort P, whereas this is absent in cohort N.

DISCUSSION AND CONCLUSIONS

Seasonal polyphenism in *Bicyclus* butterflies is well known in species inhabiting African savannah habitats (Condamin, 1973). However, we also found wide variation in eyespot diameter in many species known from rainforests without substantial seasonal variation. Furthermore, species occurring in mountain areas often have reduced eyespots reminiscent of dry season forms. Hence, wing pattern plasticity is common in most species of *Bicyclus*.

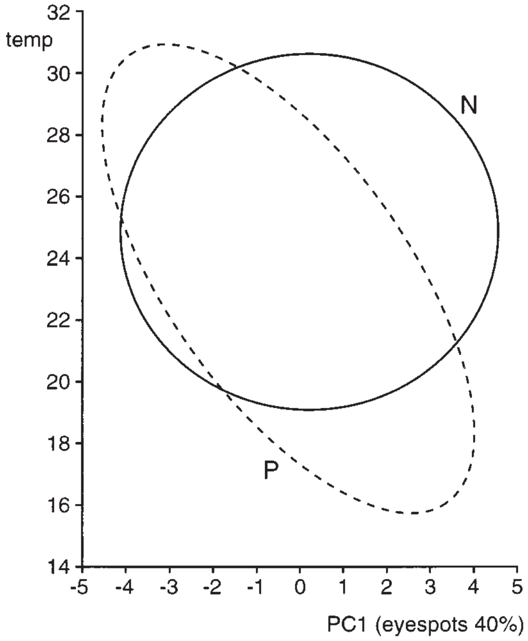

Figure 4. Comparison between scores of specimens belonging to the P- and N-cohorts, pooled in a single PCA for their six plastic wing characters. Plot of 95% confidence envelopes of scores on pc-axis 1 against temperature (°C) along pc-axis 1 (40% loading, with eyespot variation as main component).

Brakefield and Larsen (1984) and Braby (1994) reported seasonal polyphenism in *Mycalesis*, a satyrine genus close to *Bicyclus*, but occurring in the Far East through to Australia. Seasonal polyphenism is also reported in more distant groups of satyrines, especially *Melanitis* (Brakefield & Larsen, 1984; Brakefield, 1987). This means that seasonal polyphenism in Satyridae may be a phylogenetically old trait. The common ability in *Bicyclus*, but also in phylogenetically close African *Henotesia* (Condamin, 1973) to generate seasonal forms may be a vestige from adaptations to late quarternary paleoenvironments. Savannah habitats were much more common than rainforests 28 000–9000 yr BP (Maley, 1991). Under present conditions savannahs are more prone to rainfall fluctuation than rainforests. If we can extrapolate from the present day to late quarternary situations, seasonality might have been very common during that era and seasonal polyphenism might have been the dominant situation.

In general, seasonal habitats north of the equator differ from those at southern latitudes in their temperature/rainfall correlations. At southern latitudes a decline in temperature predicts the onset of the dry season and induces the formation of small eyespots in dry season butterflies. Phenotypic plasticity, however, also occurs in populations occurring in northern habitats. In summary, our multivatiate analysis found that high values for both rainfall and temperature are correlated with, and may induce high scores for eyespot diameter at localities with positive temperature/rainfall correlation, but only high values for rainfall can do so at localities with negative t/r correlation. A change in temperature can predict a response of the butterfly wing pattern, but only in populations inhabiting localities southern of the equator. In northern localities, rainfall or covarying factors other than temperature must account for any seasonal polyphenism. The yearly amplitude in temperature, moreover, is smaller in northern than in southern *Bicyclus* areas (Fig. 4) and can, also for that reason, only be a less reliable predictor. It is remarkable that conspecific populations of species of *Bicyclus* may react differently to climatic variables depending on the latitude of the area in which they occur. Hence, genetically close populations are able to respond differently to seasonal change in different habitats. This is reminiscent of other seasonal adaptations such as diapause: conspecific populations may also react differently to cues which trigger diapause, depending on their geographic situation (Tauber *et al.*, 1986). Table 1 illustrates best the impact of temperature and rainfall on wing pattern in *Bicyclus*. If t/r correlations exist a large percentage (R-SQ) of the variation in eyespot pattern is explained in many cases; rainfall alone is then most often responsible (row 'total'), even in areas where t/r are positively correlated.

It is gratifying that data obtained from often small samples present in the museum collections, where substantial noise is expected due to incomplete data on collection dates and altitude, and poor matching of collection sites to usually distant weather stations, were able to illuminate the overall effects of climate and habitat characteristics. This means that these effects will be very strong if we are able to study them in more detail. Experimental research, however, is critical for a further detailed examination of hypotheses concerning cues which may induce seasonal polyphenism in different regions, and to describe precisely how conspecific populations in different climatic regimes have adapted. The development time during the fourth and fifth larval stages may be a good candidate: development time will certainly depend on availability and quality of host plants, grasses, during the transition between wet and dry seasons (Kooi *et al.*, 1996). It will also be interesting to apply artificial selection on the sensitivity to environmental cues within a species such as *B. anynana* to examine genetic variation for the ability to respond to changing climate regimes.

ACKNOWLEDGEMENTS

For the loan of specimens in their care we thank the Zoologische Staatssammlung (Munich) and the Natural History Museum (London). Dr E. Meelis explained the intricacy of Bonferroni adjustments and Mr M. Brittijn kindly prepared the figures. Two anonymous referees are acknowledged for their comments on an earlier draft of this paper.

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