

CLIMATIC FACTORS AFFECTING THE ACTIVITY OF NATTERJACKS (*BUFO CALAMITA*) AND COMMON TOADS (*BUFO BUFO*) OUTSIDE THE BREEDING SEASON: MATHIAS REVISITED

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A multivariate analysis was performed on a set of data which contained records on the capture rates outside the breeding season, under varying environmental conditions of the two native British toads, *Bufo bufo* and *Bufo calamita*. The data were taken from a study by Mathias (1971). Although statistical relationships within the data set were generally weak, results of the analysis suggest that activity outside the breeding season of *Bufo bufo* showed the stronger dependence on the recorded environmental parameters. In particular, a striking correlation was found to exist between capture rates of *Bufo bufo* and temperatures recorded at 30 cm below ground earlier the same day.

INTRODUCTION

Relatively few studies on European amphibians have concentrated on their activity outside the breeding season. Any study which attempts to assess the effects of the environment during this terrestrial phase is likely to face great difficulty in obtaining adequate data from the field. Apart from the problem of actually finding individuals in the first place, there is the obstacle of adequately taking into account the extremely variable nature of most terrestrial environments. This is particularly true where continually changing parameters such as climatic conditions are also to be included in the assessment. In this context, previous studies which include environmental parameters have largely tended to focus on the influence of habitat as opposed to that of climate (Strijbosch, 1980; Beebee, 1985; Pavignano, Giacomini & Castellano, 1990). It is nevertheless clear that the effect of climate is of great importance in determining amphibian activity and so must be taken into account if knowledge of terrestrial amphibian ecology is to be improved. This was clearly indicated in a recent study on natterjack activity during the terrestrial phase in which greater than 81% of the variance in sightings at a particular site could be accounted for simply by using multilinear regression of temperature and rainfall readings (Denton & Beebee, 1992).

In fact, before the above recent study took place, a similar one was performed as part of a thesis by Mathias (1971) although no multivariate analysis of the data collected was carried out then. This classic comparative amphibian study of common toads, *Bufo bufo* and natterjack toads *Bufo calamita*, actually contains several data sets collected over a three year period. The data, which are generally both meticulous and extensive, were collected in one of the few British natural habitats where both species are to be found in coexist-

ence. The study location, situated on the Merseyside coast, is today one of only a few remaining areas where the natterjack toad is still to be found in reasonable abundance within Britain (Beebee, 1983). Results of a multivariate analysis on the data set relating to the above-mentioned Mathias study are now presented for the first time. The objective of this analysis was primarily to test for the possible existence of a relationship between individual toad movements and climatic conditions, outside the breeding season.

METHODS

DATA COLLECTION

Mathias assessed toad movements by carrying out night observations at two study sites termed the North and South site, respectively. Observations were carried out at night because this was found to be the most effective time at which to locate toads. Denton & Beebee (1992) also found night searching to be the best time for finding adults of both species outside the breeding season.

Regular night field trips to the sites were carried out by Mathias for the entire duration of the active part of the annual life cycle of each species during the period April 1968 to June 1970. The 'sampling method', by which the degree of toad night activity was assessed, consisted simply of noting the total number of captures made of each species on a predefined route within the field trip. After capture, each toad was marked and then released at the same point where it was caught. In addition to capture numbers, the values of ten environmental variables were obtained for the locality (Southport) for every field trip (Mathias 1971: Table 3.14, p. 204). Efforts were continually made to ensure that possible sampling bias, such as variation of route within the field trip, were kept to a minimum.

	North Site (19 trips)			South Site (20 trips)			Both Sites (39 trips)		
	Bb	Bc	total	Bb	Bc	total	Bb	Bc	total
No. of captures	9	226	235	204	159	363	213	385	598
less: recaptures	(1)	(26)	(27)	(30)	(38)	(68)	(31)	(64)	(95)
= individuals captured	8	200	208	174	121	295	182	321	503
% of total captures	2	38	40	34	26	60	36	64	100
Recapture rate %	11	12	11	15	24	19	15	17	16

TABLE 1. Summary of captures and recaptures occurring in the extracted non-breeding data set, 1968-1970. Bb - *Bufo bufo*, Bc - *Bufo calamita*.

The field sites were located at opposite ends of a nature reserve, approximately 3 km apart, and each was a few thousand square metres in area. They were selected so as to be representative of two different types of dune habitat. The North site was more exposed to wind and had little tree cover whereas the South site was less exposed because of protection afforded by the close proximity of nearby woodland. The data collected for field trips made outside of the breeding seasons of each species (39 out of a total of 55 trips) are referred to as 'non-breeding' data. It is this data set which has been extracted for analysis.

A summary of the total number of captures of each species recorded at each site, for the 39 extracted field trips is shown in Table 1. Mathias did not record the number of *individuals* captured on each trip but did, however, record those individuals that were captured more than once. This additional information enables recaptures to be individually identified and then subtracted from the captures presented in his Table 3.14., so that the total number of individuals included within the extracted data set can also be deduced. Since the recapture rate turned out to be low (16%), the number of captures (598) reasonably equates with the number of individuals that were captured (503). Either of these latter two parameters could therefore be taken as a measure of general toad movements, with negligible difference to analytic results. Capture numbers per field trip were selected as these were already presented in Table 3.14, thereby avoiding any further need for reconciliation. The respective capture variable is denoted by the following abbreviation for each species: *Bbcaught* - number of common toad (*Bufo bufo*) captures on a night field trip; and *Bccaught* - number of natterjack toad (*Bufo calamita*) captures on a night field trip.

DATA ANALYSIS

Data were analysed for dependence of capture rates on climatic conditions and also for interdependence. Abbreviations and respective definitions of each of the

ten environmental variables recorded, the lower eight (i.e. *maxtemp* down to *windspeed*) of which can be classed as strictly climatic, are: *date* - day of year (numbered 1 to 365); *site* - capture locality, North Site or South Site (numbered 1 and 2, respectively); *maxtemp* - maximum recorded day temperature; *mintemp* - minimum recorded day temperature; *grasstemp* - temperature recorded in grass (time of day not recorded); *g30temp* - temperature 30 cm below ground at 09.00 hr; *rainfall* - rainfall recorded (1/100 in); *sunshine* - sunshine recorded (1/10 hr); *winddir* - mean recorded wind direction (degrees); and *windspeed* - mean recorded wind speed (knots).

All of the above climatic recordings were made on the day prior to the night field trip. The curious variable *grasstemp* is, unfortunately, also vague since no information was given on either how or at what time of day temperature recordings in grass were made.

It can be seen from Table 1 that very few common toad captures were made at the North Site (% of total captures: 2% North, 34% South) whereas the natterjack toad captures were more evenly distributed between each site (% of total captures: 38% North, 26% South). Discriminant analysis of data collected for the field trips on the basis of *site* was therefore, unsurprisingly, found to be highly significant (null hypothesis rejected at $P = 0.001$). Hence data were also categorised as 'North Site' and 'South Site' according to the site visited in all of the subsequent analysis.

The possible interdependence between variables was investigated in two parts. Firstly, a correlation analysis was performed to generally identify the stronger and weaker relationships between all variables. Secondly, any interdependence between the eight climatic variables themselves was analysed by a principal component analysis, to assess whether the broad effects of climate could be more concisely described in terms of a few key factors.

Following the encouraging multilinear regression results obtained by Denton & Beebe (1992) between natterjack sightings vs. climatic readings, the depend-

ence of capture rates on recorded climatic conditions was assessed by a similar regression analysis on the Mathias captures of each species vs. recorded climatic data. For all of the defined data categories, *Bbcaught* and *Bccaught* were each taken as the dependent variable within the regression, initially with all climatic variables included as independent variables. A stepwise sequential selection procedure was then used to identify the key named climatic variables behind the relationships within these regressions. This technique calculates an 'optimal subset' of variables to describe any dependence, using the criterion of maximization of the R^2 -adjusted value, out of the variables defined in the original regression model (e.g. see Draper & Smith 1981). Principal component analysis would also have served to achieve a reduction in the number of variables here, but a meaningful interpretation of the main components would have been difficult.

RESULTS

CORRELATION ANALYSIS

When data for both sites were analysed collectively, the strongest general correlations were found, unsurprisingly, between the temperature-dependent climatic variables such as, for example, *g30temp* vs. *maxtemp* ($r = 0.70$, $P = 0.0001$). For some unknown reason, perhaps related to the way in which grass temperature recordings were made, the mysterious variable *grasstemp* correlated strongly with *mintemp* ($r = 0.89$, $P = 0.0001$).

The correlations of *Bbcaught* or *Bccaught* with all environmental variables, for the collective data are shown in columns 1 and 3 of Table 2. Toad captures in general can be seen to show significant correlations ($P < 0.05$) with only two climatic variables, namely *g30temp* for the common toad ($r = 0.43$, $P = 0.01$) and *maxtemp* for the natterjack ($r = 0.35$, $P = 0.03$). The number of common toad captures *Bbcaught* showed greatest correlation with *site* ($r = 0.66$, $P = 0.0001$) mainly as a result of the great disparity of capture numbers of this species with respect to the two study sites.

Table 2 also shows the correlations of *Bbcaught* or *Bccaught* with environmental variables for the separate data sets North Site and South Site. For these localized data sets, captures now showed significant correlations with a total of four climatic variables, namely *maxtemp*, *sunshine*, *g30temp* and *mintemp*. Common toad captures correlated significantly with all of these variables in turn, at one or other of the sites, but natterjack captures still only correlated significantly with *maxtemp*, at the North Site.

For the North Site, common toad captures were found to correlate significantly with *maxtemp* ($r = 0.50$, $P = 0.03$), and *sunshine* ($r = 0.48$, $P = 0.04$). No inference can be made from this though, since the actual number of common toad captures at this site were too few. For the same reason, no real significance can be attached to the apparently significant correlation between captures of the two species themselves, *Bbcaught* vs. *Bccaught* ($r = 0.60$, $P = 0.007$). However,

	Both Sites <i>n</i> = 39				North Site <i>n</i> = 19				South Site <i>n</i> = 20			
	<i>Bbcaught</i>		<i>Bccaught</i>		<i>Bbcaught</i>		<i>Bccaught</i>		<i>Bbcaught</i>		<i>Bccaught</i>	
	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>
<i>Bbcaught</i>	*	*	0.03	NS	*	*	0.60	0.00	*	*	0.30	NS
<i>Bccaught</i>	0.03	NS	*	*	0.60	0.00	*	*	0.30	NS	*	*
<i>site</i>	0.66	0.00	-0.18	NS	*	*	*	*	*	*	*	*
<i>date</i>	-0.20	NS	-0.12	NS	-0.36	NS	-0.26	NS	-0.40	NS	0.10	NS
<i>maxtemp</i>	0.29	NS	0.35	0.03	0.50	0.03	0.53	0.02	0.52	0.02	0.11	NS
<i>mintemp</i>	0.19	NS	-0.12	NS	-0.18	NS	-0.23	NS	0.46	0.04	0.00	NS
<i>grasstemp</i>	0.14	NS	-0.12	NS	-0.20	NS	-0.23	NS	0.32	NS	0.04	NS
<i>g30temp</i>	0.43	0.01	0.06	NS	0.28	NS	0.12	NS	0.77	0.00	-0.04	NS
<i>rainfall</i>	-0.15	NS	0.14	NS	0.08	NS	0.10	NS	-0.21	NS	0.19	NS
<i>sunshine</i>	0.19	NS	0.09	NS	0.48	0.04	0.17	NS	0.53	0.02	-0.13	NS
<i>winddir</i>	0.08	NS	-0.18	NS	-0.02	NS	-0.16	NS	0.21	NS	-0.26	NS
<i>windspeed</i>	-0.20	NS	-0.13	NS	-0.07	NS	-0.03	NS	-0.17	NS	-0.42	NS

TABLE 2. Correlations of the number of toad captures outside of the breeding season with recorded environmental variables, 1968 to 1970. NS not significant, ($P > 0.05$).

Climatic variable	PC1	PC2	PC3
<i>maxtemp</i>	-0.43	-0.40	-0.10
<i>mintemp</i>	-0.51	0.37	-0.08
<i>grasstep</i>	-0.43	0.45	-0.01
<i>g30temp</i>	-0.55	-0.20	-0.03
<i>rainfall</i>	-0.03	0.41	-0.06
<i>sunshine</i>	-0.23	-0.51	0.35
<i>winddir</i>	-0.10	0.15	0.67
<i>windspeed</i>	-0.01	0.14	0.64
Eigenvalue	2.51	2.02	1.56
%Explained variance	32	25	19
%Cumulative variance	31	57	76

TABLE 3. Weightings of first three principal components (PC) in principal component analysis of climatic variables ($n = 39$).

for the natterjack captures at this site, which were numerous, the significant correlation found with *maxtemp* was therefore also important ($r = 0.53$, $P = 0.02$).

For the South Site, stronger correlations between toad captures vs. environmental variables were found to exist. Since the capture numbers at this site were more evenly distributed between the two species, these data are more likely to demonstrate any comparative differences in the behaviour of each species. Common toad captures were again found to show stronger and more numerous correlations. Significant correlations for this species were with: *g30temp* ($r = 0.77$, $P = 0.0001$), *maxtemp* ($r = 0.52$, $P = 0.02$), *sunshine* ($r = 0.53$, $P = 0.02$), and *mintemp* ($r = 0.46$, $P = 0.04$). The number of

natterjack captures showed no significant correlations at $P < 0.05$ although a noteworthy negative correlation was seen with *windspeed* ($r = -0.42$, $P = 0.07$).

PRINCIPAL COMPONENT ANALYSIS OF CLIMATIC VARIABLES

Table 3 shows the weightings for the first three principal components obtained from a principal component analysis in which all the climatic data was utilised ($n = 39$). These three components accounted for 76% of the variance in the climatic data (by Kaiser's criterion the other five principal components may be discarded since their eigenvalues are less than 1). There was no significant difference between the average climatic conditions recorded for the visits to each site. The weightings for component 1 are dominated by all of the temperature variables *maxtemp*, *mintemp*, *grasstep*, and *g30temp*. This component therefore strongly reflects 'temperature'. Component 2 is more difficult to interpret, but the opposite sign of the variable pairs *maxtemp* and *mintemp*, *grasstep* and *g30temp*, and *rainfall* and *sunshine* suggests that this component may be loosely described as 'contrast between hot and cold'. Component 3 largely reflects 'wind' because of the heavy weightings with *winddir* and *windspeed*. Thus overall, the recorded climate can be roughly described in terms of the three key factors, temperature, contrast between hot and cold, and wind. Component 1 also further demonstrates the existence of interdependence between the temperature variables, observed in the correlation analysis.

REGRESSION ANALYSIS

It was found, as in the correlation analysis, that common toad captures showed the stronger relationship with the recorded environmental conditions. This

Dependent variable	Both Sites $n = 39$		North Site $n = 19$		South Site $n = 20$	
	<i>Bbcaught</i>	<i>Bccaught</i>	<i>Bbcaught</i>	<i>Bccaught</i>	<i>Bbcaught</i>	<i>Bccaught</i>
Independent variables						
All 8 climatic variables	8	9	2	3	38	0
Optimal subset*	16	16	23	27	56	17
*Optimal subsets of climatic variables in descending order significance	<i>g30temp</i>	<i>grasstep</i> <i>mintemp</i> <i>maxtemp</i> <i>sunshine</i> <i>rainfall</i>	<i>sunshine</i> <i>maxtemp</i>	<i>maxtemp</i> <i>mintemp</i> <i>sunshine</i> <i>grasstep</i>	<i>g30temp</i>	<i>windspeed</i> <i>rainfall</i>

TABLE 4. Comparison of R^2 -adjusted values (in %) obtained in linear regressions using climatic variables.

was most clearly seen in the regressions performed on the South Site data, by the value of the R^2 -adjusted multiple regression coefficient. The coefficient gives a measure of the extent of the variance in the number of captures which can be explained by the regression, simultaneously taking into account the number of variables used (hence the term 'adjusted'). This adjustment for the number of variables used is an important one, since the R^2 value alone will always "artificially" increase with an inclusion of more variables, in any regression model. Clearly then, the R^2 -adjusted value will always be more appropriate for making comparisons between any regression models which have different numbers of variables, such as those that we shall now come across.

Table 4 compares the R^2 -adjusted values found for regressions performed with the inclusion of all climatic variables against the respective figure found for regressions with the optimal set. Whereas the R^2 -adjusted value was improved in each data category by a reduction to the optimal set, the values for the South Site common toad captures are markedly better than for captures in any other category. This particular optimal variable set, which turned out only to contain the single variable *g30temp*, gave the highest R^2 -adjusted value out of all the regressions, at 56%. Thus, it turns out that the majority of the variance in common toad captures can be accounted for solely in terms of the temperature readings made at 30 cm below ground earlier in the same day as the field trip. It would be dangerous to attach too much importance to the other named sets of optimal variables since the respective R^2 -adjusted values are much too low.

DISCUSSION

The multivariate analysis demonstrates the existence of some, hitherto unnoticed, correlations within the non-breeding data. These correlations of capture numbers *vs.* recorded environmental conditions, were found to be more significant for the common toad. For this species, it was also possible to obtain a 'best fit' multilinear regression model to the data which gave a 56% R^2 -adjusted value for the South Site captures. In the case of the natterjack toad, the respective best fit only gave a 27% R^2 -adjusted value for captures, this time from the North Site. The extent to which these best fit models differ between the two species is one of the most interesting comparative aspects uncovered by this analysis.

What do the actual significant correlations between capture numbers *vs.* recorded environmental variables imply? These observed correlations only serve to *suggest* possible causes of true underlying relationships. It must be remembered that any statistical relationship, no matter how strong, can never establish causal connection. For the common toad, the extent of significant correlation with temperature-dependent variables was clear. It was apparent that the observed movement of individuals, presumably for foraging and so on, in-

creased detectably with higher temperatures. In particular, the striking correlations with recorded ground temperatures suggest that temperature below ground has a great influence in determining its night activity. The fact that interdependence existed between all of the recorded temperature variables, further accentuates the significance of the observed relationship with the *g30temp* variable alone. Are common toads, therefore, particularly sensitive to subterranean temperatures?

Why are such strong relationships absent for the natterjack toad? Could the absence of correlation with ground temperature for this species perhaps be associated with the greater depth below ground of the preferred abode, namely that of burrows in sand dunes? Or alternatively, does this absence of correlation suggest an intrinsic difference between the two species in behavioural response to either ground temperature or some other related factor?

Captures of natterjacks were only found to correlate significantly with recorded maximum temperatures. For a poikilothermic animal, such a correlation is of course, not that surprising. However, the nearly significant negative correlation observed between South Site natterjack captures and wind speed, completely absent for common toad captures made at the same site, supports the premise made by Mathias that natterjacks are more susceptible to dehydration by exposure to the wind (p. 150). It is curious then, that no support to this premise is to be found in the larger number of natterjack captures made at the more exposed North Site. How much of this discrepancy can be attributed to the actual place of capture within the site itself? A natural extension to the current analysis would be to define two new variables which combine the variables *windspeed* and *winddir*, in terms of two vector components. This would then both eliminate the awkward and discontinuous *winddir* variable and at the same time also enhance interpretation of the overall influence of the wind on captures of both species. (The variable *winddir* contributes little useful information in most statistical calculations because of a discontinuity in the scale of measurement. For example, wind directions of 2° and 359° are virtually the same but would be assigned misleadingly different calculative values.)

Further inferences beyond this are not possible, because of the lack of detail in the climatic records. These records serve only as a rough guide to prevailing conditions since they were not actually obtained at the exact time (night) or place (study site) of the field trip in question. This is a frequently encountered limitation in studies of this type (Andren & Nilson, 1985; Iverson, 1992). Even so, the recorded local conditions must still have had a strong bearing on the night 'micro-climate' of the site visited. In this respect, the correlations with ground temperature are potentially more significant because temperatures below ground are usually subject to much less daily variation, depending on the soil type and its moisture content (e.g. van Wijk & de Vries, 1963). Data on both of these unrecorded soil param-

eters would also have served to clarify the importance of the observed absence of any significant correlation of natterjack captures with *g30temp*. It is therefore a pity that no such precise information is available in respect of the soil in which the *g30temp* readings were actually recorded. Clearly, there is still scope for future practical research into this important point.

It must be stressed that only the possible existence of linear relationships is addressed in this kind of a statistical analysis. In nature, most things are not linear. Thus, it is quite possible that significant nonlinear relationships still remain hidden so that, for example, a multivariate loglinear regression analysis may help to reveal these. The comparative lack of correlation of natterjack captures with environmental variables is nevertheless surprising, especially given that a greater proportion of this species were captured (64% total captures). Also surprising for its absence, is the lack of support to the frequently held contention that 'rain brings out toads'. Denton & Beebee (1992) found in their study that natterjack sightings generally correlated with rainfall ($r = 0.6$, $P < 0.01$). Mathias commented on the absence of such anticipated correlations but then went on, overhastily, to conclude that (p. 171) 'there is no apparent correlation between the numbers of animals caught per trip and the temperature, rainfall, and wind speed recordings'. The data obtained in this unique past study may shed still greater future light on the individual movement behaviour of the two native British toads.

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