Psyche

Abiotic Factors and Insect Abundance

Guest Editors: Matilda Savopoulou-Soultani, Nikos T. Papadopoulos, Panagiotis Milonas, and Pascal Moyal

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Hindawi Publishing Corporation
Psyche
Volume 2012, Article ID 167420, 2 pages
doi:10.1155/2012/167420

Editorial

Abiotic Factors and Insect Abundance

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Received 10 December 2012; Accepted 10 December 2012

Insect abundance and distribution are regulated by several biotic and abiotic factors and their interactions. Survival and thriving at extreme physical conditions require peculiar adaptations and plastic responses. Among abiotic factors, temperature and humidity stand out as the most important ones constraining abundance and distribution of insect. Furthermore, it is well documented that abiotic factors, especially temperature, regulate the ecology of insect communities.

The current issue explores part of the effects of abiotic factors on insect abundance and provides remarkable insights on the influence and the direction of the impact that abiotic factors have on insect populations. There is a great diversity of studies included that goes across several insect taxa and ecosystems reflecting the magnitude of the effects of the physical environment on insect populations.

Although effects of temperature on survival, development, and reproduction of insects have been exhaustively explored over several decades, there is still a lot of interest on how temperature and other abiotic factors set the limits of distribution and define abundance of insect species. The present special issue includes two studies reporting on the influence of temperature on species specific population dynamics and phenology. In their study regarding the impact of climatic factors on population dynamics of *Diaphania pulverulentalis*, a devastating leafroller for mulberry, V. K. Rahmathulla and colleagues demonstrate that the interaction of low temperatures with increased rainfall and subsequent humidity is correlated with increased infestation levels. Additionally, C. P. Bonsignore studied the effect of temperature on the phenology of the buprestid beetle *Capnodis tenebrionis* that poses a serious threat especially to organic cultivation of various *Prunus* species and develops a temperature driven model that explains the activity of *C. tenebrionis* in the field. Both studies provide important tools for understanding seasonal population dynamics and making pest management decisions.

There are two more studies that explore the influence of temperature on the development and survival of insects on marginal environmental conditions. E. Müller and E. Obermaier examined the effect of daily exposure to temperatures above the developmental threshold on *Galeruca tanaceti*. Average temperatures close to or below the developmental threshold retard development and in many cases increase mortality. Nevertheless, E. Müller and E. Obermaier showed that larvae of *G. tanaceti* are capable of exploiting the daily increase of temperature in early spring above the developmental threshold and exhibit increased developmental rates and survival. This enables them to take advantage of the nutritional rich food that is only available at that time ensuring the completion of development and successful pupation. On the other hand E. Penarrubia-Maria and colleagues explore the persistence of the Mediterranean fruit fly (medfly), *Ceratitis capitata*, in north-east (NE) Spain, in an area lying within the northern limits of its distribution. The study focuses on adult survival during the winter and demonstrates that both males and females were unable to withstand the freezing temperatures of the area and, therefore, to overwinter in NE Spain.

Modelling effects of temperature on insect development is another thoroughly explored and longstanding topic in insect biology. In this issue, P. Damos and M. Savopoulou-Soultani present an extended review on temperature-driven models for insect development, describing the strengths and weakness of the most commonly used ones. In recent years, there is an increasing emphasis on modelling that based on sophisticated software tools allows projections and predictions of potential distributions for insect species based on climatic suitability. The ecoclimatic matching model CLIMEX seems to be the most commonly used tool over the last few years. Olfert and colleagues using CLIMEX provide interesting data regarding the potential distribution of the invasive species *Sitona lineatus* in North America.

Abiotic factors, as it is pointed out above, regulate insect communities and are connected with several physiological and other peculiar adaptations and plastic responses. U. Irmler studied the Staphylinidae fauna in six different habitats of the Baltic Sea coast of Schleswig-Holstein (northern Germany). Vegetation and soil moisture were the most important factors affecting species composition. Results showed that such studies provide an important tool to assess the impact of anthropogenic activities on ecosystems. Accordingly, the abundance of selected species could be used as a bioindicator to monitor pollution in tropical freshwater ponds, as shown by A. Pal and colleagues. Another study by C. J. Bidau and colleagues reported on the influence of latitude and altitude on the body size in two grasshopper species. The contribution of arboreal ants in relation to the surrounding habitat to soil fertility was examined in tropical-derived savannah ecosystems by B. C. Echezona and colleagues.

Finally, M. Eizaquirre and A. A. Fantinou reviewed dormancy responses and voltinism of *Sesamia nonagrioides* in the Mediterranean region. Facultative diapause in response to daylength has been reported in populations of the cooler Mediterranean areas; however, no such response (diapause) is reported in African populations. Voltinism depends on diapause termination, while early emergence allows the accumulation of heat units before the prevailance of the critical photoperiod for diapause induction.

Overall the current special issue contains a diverse number of papers (both original research and review papers) that contribute towards a better understanding of the effects the "abiotic factors" have on "insect abundance" and it definitely adds an asset to the growing literature on the specific subject.

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Hindawi Publishing Corporation
Psyche
Volume 2012, Article ID 186214, 6 pages
doi:10.1155/2012/186214

Research Article

Association of Climatic Factors on Population Dynamics of Leaf Roller, *Diaphania pulverulentalis* Hampson (Lepidoptera: Pyralidae) in Mulberry Plantations of Sericulture Seed Farm

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Received 6 October 2011; Revised 27 November 2011; Accepted 30 November 2011

Academic Editor: Matilda Savopoulou-Soultani

The production of quality mulberry leaf and subsequent production of quality silk is hampered due to the incidence of various insect pests. The present study analyses the population dynamics of *Diaphania pulverulentalis* (leaf roller), a serious pest of mulberry in a sericulture seed farm. The results indicated that maximum population buildup of the pest was recorded during rainy season. High humidity coinciding with low temperature because of southwest and northeast monsoon was conducive for breeding and multiplication of the pest. Correlation studies revealed that there was a significant negative correlation between increase in temperature and pest infestation. All other weather factors recorded from the study location have a positive correlation with incidence of the pest. The regression model developed also supported the relationship between the pest population buildup and weather factors.

1. Introduction

The existence and prosperity of sericulture industry depends upon the production of quality silk. For production of quality cocoon and silk, silkworm larva should feed with quality mulberry leaves, which is the exclusive food plant of the *Bombyx mori* L. The process of mulberry leaf production is suffering due to the attack of various insect and noninsect pests. Being, a perennial blooming and high biomass producing plant with luxuriant growth under irrigated condition of recommended package and practices often leading to the breeding and multiplication of various pests. This condition leads to rapid pest proliferation, which resulted qualitative and quantitative loss of mulberry plants and ultimately low productivity in sericulture.

Diaphania pulverulentalis is one of the devastating pests of mulberry in southern states, namely, Andhra Pradesh, Karnataka, and Tamil Nadu. The pest reported from different locations of India (Nagaland [1]; Jammu [2]; Kashmir [3]; Punjab [4]) and the incidence reported from sericulture countries like China and Japan [5]. The early stages, larvae of the pest inhabits apical succulent portion of the shoot and leads to its destruction, resulting in stunted growth thereby affecting considerable decline in leaf yield about 12.8% with an average incidence of 21.77% [6, 7]. The incidence of pest occurs during June–February months and causing severe damage to young plantation and it affects severe loss in tender chawki leaves, which is very much essential for young age silkworm larvae. The infestation and population buildup of a pest is greatly affected by weather parameters like temperature, relative humidity, rainfall, and so forth. Climatic factors also have a dominating influence on the survival, development, and reproductive capacity of insect pests. In recent years, many pests and diseases have been reported to be the major limiting factors affecting the production of mulberry leaves due to intensive cultivation practices and indiscriminate use of nitrogenous fertilizers and pesticides. There is a change in the insect pest scenario in mulberry due to changes in climate and agro ecosystem. Besides, the above practices, the use of high-yielding varieties and monoculture also invited pest problems and minor pests have become major ones. Several workers studied the seasonal incidence of the pest and higher infestation was reported during October to February months in Krishnagiri [8, 9] and October to December in Salem areas of Tamil Nadu [10]. Since an understanding of the population dynamics of the pest species is vital for evolving appropriate and timely management strategies, the study was conducted to estimate the seasonal population variations of *D. pulverulentalis* in relation to climatic conditions. The present study was taken up in mulberry plantations of a Sericulture Basic Seed Farm about the population dynamics of leaf roller and seasonal incidence of the pest. The study results may bring out appropriate ecological requirements, particularly weather factors like temperature, relative humidity, and rainfall, that play a vital role in multiplication and distribution of insect pests, and these factors will give momentum to research on pest management strategies.

2. Methodology

2.1. Study Location. The study area P3 Basic Seed Farm is located in Mysore, Karnataka, India and it was situated at 12° 18′N 76°39′E and has an average altitude of 770 meters (2,526 ft). It is in the southern region of the state of Karnataka and spreads across an area of 128.42 km^2. The summer season is from March to middle of June, followed by the monsoon season from the middle of June to October and the winter season from November to mid-February. The highest temperature recorded in Mysore was 38.5°c (101°F) and in winter, temperatures as low as 9.6°C (49°F). The average annual rainfall received was 798.2 mm. The parental silkworm rearing at basic seed farm has to be organized in a manner to ensure that silkworm rearing is free from disease menace. Besides, these various cocoon characters and fecundity, have to be according to the norms fixed for each race. The mulberry garden has to be managed with due care and right input has to be added to produce healthy and succulent leaf.

2.2. Study Material. Diaphania pulverulentalis is a major pest of mulberry and it belongs to family Pyralidae. It was reported as a major pest of many agricultural and horticultural crops and lay about 80–150 eggs on tender apical leaf buds of mulberry and hatching generally take place within 2-3 days. The larval stage, which causes severe damage to apical portion of the plant and the period, completes 8–12 days. The pupation takes place in the soil and the period takes 7–9 days. The adult longevities of 7–12 days and 9–14 days were recorded for male and female respectively. The target area of the leaf roller is the apical portion of the mulberry shoot. The young caterpillar binds the leaflets together with silky secretion, settles inside, and devours the soft tissues of the leaf surface and so the pest is popularly called as leaf roller or leaf webber. The web protects the larvae from natural enemies and even spraying of insecticide and killing the target pest become difficult. Late instar caterpillars feeds, on tender leaves and cause severe damage.

2.3. Host Plant. Mulberry (*Morus* sp.) is exclusive food for economically important silkworm (*Bombyx mori* L.), which is cultivated in tropical and temperate countries of the world. In India, it is cultivated mostly in the tropical region, evergreen throughout the year. Due to continuous crop improvement in the field of mulberry breeding and genetics, many new mulberry varieties have been evolved, much better than the local varieties in respect of quality and quantity of leaf produced. At the same time, these improvements paved ways for their susceptibility to be attacked by pests and diseases.

2.4. Sampling and Statistical Analysis. The mulberry garden of the basic seed farm was divided into six sub plots, and pruning schedule was adjusted to conduct six silkworm crops annually. Luxuriant growth and availability of different qualities such as tender, medium, and coarse leaves are assured throughout the year. For observations of pest incidence, ten plants from each subplots were selected at random. Thus, 60 plants were observed every week for a period of three years. The incidence of *D. pulverulentalis* was observed and the number of insects on each selected plant was counted and the total pest infestation was calculated. The data were tabulated in different months and the experiment was continued for three years (2008-2009, 2009-2010 and 2010-2011) and leaf roller infestation for each month was calculated. The weather factors like maximum temperature, minimum temperature, maximum humidity, minimum humidity, and rainfall data were recorded from the study location every day and month wise data were tabulated. The influence of weather factors on population density of leaf roller was analyzed by a simple correlation study and coefficients were worked out for a period of three years. In order to investigate the simultaneous influence of the climatic factors on pest incidence, a multiple linear regression analysis was accomplished.

3. Results and Discussion

3.1. Population Dynamics. The percentage of infestation varied in different months of the year, with a seasonal influence and a difference in the insect population in each year was observed. The three-year observation for the incidence of leaf roller indicated that during the year 2008-2009, mild infestation was started in the month of April (0.56%) and an increase was recorded on subsequent months and after the onset of monsoon rain, the infestation was further intensified. The larval establishment severe damage was found during the months of June–October and the peak infestation was observed in September (39.56%). After October infestation was gradually declined, and again a slight increase was recorded during December (17.86%). This may be due to the unexpected cyclonic rainfall received, which resulted increase in relative atmospheric humidity and a further population buildup of the pest. During January, the infestation was lowest (4.3%) and subsequent two

Table 1: Leaf roller infestation during different months (percentage).

Years	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan	Feb.	Mar.	Range of infestation
2008-09	0.56	12.45	32.56	38.56	31.78	39.56	38.45	12.78	17.86	04.3	0	0	0.56–39.56
2009-10	0.36	16.45	32.66	39.46	35.78	40.16	39.35	11.78	06.76	02.3	0	0	0.36–40.16
2010-11	6.56	12.15	31.26	39.23	31.12	38.56	37.45	14.78	28.86	05.2	0	0	05.2–39.23
Average	2.49	13.68	32.20	39.08	32.89	39.43	38.42	13.11	17.83	03.93	0	0	2.49–39.43

Table 2: Association of climatic factors with leaf roller infestation during 3 years.

Year	Maximum temperature	Minimum temperature	Maximum humidity	Minimum humidity	Rainfall
2008-09	−0.473**	0.328*	0.594**	0.584**	0.396*
2009-10	−0.548**	0.347*	0.741**	0.835**	0.378*
2010-11	−0.666**	0.411**	0.566**	0.802**	0.410*
Pooled	−0.562**	0.362*	0.633**	0.740**	0.395*

** Significant at 1% level; * Significant at 5% level.

months (February and March) infestation was zero. High temperature and low humidity prevailing during February–March in the study location created an unfavorable ecological condition for the development and population buildup of leaf roller. Studied the infestation of leaf roller in dry areas of Chamaraj Nagar, Karnataka (India) and found that the infestation was recorded maximum during rainy season and least in summer [11]. However, some workers reported infestation was high during January [12, 13]. During 2009-2010 almost the same line of observations was made and the infestation was started at a low level during April (0.36%) and it was recorded slightly higher in succeeding month (16.45%) when compared with the previous year (Table 1). This may be due to the early showers received during the end of April. The trend was followed similar to the previous year and the infestation was increased during subsequent months until the commencement of the winter season. The peak infestation was recorded during September (40.16%) and from November onwards infestation was marginally reduced. There was a rapid buildup of the pest population in the middle of each year beginning with June and ending in December. The influences of climatic factors on the incidence pest during different months are summarized in Figure 1. The peak relative humidity that occurred during August–September months influenced the highest incidence of the pest. The gradual decline in the population of leaf roller in January onwards was in consonance with the drop in the relative humidity.

During the year 2010-2011 the infestation of the leaf roller was started little early in April (Table 1) and higher infestation was recorded when compared with previous years (6.56%). This is also may due to early rain fall received at the end of March and as a result a favorable climatic condition was created for population buildup of leaf roller in the field. Similar, to previous two years the population was recorded peak during June–October and highest infestation was recorded during the month of July (39.23%). After October, during the beginning of the winter season there was a decline in population and again a slight increase was observed during the month of December (28.86%) due to the unexpected cyclonic rainfall.

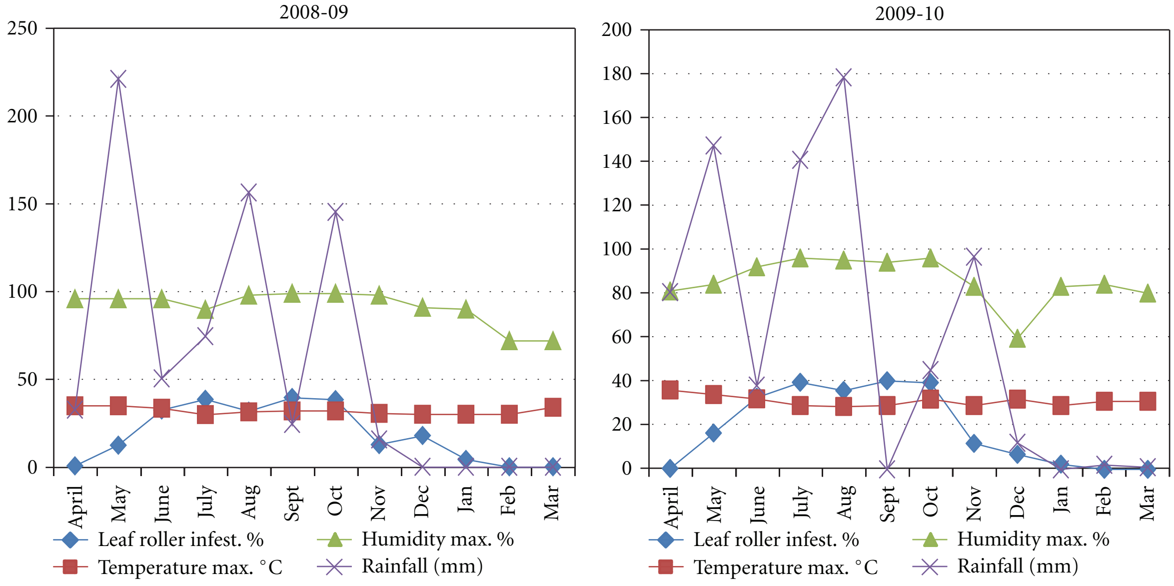
3.2. Correlation between Incidence of Pest Population and Abiotic Factors. The infestation of leaf roller showed a great sensibility to weather variations occurring over the period studied. A significant and negative correlation was observed between the percentage of leaf roller infestation and maximum temperature recorded from the study location ($r = -0.473$ in 2008-2009, $r = -0.548$ in 2009-2010, and $r = -0.666$ in 2010-2011). The study results were in accordance with the results of earlier workers [12]. The correlation coefficient data indicated that when the temperature rises up during the hottest months of February–April the infestation was recorded very low or nil (Table 2). However, a positive correlation was recorded between the infestation and minimum temperature. Similarly, correlation studies were worked out between infestation of leaf roller and maximum humidity, minimum humidity, and rainfall recorded during different months for a period of three years. All correlation coefficient (r) data showed a positive correlation between the two variables. Significant ($P \leq 0.\ 1$) correlation was observed between maximum humidity and leaf roller infestation (0.594 in 2008-2009, 0.741 in 2009-2010, and 0.566 in 2010-2011). The analysis also revealed a positive and highly significant correlation between leaf roller infestation and minimum humidity (0.584 in 2008-2009, 0.835 in 2009-2010, and 0.802 in 2010-2011). The results indicated that weather factors have greatest importance upon the population fluctuation of leaf roller. Quite a few workers reported similar results from Tamil Nadu climatic conditions [13, 14]. The rainfall data of the study location also significantly correlated with leaf roller infestation (0.396 in 2008-2009, 0.378 in 2009-2010, and 0.410 in 2010-2011). The results of the analysis showed that due to continuous rain (June–October) naturally increased relative atmospheric humidity as well as percentage of soil moisture. It created a suitable condition for the luxuriant growth of mulberry and

Larva of leaf roller

(a)

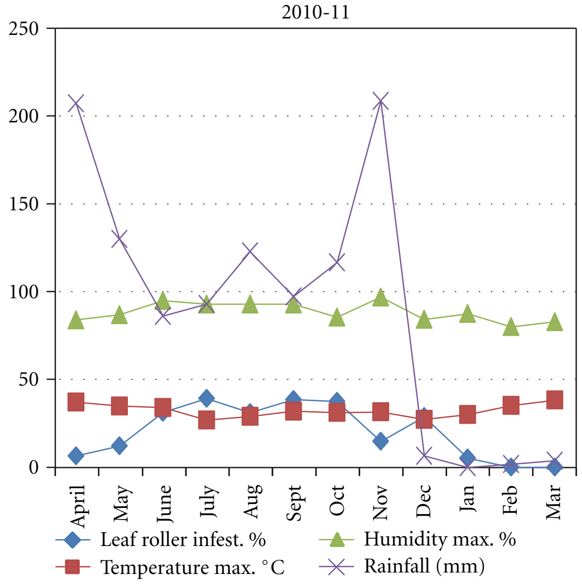
Adult moth of leaf roller

(b)



(c)

(d)



(e)

FIGURE 1: Association leaf roller (*Diaphania pulverulentalis*) infestation and abiotic factors of the study location (3-years period).

Table 3: Regression model developed for Leaf roller infestation.

Years	Maximum temperature ($X1$)	Minimum temperature ($X2$)	Maximum humidity ($X3$)	Minimum humidity ($X4$)	Rainfall ($X5$)
2008-09	$Y = -64.291+1.415X1$ $R^2 = 0.171^*$	$Y = 17.160 - 0.107X1$ $R^2 = 0.190^*$	$Y = 72.168 - 0.998X3$ $R^2 = 0.350^*$	$Y = 0.257 - 0.363X4$ $R^2 = 0.281^*$	$Y = 15.765 - 0.123X5$ $R^2 = 0.003$
2009-10	$Y = -99.537+2.605X1.$ $R^2 = 0.120^*$	$Y = 17.370 - 2.012X2$ $R^2 = 0.122^*$	$Y = 87.908 - 1.245X3$ $R^2 = 0.541^{**}$	$Y = -49.670 - 1.458X4$ $R^2 = 0.694^{**}$	$Y = 12.546 - 0.101X5$ $R^2 = 0.146$
2010-11	$Y = -110.883 + 2.798X1.$ $R^2 = 0.441^{**}$	$Y = 06.104 - 1.492X2$ $R^2 = 0.173^*$	$Y = 122.281 - 1.661X3$ $R^2 = 0.324^*$	$Y = 12.542 - 0.321X4$ $R^2 = 0.641^{**}$	$Y = 14.431 - 0.165X5$ $R^2 = 0.055$

**Significant at 1% level; *Significant at 5% level.

availability of more nutritious and succulent leaves naturally favored a population buildup of leaf roller. Same results were observed and concluded the peak leaf roller infestation occurs both in southwest and northeast monsoon period, and showed that rainfall, and humidity were conducive for the multiplication of the pest [15]. However, maximum infestation was reported during the winter season in Kerala, (India) climatic condition [16]. These reports make it clear that there was a linear relationship of decreasing atmospheric temperature and increasing relative humidity with increased pest incidence. The significant correlation found between the leaf roller infestation and abiotic factors definitively help to develop a predictive model, by which the outbreak of this pest could be known in advance, so that timely control measures can be taken up to curtain the problem. The climate change can affect the response of insect pests to the host plants, although it is difficult to predict the impact of climate changes on various insect pests; the overall response is dependent on the impact of climate change on the insect, plant host and natural enemy relationship.

3.3. Regression Model. Linear regression analysis revealed that measured environmental variables have significant effects on leaf roller pest densities ($P < 0.05$) confirming results of correlation analysis. The importance of relative humidity and pest incidence for explaining significant portions of the independent variable for densities of leaf roller is also emphasized. The stepwise regression analysis constructed to investigate the abiotic factors contributed the most to the variance of the leaf roller population (Table 3). Regression analysis showed that minimum humidity recorded from the study location significantly contributed to the population variation of the pest (28% in 2008-2009, 69% in 2009-2010, and 64% in 2010-2011). Similarly, maximum humidity also significantly and positively contributed for variations in the population buildup (35% in 2008-2009, 54% in 2009-2010, and 32% in 2010-2011). Analysis also showed that the maximum temperature significantly and negatively contributed to the variation of leaf roller population (17%, 12%, and 44% for 2008-2009, 2009-2010 and 2010-2011 resp.). The optimum regression model indicated the strong influence of maximum humidity and minimum humidity on variation in pest population in mulberry plantation. The forecast model can be used to predict the initiation and "red alert" season of the pest attack. This serves as a scale for the sericulturist to adopt effective crop protection measures at the appropriate time.

Timing of the insect pest appearance varies, depending on differences in temperature throughout the years, which makes the pest's forecasting and management difficult. One way to promote our understanding of the phrenology of *Diaphania pulverulentalis* is to develop a population dynamics model that explicitly incorporates temperature-dependent development. Indeed, models for temperature-dependent development of insect pests have been widely used as decision-support tools to improve the efficiency of pest management.

Forecasting the peak abundance of pest and diseases in advance helps in timely management of crop pests. The correlation and multiple regression analysis clearly showed the importance of weather factors in the pest incidence. Among the models regression can be used for forecasting the pest and also these models can be utilized in agroadvisories after validating with individual seasonal data.

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Hindawi Publishing Corporation
Psyche
Volume 2012, Article ID 863947, 11 pages
doi:10.1155/2012/863947

Review Article

Effects of Abiotic Factors on the Geographic Distribution of Body Size Variation and Chromosomal Polymorphisms in Two Neotropical Grasshopper Species (*Dichroplus*: Melanoplinae: Acrididae)

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Received 19 August 2011; Revised 28 December 2011; Accepted 3 January 2012

Academic Editor: Matilda Savopoulou-Soultani

We review the effects of abiotic factors on body size in two grasshopper species with large geographical distributions: *Dichroplus pratensis* and *D. vittatus*, inhabiting Argentina in diverse natural habitats. Geographical spans for both species provide an opportunity to study the effects of changes in abiotic factors on body size. The analyses of body size distribution in both species revealed a converse Bergmannian pattern: body size is positively correlated with latitude, altitude, and seasonality that influences time available for development and growth. Allen's rule is also inverted. Morphological variability increases towards the ends of the Bergmannian clines and, in *D. pratensis*, is related with a central-marginal distribution of chromosomal variants that influence recombination. The converse Bergmannian patterns influence sexual size dimorphism in both species but in different fashions. Body size variation at a microspatial scale in *D. pratensis* is extremely sensitive to microclimatic clines. We finally compare our results with those for other Orthopteran species.

1. Introduction: Ecogeographic Rules, Body Size, and Abiotic Factors

Body size, one of the most important characteristics of animals, is strongly influenced by abiotic factors [1, 2]. One of the main causes of the importance of body size in determining many characteristics of the life history of organisms is that it scales with metabolic rate which, in turn, influences the rate at which an individual grows, acquires resources, and reproduces [3]. In Orthoptera, a interspecific analysis using 32 species of 7 families (both Ensifera and Caelifera) showed that the scaling exponent between metabolic rate and body size was 1.06 [3] supporting the model of Kozlowski et al. [4, 5] that cell size and number influence the metabolic scaling of organisms.

The influence of body size in a large number of life history characteristics of organisms including grasshoppers has been repeatedly stressed [2, 6–8]. Examples of this in grasshoppers are the relationship between body size and fecundity [7] or survival [9]. Thus, analyzing large-scale geographic variation of body size in different organisms is of importance in order to understand both the abiotic and biotic factors that may modify it through several mechanisms and the ecological and evolutionary consequences of this variation [2, 10–12].

The concept that abiotic factors are relevant to the evolution and adaptation of living beings has been present since the early days of modern biology [13–15]. Because abiotic factors vary geographically, their effects on organisms should change in consequence. A number of the so-called "ecogeographic rules" (Bergmann's rule, Allen's rule, and others) try to describe geographic patterns of body size observed across the geographic (essentially latitudinal and altitudinal) distributional range of species. Bergmann's rule [16] was originally formulated for endothermic animals (mammals and birds) at an interspecific scale. This rule states that body size tends to increase with latitude (or altitude) because of the ecological advantage of being larger, thus having lower surface/volume ratio, when temperature is lower. Heat loss is minimised (or heat conservation is increased) due to a larger body size. Allen's rule [17] is usually seen as a complement to Bergmann's rule because it describes geographic patterns of decreases in relative size of protruding parts of animals (ears, tails, wings, and limbs) as latitude increases (and mean temperature decreases), as a means for avoiding heat loss. Another important ecogeographic principle relating to adaptation to different environments both within and between species is Gloger's rule [18], which states that birds in climates with high relative humidity tend to be darker than conspecifics in climates with low relative humidity. However, this rule has not been thoroughly explored, especially in insects. A further ecogeographic rule, Jordan's rule or the Law of Vertebrae [19], states that the number of vertebrae in fish increases with latitude and thus decreases with temperature. In this sense it intersects with Bergmann's rule, but also with many other possible environmentally and genetically related mechanisms [20], and of course is not applicable to insects.

It is important to note that all these ecogeographic rules proposed, at their inception, a thermoregulatory explanation for the observed clinal trends (either latitudinal or altitudinal [21]). However, there has been growing concern that these patterns are probably the result of many factors (abiotic and biotic) acting jointly, which makes the situation far more complex than originally thought [20, 22–24], a suggestion that was already present in an early paper by Scholander [25].

With time, Bergmann's and Allen's rules became modified in their original sense. Both Mayr and Rensch [21, 26–29] transformed the original concept of Bergmann's (and by extension, Allen's) rule to an intraspecific pattern: races or populations (not necessarily species) varied in size according to temperature gradients. Also, a number of studies were undertaken to try to apply these rules to ectotherms, that of Ray being one of the first [30]. However, his results [30] were inconclusive mainly because he freely compared different kinds of ectotherms (including insects and amphibians) and mechanisms underlying ecogeographic patterns in different organisms that probably obey different mechanisms. In fact, in the case of endotherms for which the ecogeographic rules were originally formulated, a number of discrepancies occur and it is not always possible to explain the geographic body size trends by simple thermoregulatory models. This situation becomes more complex when trying to verify the rules in ectotherms that, in most cases, regulate body temperature behaviourally, as is the case of most studied Orthoptera [31–35].

For endotherms, a number of non-Bergmannian physiological or ecological explanations have been developed to explain clinal patterns of body size variation, especially when this variation does not conform to Bergmann's rule [36–38]. This situation is complicated in ectotherms and particularly in insects, which tend to show geographic body size patterns that represent a continuum between fully empirical Bergmannian trends to its converse [39] and where classical thermoregulatory explanations are difficult to apply [10, 11].

We have studied two closely related species of Neotropical Melanopline grasshoppers, *Dichroplus pratensis* and *D. vittatus*, both of wide geographic distribution in Argentina in order to describe and understand their patterns of body size variation across climatic gradients.

2. Study Species

Dichroplus pratensis Bruner, 1900, and *D. vittatus* Brunner, 1900, belong to a large genus of Melanopline grasshoppers widely distributed in South America. Both species have the largest geographic distributions within the group, essentially in Argentina. Although *Dichroplus* has been recently the subject of revision and a number of species were placed in new genera, the *maculipennis* group, containing 9 species, seems to be well based and monophyletic on the grounds of structure of the phallic complex and external morphology [40].

Dichroplus pratensis distribution spans more than 23 degrees latitude, from the Puna highlands of Jujuy province to Santa Cruz province in Southern Patagonia. It is found from 0 to at least 2,500 masl, and longitudinally it is found from the Atlantic Ocean shore to the Andes [10, 12]. *D. pratensis* is more frequent in elevated, dry grasslands. It is found in an astonishing variety of habitats including the Patagonian steppe, the Puna highlands, and the humid Pampas. It is obviously a species of wide ecological tolerance, which is probably related to its nonselective polyphagous herbivorous habits. However, there is some evidence that it prefers forbs, which would explain its presence in nongrassland territory [41].

Dichroplus vittatus also has a wide distribution in Argentina partially overlapping that of *D. pratensis* although only seldom both species are found in strict sympatry, probably due to competitive exclusion. *D. vittatus* is more common in semiarid and arid habitats, and populations have been found at over 3,000 masl in Catamarca and La Rioja provinces [40]. Large populations are found in central Chubut on natural grasses and on "*Jarilla*" (*Larrea divaricata*) in the Monte phytogeographic region of Argentina [40]. Both species are univoltine, and the length of their adult reproductive periods depends largely on latitude and altitude [10, 11].

Twenty five population samples of adult *D. pratensis* Bruner (343 males, 352 females) were collected at localities from Argentina spanning 22° of latitude and 0 to 2,474 m elevation during February and March, 2001. Population samples of adult *D. vittatus* Bruner were obtained at nineteen Argentine localities (190 males and 174 females) spanning almost 20° of latitude and 36 m to 2,758 m above sea level during February and March, 2001. We used SPSS for Windows (Statistical Package for the Social Sciences) software to perform all statistical tests, mainly OLS regression and parametric and nonparametric correlation between body size estimators and geographic and climatic variables. Reduced major axis (RMA) regression was used in tests of allometry and sexual size dimorphism (SSD). Principal components analysis (PCA) was usually performed to reduce dimensionality of predictors because most environmental variables tend to show a high degree of colinearity. Prior to statistical analysis, all measurements were log-transformed and then tested for normality using the Kolmogorov-Smirnov test to determine the appropriateness of subsequent parametric or nonparametric analysis.

2.1. Clinal Variation of Body Size in Dichroplus pratensis and D. vittatus: The Converse to Bergmann's Rule. Bergmannian patterns in insects remain controversial. Some species or species groups tend to show clinal variation of increasing body size or body mass towards higher latitudes or altitudes and lower temperatures. However, in a large number of cases converse trends (or even the absence of a trend) have been observed at intra- and interspecific levels [39, 42–45].

We studied geographic body-size variation in 25 populations of *Dichroplus pratensis* (along more than 22 degrees of latitude (*S*) and between 0 and almost 2,500 m altitude) and 19 populations of *Dichroplus vittatus* spanning 20 degrees of latitude and 2,700 m altitude. Geographic size variation is wide in both species. Mean male body size (populational means) varied between 18.9 and 26.4 mm in *D. pratensis* and 16.43 and 21.62 mm in *D. vittatus*. For females, size ranges were 22.2–28.2 and 20.26–28.13 mm, respectively.

Using mean body length of each sex and factors obtained from PCA analyses of six morphometric linear characters (body length, length of left hind femur, length of left hind tibia, length of tegmina, middorsal length of pronotum and height of pronotum), it was shown that *D. pratensis* and *D. vittatus* follow the converse to Bergmann's rule, becoming smaller at higher latitudes and altitudes (Table 1). In *D. pratensis* variability of body size increased with latitude and altitude in both sexes (Table 3). Body size trends were significantly correlated with mean ambient temperatures (annual mean, minimum, and maximum), precipitation (annual mean, minimum, and maximum), and two estimators of seasonality, the difference between the maximum and minimum temperatures and the difference between maximum and minimum precipitation; all nonparametric correlations were positive (Table 2). Body size was also positively and significantly correlated with actual evapotranspiration (AET), a measure of primary productivity, and with potential evapotranspiration (PET), a measure of ambient energy (Table 2). Some allometric relationships also showed geographic variation (see the section on Allen's rule) [10, 46]. We proposed that the observed decrease in size with latitude and the increase in morphological variability are joint consequences of the shortening of the growing season, the increasing seasonality and climatic unpredictability and lower primary productivity towards the south (as represented by AET) and that the species exhibits protandry, which contributes, in the south, to smaller and more variably sized males and smaller but more constant body sizes in females. A further factor increasing variability at marginal localities has a genetic component (see below).

A parallel study was performed in the closely allied *D. vittatus*. This species also follows the converse to Bergmann's rule latitudinally but not altitudinally where no significant trends were observed (Table 1). For males, variability of body size increased with latitude but not altitudinally (Table 3). Both trends (size and variability) were significantly and positively correlated with mean annual temperature and minimum annual temperature and two estimators of seasonality: the coefficients of variation of mean annual temperature (negative correlation) and mean annual precipitation (positive correlation) (Table 1). As in *D. pratensis*, some allometric relationships also showed geographic variation. It was suggested that the observed decrease in size with latitude together with the increase in morphological variability is a consequence of a number of factors, which parallel those that predict body size in the sister species: the shortening of the growing season southwards, the increasing seasonality and climatic unpredictability, and the fact that the species exhibits protandry which contributes to smaller and more variable size in males and smaller but more constant body sizes in females [10].

Thus, both species seem to obey the same environmental pressures (either because of phenotypic plasticity or natural selection in different habitats), and the correlations with abiotic factors result from the large geographic distribution of both species which extend progressively into areas of increasing seasonality, lower resource availability, and shorter time for growth, development, and reproduction. These results are in close agreement with those obtained for crickets [43–45] but were reported by us for the first time in species of Acrididae.

2.2. Allen's Rule in D. pratensis and D. vittatus. The relative length of protruding parts of endothermic animals tends to decrease with increasing latitude and altitude as Allen proposed almost a century and a half ago [17, 47]. This pattern, as Bergmann's rule, has been usually regarded as a means of decreasing area/volume ratios in order to minimize heat loss and as a thermoregulatory evolutionary adaptation [48]. It has recently been suggested that a further physiological explanation could explain the effect of temperature on limb length in endotherms. In an experiment using mice it was shown that peripheral tissue temperature closely reflects housing temperature *in vivo*. Also, tissue temperature was significantly correlated with the proliferation of chondrocytes in *in vitro* cultures of metatarsals without vasculature [49]. This provides a novel, nonthermoregulatory explanation to limb length variation by a direct effect of ambient temperature.

However, with very few exceptions, application of Allen's rule to insects has not been explored [30, 48]. We studied the geographic variation of three morphometric characters in relation to body size in *Dichroplus vittatus* and *D. pratensis* to test Allen's rule in these ectotherms. Since both

Table 1: Correlation coefficients and their statistical significance between an estimator of body size (BL: body length) and several geographic and environmental predictors for males (M) and females (F) of two grasshopper species.

Variable*	Correlation coefficient (*P*)			
	Dichroplus pratensis		*Dichroplus vittatus*	
	$\log_{10}$MBL	$\log_{10}$FBL	$\log_{10}$MBL	$\log_{10}$FBL
LAT	−0.70 (<0.001)	−0.76 (<0.001)	−0.64 (0.003)	−0.65 (0.003)
ALT	−0.39 ns	−0.51 (<0.001)	ns	ns
TMEAN	0.71 (<0.001)	0.65 (<0.001)	0.52 (0.021)	0.60 (0.006)
TMAX	0.70 (<0.001)	0.63 (<0.001)	ns	ns
TMIN	0.59 (0.002)	0.53 (0.007)	0.58 (0.010)	0.70 (0.001)
CVT	ns	ns	−0.67 (0.002)	−0.75 (<0.001)
TMm	0.73 (<0.001)	0.44 (0.029)	ns	ns
PANNU	0.56 (0.004)	0.40 (0.044)	ns	ns
PMAX	0.43 (0.031)	0.42 (0.039)	ns	ns
PMIN	0.48 (0.014)	ns	−0.53 (0.020)	−0.50 (0.028)
CVP	ns	ns	0.56 (0.012)	0.52 (0.024)
PMm	0.49 (0.013)	0.42 (0.039)	0.47 (0.043)	ns
PET	0.59 (0.002)	0.48 (0.016)	ns	0.46 (0.047)
AET	0.48 (0.014)	0.50 (0.011)	ns	ns
WB	ns	ns	ns	ns

* LAT: latitude in decimal degrees; ALT: altitude in metres above sea level; TMEAN: mean annual temperature (in Celcius degrees); TMAX: mean annual maximum temperature; TMIN: mean annual minimum temperature; CVT: coefficient of variation of TMEAN; TMm: mean difference between maximum and minimum monthly temperatures; PANNU: total annual precipitation (in mm/year); PMAX: mean maximum monthly precipitation; PMIN: mean minimum monthly precipitation; CVP: coefficient of variation of PANNU; PMm: mean difference between maximum and minimum monthly precipitation; PET: potential evapotranspiration (the Priestley-Taylor equation); AET: actual evapotranspiration (the Thornthwaite formula); WB: water balance; ns = non-significant.

Table 2: Spearman correlation coefficients and their statistical significance (in parentheses) between the *arsin*-transformed proportions of three morphometric traits (F3L: femur 3 length; T3L: tibia 3 length; TeL: tegmina length) and body length (BL) with respect to latitude (LAT), altitude (ALT), and three selected abiotic factors (TMEAN: mean annual temperature; PMm: mean difference between maximum and minimum mean monthly precipitation; WB: water balance) in males and females of 25 and 19 populations of *D. pratensis* and *D vittatus*, respectively.

Species (sex)	*arsin* Proportion	LAT	ALT	TMEAN	PMm	WB
D. pratensis M	F3L/BL	0.55 (0.004)	−0.47 (0.018)	−0.03 (ns)	0.19 (ns)	0.73 (<0.001)
	T3L/BL	0.55 (0.004)	−0.68 (<0.001)	−0.10 (ns)	0.04 (ns)	0.57 (0.003)
	TeL/BL	0.53 (0.006)	−0.56 (0.004)	0.07 (ns)	0.18 (ns)	0.77 (<0.001)
D. pratensis F	F3L/BL	0.63 (0.001)	−0.46 (0.022)	−0.61 (0.001)	−0.005 (ns)	0.39 (0.005)
	T3l/BL	0.66 (<0.001)	−0.58 (0.002)	−0.61 (0.001)	−0.22 (ns)	0.31 (ns)
	TeL/BL	0.71 (<0.001)	−0.73 (<0.001)	−0.14 (ns)	−0.13 (ns)	0.64 (0.001)
D. vittatus M	F3/BL	0.32 (ns)	−0.10 (ns)	0.10 (ns)	−0.63 (0.004)	0.07 (ns)
	T3/BL	−0.50 (ns)	−0.05 (ns)	0.32 (ns)	0.70 (0.001)	−0.32 (ns)
	Te/BL	−0.34 (ns)	0.10 (ns)	0.43 (ns)	0.66 (0.002)	−0.11 (ns)
D. vittatus F	F3/BL	−0.32 (ns)	0.06 (ns)	0.07 (ns)	0.51 (0.026)	−0.16 (ns)
	T3/BL	−0.49 (ns)	0.08 (ns)	0.26 (ns)	0.34 (ns)	−0.33 (ns)
	Te/BL	−0.60 (0.007)	0.002 (ns)	0.54 (0.016)	0.61 (0.006)	−0.37 (ns)

ns = non-significant.

species follow the converse to Bergmann's rule owing to latitudinal and/or altitudinal variation in time available for growth and reproduction, geographic variation in body size proportions of protruding parts may obey differential allometric growth in different geographic areas owing to time constraints on development and growth imposed by abiotic factors that in turn regulate adult season and time available for reproduction (see above). Alternatively, it could reflect true Allenian variation related to thermoregulation. Body proportions (hind femur, hind tibia, and tegmina with respect to total body length measured from the tip of the head up to the distal portion of the hind femur length

Table 3: Mean body length in mm (BL) and coefficients of variation (CV) in selected marginal and central populations of two species of grasshoppers. LAT: latitude in decimal degrees; ALT: altitude in metres above sea level.

Species	Population	LAT	ALT	Male BL/CV	Female BL/CV
D. pratensis	Volcán	23.92	2574	22.36/5.56	24.34/4.69
	Estación Mazán	28.73	646	23.83/4.56	26.48/5.71
	Don Tomás	36.68	175	24.24/4.00	25.41/3.51
	Olavarría	36.92	162	22.57/3.95	24.34/4.30
	Diadema Argentina	45.78	326	19.29/5.86	22.18/6.21
	Villa Rada Tilly	45.95	0	18.21/6.33	23.17/6.37
D. vittatus	Huacalera	23.43	2758	17.30/4.05	21.66/6.09
	Santiago del Estero	26.02	174	21.62/4.38	24.83/3.71
	Valle Fértil	30.63	828	18.55/4.64	24.68/2.35
	Villa del Rosario	31.57	248	19.19/3.65	26.08/3.26
	Toay	36.57	174	16.77/7.69	20.76/2.89
	Playa Unión	43.07	36	16.43/5.78	20.26/8.29

when parallel to the longitudinal axis of the body) were studied by correlation/regression analyses with geographic and climatic variables (temperature, precipitation, evapotranspiration, and water balance) (Table 2). In *D. pratensis*, body proportions increased with latitude and decreased with altitude (Table 2). These results probably obey the effects of water balance and seasonality on final body size, and on the allometric growth of the three studied characters not being related to thermoregulation. In *D. vittatus*, a generally nonsignificant trend towards the decrease of the mean proportions of all three characters with increasing latitude was observed (Table 2). Nevertheless, also in this species, it is probable that the environmental gradient responds to seasonality factors (although not to water balance) that affect the length of growing season and, in consequence, body size and its allometric relationships. We conclude that the regularities in the geographic distribution of body proportions of *D. pratensis* and *D. vittatus* do not follow Allen's rule in the sense of thermoregulation and result from variables that determine growing season length and the allometric growth of different body parts, closely correlated with the converse Bergmannian body size trends [46].

2.3. The Central Marginal Distribution of Chromosomal Polymorphisms of D. pratensis and Its Relationship with Body Size and Abiotic Factors. Dichroplus pratensis has a standard all-telocentric chromosome complement of $2n = 18 + X0♂/18 + XX♀$ but is polymorphic and polytypic for Robertsonian (Rb) fusions that involve the six larger autosomes (L1–L6). Each population may be polymorphic (or eventually may have become fixed) for one to three Rb fusions (except in monobrachial chromosomal hybrid zones in which four fusions may coexist), which vary in quality and frequency in different populations. Fusions in this species produce profound changes in inter- and intrachromosomal genetic recombination by reducing the number of linkage groups that assort independently and by creating, through a reduction of chiasma frequency, large pericentromeric recombination-free chromosomal regions that may house adaptive supergenes [50].

Distribution of Rb polymorphisms is not random in *D. pratensis*: different fusion systems characterize different chromosomal races that inhabit radically different environments. Moreover, the highest number of fusions and their highest frequencies are associated with ecologically optimal (central) environments. In these not highly seasonal habitats, primary productivity is high and resources are abundant in quantity and variety. Populations tend to be very large and extremely dense in some years. Rb frequencies decrease clinally and steeply towards the margins of the geographic distribution until in the most extreme environments (i.e., the Patagonian steppe towards south and the Puna highlands towards north) fusions completely disappear, populations being strictly monomorphic for the standard karyotype. Those extreme habitats are harsh, unpredictable, and highly seasonal. Populations are rare, very small, and of very low density, and the distribution of the species is extremely patchy and not continuous as in central habitats [50, 51].

The central-marginal model relates the complex Rb polymorphisms with the distribution of abiotic and biotic factors along latitudinal and altitudinal gradients and variation in body size which, as stated before, follows the converse to Bergmann's rule. We have proposed that, in central regions, high frequencies of Rb polymorphism would maintain coadapted supergenes adaptive to these stable and favorable environments; thus, restriction of genetic recombination would be essential to impede supergenes breakdown through crossing-over. In marginal habitats, however, which are changing and unpredictable, where resources are low and populations probably endure continuous cycles of extinction and recolonisation, high recombination is essential for the liberation of genetic variability that would be the substrate of natural selection for allowing adaptation to these harsh environments.

The former was in part corroborated by studies of morphological diversity along the range of the species. It has been shown that, although body size decreases clinally

Table 4: Reduced major axis (RMA) regressions of male body length on female body length under the null hypothesis of $\beta = 1.0$ in *Dichroplus pratensis* and *D. vittatus*. r: pearson's correlation coefficient; T: student's t-statistic; df: degrees of freedom; P : probability; β: slope of RMA regression; S_ξ: standard deviation; T: Clarke's T-statistic; CI: confidence interval; a: RMA regression intercept.

		Correlation coefficient				RMA slope					RMA intercept	
SPECIES	TRAIT	r	t	df	P	β (S_ξ)	T	df	P	95% CI	a (S_ξ)	95% CI
D. pratensis	BL	0.79	5.12	23	<0.001	1.328 (0.171)	2.60	20.33	0.009	0.975, 1.681	−0.493 (0.239)	−0.988, 0.002
D. vittatus	BL	0.83	6.15	17	<0.001	0.767 (0.104)	2.40	15.38	0.015	0.549, 0.986	0.221 (0.143)	−0.080, 0.522

towards the margins, morphological variability increases significantly (especially in adult males) despite the fact that, in marginal populations, the time available for development and growth is much lower than in optimal central environments (Figure 1). This fact has been interpreted as a result of increased recombination and release of genetic variability (Figures 1(c)–1(f)). The same phenomenon has been observed in the sister species, *D. vittatus* whose geographic distribution mostly overlaps that of *D. pratensis* (see below).

2.4. Rensch's Rule Is Affected by Bergmann's Rule or Its Converse. In 1950, Berhard Rensch [52] described, in phylogenetically related species (including mammals, birds, and carabid beetles), an interspecific pattern, now called Rensch's rule, by which sexual size dimorphism (SSD) tends to increase as general body size increases. Later, Rensch expanded his definition as follows: "In species of birds in which the male is larger than the female, the relative sexual difference (in size) increases with body size. If by way of exception, the females are larger than the males, as among many species of birds of prey, the opposite correlation applies, that is, the greater sexual difference is found in the smaller species". The latter has become to be considered the standard definition of Rensch's rule [53, 54] but its interpretation is ambiguous. Although in male-biased SSD the rule is usually clearly demonstrated, in the opposite situation (female-biased SSD) the situation is far from clear [55]. This is most relevant because in a vast majority of insects and particularly in grasshoppers females are usually larger than males. In grasshoppers, there are many cases of extreme female-biased SSD in families such as Proscopiidae, Ommexechidae, and Romaleidae but information regarding Rensch's rule is extremely scarce [56]. Furthermore, since patterns of SSD are probably heavily influenced by Bergmannian or converse-Bergmannian body size patterns, which in turn depend on clinal variation of abiotic factors [57], a clarification of Rensch's rule in grasshoppers is needed.

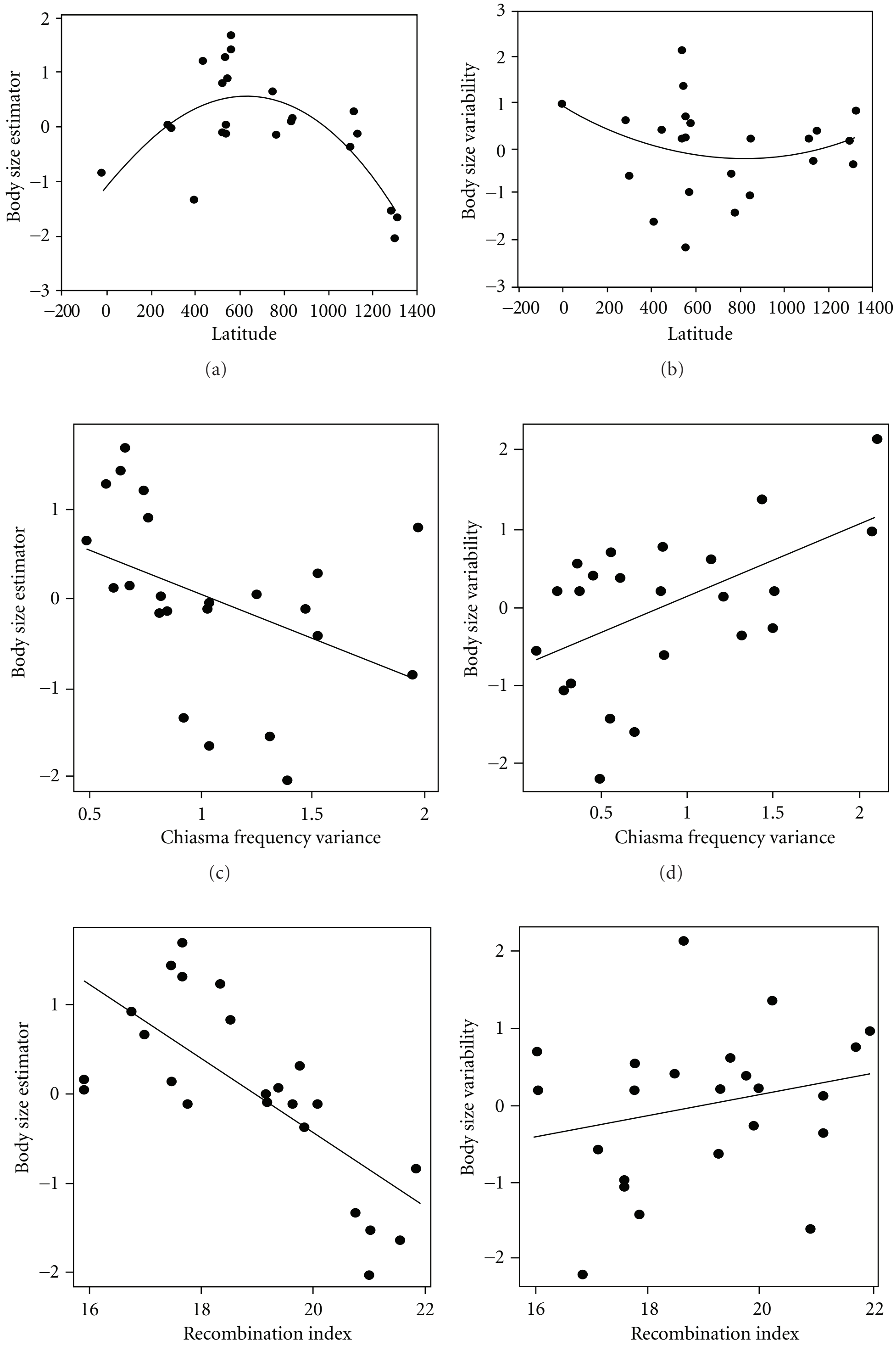
The case of both *Dichroplus* species here reviewed is clear in this respect: both species have overlapping geographic distributions in Argentina, and both are sister species belonging to the same *Dichroplus* species group (the "*maculipennis*" group) and follow the converse to Bergmann's rule. Although Melanoplinae Acrididae do not show extreme SSD, males and females are readily distinguished by size in the field and all species show female-biased SSD. However, both species exhibit completely opposite patterns of SSD regarding Rensch's rule.

SSD can be the result of sexual or natural selection. Due to male-male competition for access to females, SSD could favor an increase in male body size. On the other hand, larger size in females could be favored by natural selection since fecundity is directly correlated with body size [56, 58].

SSD occurs in both species across their geographical distribution ranges, also involving differences in allometry and shorter developmental times in males. In *D. vittatus* the degree of SSD increased significantly with general body size (classical definition of Rensch's rule), whereas in *D. pratensis* SSD decreased as body size increased (as predicted by the extended definition of Rensch's rule) (Table 4). A plausible explanation of SSD is that sexual selection favors a differential increase in female body size related to a preference by males for more fecund females. Given the close phylogenetic relationship between both species, the differences in SSD between them may be the result of differential natural and sexual selective pressures. In *D. vittatus* both sexes may be reacting differently to environmental conditions regarding body size, while in *D. pratensis* protandry could be the main factor behind SSD, although both react to ambient conditions following the converse to Bergmann's rule [58].

Considering that both species exhibit converse latitudinal Bergmannian patterns related to environmental conditions and that SSD depends on general body size according to Rensch's rule (independently of definition), the steeper latitudinal body size cline shown by males of *D. vittatus* with respect to females would be a consequence of male differential responsiveness to seasonality and season length, determining the decrease of SSD towards South.

2.5. Microspatial Body Size Variation in D. pratensis. In a recent study [59], variation in six morphological measurements in *D. pratensis* sampled at a microspatial scale within the Sierra de la Ventana chromosomal hybrid zone was analyzed. The Sierra de la Ventana region (Buenos Aires province, Argentina) is a heterogeneous environment spread over the southern portion of the transitional zone between wet and dry pampas of Argentina. As a consequence of the interaction among climatic and geological factors (i.e., 16 different vegetation units, transitional annual rainfall regime, and diversity of soils, environments, and topographical design) this region displays diverse microclimates (see references in [59]). Despite its habitat heterogeneity, the Sierra de la Ventana area belongs to the central, ecologically favorable, range for *D. pratensis* characterized by higher food availability and less strenuous environmental conditions [58]. In this hybrid zone, two chromosomal races, polymorphic for different Rb fusions, encounter and hybridize [60, 61].



(a) (b) (c) (d) (e) (f)

Figure 1: Regressions of body size and body size variability of *D. pratensis* on latitude and two estimators of genetic recombination. Body size and its variability are represented by the first and second principal components of a PCA analysis of six linear morphometric measurements and their coefficients of variation. PC1 showed high loadings for the six measurements and PC2 for the six CVs. (a) Distribution of body size along the studied gradient. Marginal populations show smaller body sizes than central ones. (b) Distribution of body size coefficients of variation along the studied gradient. Marginal populations show higher variability than central ones. (c) and (d) Regression of body size and body size variability on between-cell variance of mean chiasma frequency. Body size decreases but its variability increases with higher chiasma variance. (e) and (f) Regression of body size and body size variability on an *ad hoc* recombination index. Body size decreases but its variability increases with higher recombination frequency.

The "Northern" race, widely distributed in central Argentina, polymorphic for fusions L1 and L6 (L1/L6) and L3 and L4 (L3/L4), contacts a geographically restricted "southern" race, polymorphic for fusions L1 and L2 (L1/L2), L3/L4, and L5 and L6 (L5/L6). Complex Rb heterozygotes with reduced fertility occur at this mosaic hybrid zone [51] and chromosome frequencies change abruptly over rather short distances and altitudes (ca. <1,000 m and <500 m, resp.) with fusions L1/L2 and L5/L6 occurring more frequently at higher altitudes [51, 59].

Miño et al. [59] investigated morphometric (total body length, pronotum height and length, left third femur length, left third tibia length, and tegmina length), chromosomal, and molecular (genetic) variation in males and females of *Dichroplus pratensis*, at a microspatial scale. A microspatial altitudinal gradient was studied: samples were taken from the base to the top of Cerro Ceferino Hill, a hill of about ~456 masl. Both male and female grasshoppers showed extensive morphometric variation at a microspatial scale. Highly significant differences were observed between samples and sexes, as indicated by GLM (General Linear Model), with all six morphometric characters separately measured in both sexes from each sample as dependent variables [59]. Specifically for body length, significant differences were observed among grasshoppers from the hill base (~440 masl) and the hill top (~650 masl). Insects from the hill base were smaller (mean/CV body length in males = 21.73 mm/1.2; mean/CV body length in females = 23.86 mm/1.04) than those from the hill top (mean/CV body length in males = 23.12 mm/1.08; mean/CV body length in females = 24 mm/1.19). In Miño et al. [59], body length was significantly positively correlated with altitude in males. Furthermore, a PCA performed to investigate the relationship between body size and altitude, revealed that the first PC, a size estimator, showed the highest loadings for the majority of traits. Also within the Cerro Ceferino hill the trend for male body size was significant and positive. However, no significant correlations between altitude and body size were apparent for females despite a slightly increasing trend.

An additional dimension of intraspecific morphometric variation was analyzed in Miño et al. [59], and sexual size dimorphism was also present in *D. pratensis* samples from a microspatial altitudinal gradient. Sexual size dimorphism was female-biased for all traits in most samples. However, there was no significant relationship between SSD and altitude (ALT) although third tibia length was significantly correlated with ALT in an inverse function. Also, in male grasshoppers from Cerro Ceferino, body length increased significantly and linearly with mean fusion frequency, with frequency of fusions L5/L6 and L3/L4. No trend was statistically significant in females. The body size pattern observed at a microspatial scale in *D. pratensis* [59] differentiates from that observed at a large geographic scale where size shows an inverse correlation with altitude and latitude [10, 12]. It was proposed that in Sierra de la Ventana the body size trend is a likely consequence of habitat segregation of two forms well adapted to contrasting microhabitats within the hybrid zone; this zone, although environmentally heterogeneous, only represents a very small fraction of the species total geographic range and environmental variability.

In this study [59] it was also shown that chromosomal variation of insects was also correlated to microgeographic location: in the Cerro Ceferino Hill, the four fusions characteristic of the hybrid zone varied widely in the sampled grasshoppers, with mean frequency values (F) ranging from 2.5 to 3.0. Fusion L1/L6 was only recorded at the hill base. The frequencies of L1/L2 and L5/L6 increased towards the top of the hill reaching fixation in most samples; fusion L3/L4, showed high frequencies in all samples. Mean fusion frequency and frequencies of fusions L1/L2, L3/L4, and L5/L6 were positively correlated with altitude.

Molecular variation in *D. pratensis* from the Cerro Ceferino, a microspatial altitudinal gradient within the Sierra de la Ventana hybrid zone, was also assessed by Miño et al. [59] using RAPD primers. Significant differences were found in mean heterozygosity values among samples from the hill base to the top, samples from the slope being the more genetically variable. Moreover, samples from the hill base and top were significantly differentiated genetically (as revealed by Wright's 1951 F_{ST}; see Table 5 in [59]).

In conclusion, data of this study [59] revealed a pattern of morphological variation and genetic differentiation within very short distances in *D. pratensis* populations from Sierra de la Ventana hybrid zone. It was proposed that the observed pattern reflects local adaptation at a very small geographical altitudinal gradient, favored by differential adaptation of chromosomal hybrids (genotype combinations) that vary in fitness to heterogeneous abiotic and biotic conditions.

3. Discussion and Conclusions

The results reviewed in this paper have shown that two neotropical melanopline species, *Dichroplus pratensis* and *D. vittatus*, with largely overlapping but usually not locally sympatric geographic distributions, follow the converse to Bergmann's rule. These inverted patterns cannot be attributed to thermoregulatory responses but to interaction with abiotic environmental factors such as seasonality that shorten the time available for development, growth, and reproduction and others that control primary productivity and access to resources. Allen's rule was also not verified but a converse pattern or absence of pattern indicating that, again, thermoregulation is not involved in the proportion of protruding body parts. The observed trends are probably a byproduct of the converse Bergmannian pattern and allometric growth. The countergradient body size variation also indirectly affects Rensch's rule but in opposite ways in both species so that *D. vittatus* follows the rule while *D. pratensis* inverts it. It is important to note that the relationship between body size and abiotic factors produces in both cases a central-marginal size pattern, which in both species involves also an increase of size variability towards the margins. Furthermore, in *D. pratensis* the pattern is closely followed by a complex polymorphic chromosomal system that regulates genetic recombination probably as a selective response to increasing unpredictability of the environment towards the margins of the distribution. Most of these patterns are repeated at a microspatial scale in *D. pratensis*.

However, it is possible that the effect of abiotic factors on body size and life history characteristics follows different paths in different species. A brief survey of the orthopteran literature in this respect suggests the former but also highlights some common points. In the bushcricket *Poecilimon thessalicus* (Phaneropterinae), collected at three mountain ranges in eastern Greece, it has recently been demonstrated that individuals of populations from the eastern slopes were consistently larger than those from the western slopes. Since these size differences cannot be attributed to a large geographic distribution (less than 1 degree latitude and longitude although altitude varied between 400 and 1,800 masl), no large temperature differences are expected to exert profound effects on body size. Thus, the most probable explanation of this size variation is that, in the dryer western slopes, growing season is shorter thus producing smaller individuals [62].

Another study involving the flightless bushcricket *Pholidoptera frivaldskyi* analysed three extremely isolated populations of this species. This bushcricket is endangered and inhabits fragments of mountainous areas (550–1800 masl in elevation) at the Carpathian Mountains and montane areas in Bulgaria, Serbia, Bosnia, and Macedonia. However, it has not been recorded out of Slovakia for more than 40 y. Despite their isolation, all three populations did not show consistent differences in body size apart from the intrapopulational ones. This may indicate a similar environmental effect of ambient conditions on the phenotypic plasticity of the populations and a genetic uniformity aided by the small size of the populations and a relatively recent origin before fragmentation [63].

In a study of species composition and body size of Tettigoniid species in Atlantic coast salt marshes on *Spartina alterniflora* (Poaceae) communities (latitudinal range, 13.19°), Fabriciusová et al. [63] showed converse Bergmannian patterns for two species, *Orchelimum fidicinium* and *Conocephalus spartinae*. *O. fidicinium*, the largest species, dominated the tettigoniid community at low latitudes and *C. spartinae,* the smallest species, at high latitudes. Furthermore, both species showed a converse Bergmannian pattern at the intraspecific level, individuals being progressively smaller towards higher latitudes. According to the authors several factors might explain this shift in dominance and size trends, including changes in climate, plant phenology, and plant zonation patterns.

Altitudinal body size clines have been less explored in Orthoptera. However, recently, Ciplak et al. [64] have shown converse Bergmannian clines for a grasshopper (*Oedipoda miniata*) and a katydid (*Poecilimon birandi*) along a 2,000 m altitudinal gradient in Anatolia (Turkey). Although the authors did not explore the relationship between body size and abiotic factors, they found that, in both species, larger *O. miniata* individuals were found at sites of higher densities of the species and lower sizes where grasshopper diversity was higher (thus suggesting that interspecific competition could play a role in determining body size). Nevertheless, they suggested that sites of high density are the most ecologically favourable (central), which possibly depend on a combination of abiotic factors that maintain an environment supportive of larger body sizes.

It is thus clear that most well-studied Orthoptera follow the converse to Bergmann's rule and that the most probable explanation for these trends is not thermoregulatory but has to do with increasing seasonality, availability of resources, and growth and developmental time [10, 12, 42–45, 65, 66].

The study of abiotic factors that influence the distribution of geographic body size of animals is thus relevant from several points of view. The confluence of climatic and ecological factors affects so many life history characteristics that knowledge about the trade-offs between the biology of organisms and the environment is essential for a true comprehension of the evolutionary history of species and higher taxa as well as the impact of ongoing and prospective climatic change on their geographic distribution. In the case of Melanopline grasshoppers, and especially those of the *maculipennis* group treated in this paper, biotic and abiotic factors and body size variation may be correlated with complex chromosome polymorphisms. As we demonstrated in *D. pratensis* marginal populations occupy ecologically suboptimal environments in southern margins (Patagonia) and in high altitude in the sub-Andean populations at more than 2,400 m above sea level in the northwest. In these populations the morphological (and genetic) variability increases with the decrease in body size. The release of genetic variability due to high recombination would favor adaptation of natural populations to harsh environments in marginal regions. Although *D. vittatus* is not chromosomally polymorphic, it exhibits the same body size trends of *D. pratensis* (except for sexual size dimorphism) within the same general geographic area. Harsh abiotic and biotic conditions in marginal areas and increasing seasonality determine the shortening of the time available for growth and development, thus allowing for lower body sizes as well as small, low-density, sparsely distributed populations. Marginal areas are zones of continuous extinction and recolonisation according to changing climatic conditions. This is of relevance in the context of current climatic change because increasing temperature may allow the expansion of these species, which are serious crop pests in some parts of their ranges, allowing for the transformation of previous marginal areas into more favorable ones. It is thus of utmost importance to recognize abiotic and ecological body size predictors that may help understand future range expansions and prospective outbreaks.

Acknowledgments

The authors wish to thank Dr. Matilda Savopoulou-Soultani for her kind invitation to participate in this special issue of *Psyche*. An anonymous referee provided valuable suggestions. Valeria Ximena Rodríguez was extremely helpful in the preparation of the definitive manuscript. This work was partially financed through Grant PICTO 37035 FONCyT to D. A. Martí. E. R. Castillo is a Ph.D. candidate at Universidad Nacional de Córdoba (Ph.D. in Biological

Sciences). C. I. Miño is thankful to CAPES (Brazil) for her postdoctoral fellowship (PRODOC 2637/2010). D. A. Martí acknowledges the continuous support of Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET). C. J. Bidau acknowledges Universidad Nacional de Río Negro (Argentina) for numerous benefits in his present professorial position and dedicates this paper to his dear friend Alejandra Pilar Rendina for her endless love, continuous support, and stimulating discussions.

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Hindawi Publishing Corporation
Psyche
Volume 2012, Article ID 235840, 11 pages
doi:10.1155/2012/235840

Research Article

Properties of Arboreal Ant and Ground-Termite Nests in relation to Their Nesting Sites and Location in a Tropical-Derived Savanna

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Received 11 July 2011; Revised 5 October 2011; Accepted 19 December 2011

Academic Editor: Panagiotis Milonas

Ecosystem engineers such as ants and termites play an important role in the fertility of tropical soils. Physicochemical analyses were thus carried out on some arboreal ant nests collected from mango (*Mangifera indica*), bush mango (*Irvingia gabonensis*), kola (*Cola nitida*), newbouldia plant (*Newbouldia laevis*), and oil bean plant (*Pentaclethra macrophylla*) and on ground nest of termite, *Odontotermes sudanensis* Sjost. (Isoptera: Termitidae) in Nigeria. Arboreal nests, particularly those of *M. indica*, were significantly richer in the chemical constituents sampled, compared to those of ground-termite nests or adjacent unaffected soils. Available water capacity of nests from *M. indica* (60.0%) was significantly higher than those of other sites or locations sampled. While biogenic structures were sandy-loamy in texture, their corresponding adjacent soils were either sandy or sandy-loamy. Soils worked by ants and termites had greater proportions of silt-sized (17.9 versus 9.7) and clay-sized (19.2 versus 9.3) to the detriment of coarse-sized particles (51.2 versus 60.9) and fine-sand-sized particles (11.7 versus 20.1) relative to the adjacent soils. Generally, biogenic structures were about 348% richer in P than their corresponding adjacent soils; an attribute, which holds a strong promise in bioremediation and biofortification of soils especially during amendment.

1. Introduction

Tropical-derived savannah ecosystems are often dominated with patches of arboreal ant and epigeous termite nests (≈5 mounds/m^2). Ants are ubiquitous, diverse, and abundant in tropical ecosystems and represent up to 80% of animal biomass [1]. Tree crops are of great economic significance in the forests of Nigeria, and the ants which inhabit those trees profoundly affect the ecosystem dynamics through the modification, maintenance, and/or creation of habitats for other organisms in the forest ecosystem [2].

Ecosystem engineers such as ants and termites play an important role in the fertility of tropical soils. Physicochemical analyses were thus carried out on some arboreal ant nests collected from mango (*Mangifera indica*), bush mango (*Irvingia gabonensis*), kola (*Cola nitida*), newbouldia plant (*Newbouldia laevis*), and oil bean plant (*Pentaclethra macrophylla*) and on ground nest of termite, *Odontotermes sudanensis* Sjost. (Isoptera: Termitidae) in Nigeria. Arboreal nests, particularly those of *M. indica*, were significantly richer in the chemical constituents sampled, compared to those of ground-termite nests or adjacent unaffected soils. Available water capacity of nests from *M. indica* (60.0%) was significantly higher than those of other sites or locations sampled. While biogenic structures were sandy-loamy in texture, their corresponding adjacent soils were either sandy or sandy-loamy. Soils worked by ants and termites had greater proportions of silt-sized (17.9 versus 9.7) and clay-sized (19.2 versus 9.3) to the detriment of coarse-sized particles (51.2 versus 60.9) and fine-sand-sized particles (11.7 versus 20.1) relative to the adjacent soils. Generally, biogenic structures were about 348% richer in P than their corresponding adjacent soils; an attribute, which holds a strong promise in bioremediation and biofortification of soils especially during amendment.

Ants and termites as decomposers have been reported as the basis for soil formation [3]. Some of the outcome of this decomposition is nutrient release to the soil worked upon by these organisms. Extensive works have been done on the nutrient recycling, soil formation, and soil structural modification by these animals. Lee and Foster [4] observed that the activities of ants and termites together with their abiotic physical and chemical processes regulate the soil fertility and counteract the physical and chemical processes of soil degradation. Leprun and Roy-Noël [5], Boyer [6], and Mahaney et al. [7] reported a remarkable increase in the mineralogical properties of mounds built by ants and termites. Jouquet et al. [8] and Holt and Lepage [9] found enrichment in mineral nutrients (e.g., NH_4^+, NO_3^-) and exchangeable cations (e.g., Ca^{2+}, Mg^{2+}, K^+, and Na^+) on biogenic (nest) structures of termites as compared to that of the surrounding soils. Konaté et al. [10], Macmahon et al. [11], Kristiansen et al. [12] and Jouquet et al. [13] also observed that through the impact on soil by termites, their biogenic structures can constitute patches in the landscape where the availability of soil nutrients for plants is improved. Nests of the harvester ant *Pogonomyrmex barbatus* typically contain higher concentrations of organic matter, nitrogen, and phosphorus than surrounding soils [14]. Comparative studies by Jouquet et al. [15] on nests made by ants and termites revealed some changes in their soil nutrient properties. They suggested that these changes could be due to greater litter associated with ant nest relative to termite nests, which also could be responsible for changes in the morphology and performance of plants and the composition of plant communities in any agroecology.

Very special biogenic structures created by ants are the so-called ant gardens [2]. Jouquet et al. [2] also indicated that a clear agreement has been established between plant preferences for soil altered by termite activity and termite preferences for plant species growing on their own nests. Ants also have been reported to be capable of building nests of carton materials constructed around epiphytic roots thereby developing aggregation of artificial soil [16, 17]. Buckley [18] noted that direct positive effect of the engineering activity of ants lies in the development of a mutualistic relationships between the ants and the epiphytes, whereby the ants profit from the roots forming an integral part of the nest and increasing its structural stability and an abundant food source close to the nest. It could therefore be suggested that these soil engineers indirectly invade their own availability through the increase in colony fitness (i.e., better nourishment of nymphs, higher alate production, and survival) [2].

While the biogenic structures of these organisms have been shown to influence soil quality, microorganism activities, and plants, very little information is available about the differences in the nutrient status of the nest soils based on their nesting sites, biota, and soil locations. We therefore wanted to test the hypotheses that nest substrate (sites) does not influence nest soil properties and that nest soil properties are not a reflection of the initial soil properties when it was unaffected by soil engineers. The aims of this study therefore were to determine the physicochemical properties of the biogenic structures in relation to their nesting sites and biota nests and to compare the characteristics of these nests and their adjacent surface soil. Particle-size analyses of soils were used to assess the physical properties of the soils. The chemical properties of the soils were determined by estimating their C, N, organic matter, base saturation, cation exchange capacity (CEC), exchangeable bases, and P-contents, as well as their pH in both water and in KCl. To determine the availability of the chemical nutrients to plants and thus assess the relative importance of the various soil characteristics in the ecosystem, we also estimated the available water capacity (AWC) and the dispersion ratios (DR) of the various soils, in addition to the dispersibilities of their clay and silt fractions in both calgon and water. The specific objectives of this study thus were to

(i) determine the effect of different tree hosts on the physiochemical properties of nests they inhabit,

(ii) compare the physiochemical properties of biogenic structures with that of their adjacent unmodified soils,

(iii) ascertain the interaction effects of the nesting sites and soil location on the physiochemical properties of their soils.

2. Materials and Methods

2.1. Study Site and Species Studied. Field samples of arboreal-ant and ground-termite nests were collected at Orba Nsukka in Udenu Local Government Area of Enugu State in Southeast Nigeria (06° 52′N, 07° 24′E; altitude 442 m above mean sea level). Nsukka is situated in a derived savannah belt with some relics of rainforest distributed in patches [19]. The soil is well-drained reddish-brown Typic Paleustult [20]. The annual bimodal rainfall is 1800 mm and spans from April to November of each year [21], with peaks around July and September. The mean monthly temperatures vary between 25°C and 32°C [22]. The study site is a grassy humid savannah with sparse shrub vegetations intermingled with palm trees and some other tree plants forming patches of thickets.

2.2. Field Sample Collection. Six biogenic structures (comprising five from different trees and one from ground soil termite nest—termitarium) were sampled for this study. The five trees were mango (*Mangifera indica*), bush mango (*Irvingia gabonensis*), kola (*Cola nitida*), newbouldia (*Newbouldia laevis*), and oil bean plant (*Pentaclethra macrophylla*). Biogenic structures (nests) collected from ants and termite nests and the adjacent surface soils (control) were regarded as two soil locations. This is to be able to compare the constituents of nest and unmodified surface soil. Ant arboreal nests were built by *Camponotus acvapimensis* Mayr. (Hymenoptera: Formicidae), while the termite nest was built by *Odontotermes sudanensis* Sjost. (Isoptera: Termitidae). Each ant arboreal nest sample was collected from two trees of the same tree species and about the same age and height to represent the two replications of each treatment. Ground-termite nest samples were taken in pairs from the same soil type (Typic Paleustult) also. Termite mounds were collected and excavated from 0 to 10 cm depth from actively forming nests from the open field. Adjacent soils (without any visible termite—or ant—activity) were sampled at the same depth

(0–10 cm depth) and 6 m away from each habitat tree and termite mound. Sampling from adjacent unaffected soils was conducted in pairs from their surrounding environment. Nest samples were randomly collected from actively forming mound samples.

The entire arboreal carton ant nests were pried from their host trees, placed in plastic bags and taken to the laboratory for analysis. The nests were dissected by segmental shaving after being air-dried for seven days to remove the ants. The corresponding termite nests collected were also placed inside plastic bags and taken to the same laboratory after being air-dried for seven days. All samples were sieved with 2 mm mesh and used for laboratory analysis. Each laboratory result was read in triplicate for each sample.

2.3. Laboratory Analysis. The particle-size analyses of soils, termite, and carton nests were determined by the hydrometer method as described by Gee and Bauder [23] using sodium hexametaphosphate (Calgon) dispersant while dieonised water was used separately to disperse soil mechanically only after soaking for 24 hours and distilled water separately as dispersants. The percentage clay-sized and silt-sized particles obtained using calgon were regarded as the total clay and total silt while those obtained with water alone were assumed to be water dispersible clay and silt.

Soil pH for soils and ant/termite affected soil in both 1 : 2.5 soil: 0.1 M KCl suspension and in a soil/water suspension ratio using a Beckman Zeromatic pH meter were determined. The soil organic carbon was determined by a modified acid dichromate oxidation procedure according to Walkey and Black [24] as described by Nelson and Sommers [25]. The percentage organic matter was calculated by multiplying values obtained by "Van Benmelin" factor of 1.724. The exchangeable cations and acidity were determined by the method described by Thomas [26]. The cation exchange capacity (CEC) was calculated as the total of all the exchangeable cations.

Total (Kjeldahl) nitrogen was measured with a block digester [27] and distilled using NaOH. Available P was determined using Bray and Kurtz [28] method. AWC was calculated by Klute [29] method.

Dispersion ratio (DR) was calculated as (WDSi + WDC)/(Tsilt + Tclay), where WDSi is the water dispersible silt, WDC is the water dispersible clay, Tsilt is the total silt and Tclay is the total clay.

The laboratory analyses results were read in triplicates (three times) for each sample.

2.4. Data Analysis. Treatments comprised factorial combinations of six nesting sites of ants and termites nests and two soil locations (adjacent soils and biogenic structures) arranged in a completely randomized design (CRD). These treatment combinations were each replicated two times. The laboratory results were read in triplicates (three times) for each sample making a total of six replications on the whole. Treatment effects were tested through analysis of variance (ANOVA) and differences between means were tested with Duncan's New Multiple Range Test (DNMRT). Differences were only considered significant when P values were lower than or equal to 0.05. Percent values were subjected to angular (inverse sine) transformation (arcsin $\sqrt{x}$), before analyses of variance were carried out on them.

3. Results

The AWC of ant nests from *Cola, Irvingia*, *Newbouldia,* and termitaria did not differ ($P > 0.05$) with one another statistically, but were significantly ($F = 4.08$; d.f. $= 5$; $P < 0.05$) lower than the AWC of ant nests collected from *Mangifera* (Table 1). The AWC of *M. indica* hosted nests (60%) was significantly higher than the AWC obtained from *C. nitida* (42.3%), *I. gabonensis* (30.4%), *N. leavis* (43.3%), termitaria (44.6%), and *P. macrophylla* (46.7%). Differences amongst the nesting site effects on dispersion ratios (DRs) of nest soils, calgon and water dispersible clay, clay + silt, and silt were not significant. However, there were evident trends of higher calgon dispersible clay + silt and silt and water dispersible clay and clay-silt on arboreal ant nests than on epigeous termite ground mounds. Similarly the AWC (53.8%), calgon dispersible clay (19.2%), clay + silt (36.5%), and silt (15.9%) and water dispersible clay (22.1%), clay + silt (32.8%), and silt (7.7%) were found to be significantly higher on biogenic structures compared to their corresponding adjacent surface soil values of 36.0%, 9.3%, 19.4%, 8.8%, 9.5%, 12.7%, and 3.3%, respectively (Table 2). Although the differences produced by the effect of soil location amongst the dispersion ratio (DR) were not statistically significant, the DR of the biogenic structure was relatively higher compared with those of their adjacent soils.

Except for the total dispersible silt which differed significantly when the effect of the nesting sites was combined with the soil types, the AWC, DR, and other calgon or water dispersible soil fractions did not show such statistical differences ($P > 0.05$) under comparable combined treatment effects (Table 3). This is such that ant nests of biogenic structure on *I. gabonensis* contained significantly ($F = 3.75$; d.f. $= 5$; $P < 0.013$) higher calgon dispersible silt (28.6) than other nest structures or adjacent soil, while the adjacent soil around *C. nitida* (5.6), *I. gabonensis* (6.6), *M. indica* (13.6), *N. leavis* (8.5), *P. macrophylla* (9.6), and the termitaria contained significantly ($F = 3.75$; d.f. $= 5$; $P < 0.013$) lower calgon dispersible silt than other soils. However, there were glaring trends of numerically higher AWC, DR, and soil dispersibilities amongst the nest structures collected from any of the substrates than their corresponding adjacent soils.

The percent C and N, SOM, base saturation, exchangeable bases, and pH values differed significantly amongst the various soil engineering host substrates (Table 4). The carbon contents of kola (7.32%), bush mango (9.14%), mango (6.98%), newbouldia (7.01%), and oil bean (8.27%) were significantly ($F = 11.94$; d.f. $= 5$; $P < 0.001$) higher than the C content of termitarium (1.23%). The same trend also followed in Mg^{2+}. N was significantly ($F = 15.28$; d.f. $= 5$; $P < 0.001$) higher in oil bean compared to samples, while Ca^{2+} was higher in Kola (5.15 meq/100 g sample) and newbouldia (6.0 meq/100 g sample) compared to others.

Table 1: Main effects of soil engineers nesting substrates (sites) on the mean available water capacity (AWC), dispersion ratio (DR), and calgon and water dispersibilities of the biogenetic structure's clay, clay and silt, and silt.

Soil engineer	Nesting Site	AWC^1 (%)	DR	Calgon dispersed			Water dispersed		
				Clay	Clay + silt	Silt	Clay	Clay + silt	Silt
Ant	*C. nitida*	42.3_{ab}	0.72_{a}	12.5_{a}	23.5_{a}	10.6_{a}	15.2_{a}	17.8_{a}	2.5_{a}
Ant	*I. gabonensis*	30.4_{a}	0.71_{a}	16.0_{a}	34.0_{a}	17.6_{a}	20.7_{a}	24.8_{a}	4.1_{a}
Ant	*M. indica*	60.0_{c}	0.76_{a}	17.5_{a}	35.0_{a}	14.5_{a}	16.2_{a}	24.8_{a}	8.8_{a}
Ant	*N. leavis*	43.3_{ab}	0.70_{a}	10.5_{a}	25.0_{a}	11.1_{a}	10.4_{a}	19.8_{a}	5.6_{a}
Ant	*P. macrophylla*	46.7_{b}	1.16_{a}	15.5_{a}	27.5_{a}	11.6_{a}	21.7_{a}	33.7_{a}	7.1_{a}
Termite	Ground	44.6_{ab}	0.71_{a}	13.5_{a}	22.5_{a}	8.6_{a}	10.7_{a}	15.8_{a}	5.1_{a}
	F-value	4.08	2.11	2.10	0.94	1.16	0.91	0.93	1.60
	d.f.	5	5	5	5	5	5	5	5
	P value	0.005	0.087	0.088	0.469	0.348	0.485	0.471	0.201

AWC: available water capacity and DR: dispersion ratio.

[1] Results of angular transformed data presented in the original scale.

Values within a column followed by the same letter are not significantly different.

Table 2: Main effect of soil locations on the mean available water capacity (AWC), dispersion ratio (DR), calgon and water dispersed clay, clay/silt, and silt of different soil locations.

Soil location	AWC^1 (%)	DR	Calgon dispersed			Water dispersed		
			Clay	Clay + silt	Silt	Clay	Clay + silt	Silt
Adjacent soil	36.0_{a}	0.69_{a}	9.3_{a}	19.4_{a}	8.8_{a}	9.5_{a}	12.7_{a}	3.3_{a}
Biogenic structures	53.8_{b}	0.89_{a}	19.2_{b}	36.5_{b}	15.9_{b}	22.1_{b}	32.8_{i}	7.7_{a}
t-value	961.23	6.07	39.68	108.0	87.6	287.41	164.28	480.00
d.f.	1	1	1	1	1	1	1	1
P value	<0.001	0.220	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001

AWC: available water capacity and DR: dispersion ratio.

[1] Results of angular transformed data presented in the original scale.

Values within a column followed by the same letter are not significantly different.

Table 3: Interaction effects of soil engineers' nesting substrates (sites) and soil locations on the values of some soil properties of biogenic structures and their adjacent soils.

Soil engineer	Nesting site	Soil location	AWC^1 (%)	DR	Calgon dispersed			Water dispersed		
					Clay	Clay + silt	Silt	Clay	Clay + silt	Silt
Ant	*C. nitida*	Adj. soil	30.3_{a}	0.65_{a}	6.5_{a}	12.0_{a}	5.6_{a}	7.2_{a}	7.8_{a}	0.56_{a}
		B. structure	54.2_{a}	0.68_{a}	19.6_{a}	13.0_{a}	15.6_{b}	23.2_{a}	27.8_{a}	4.56_{a}
Ant	*I. gabonensis*	Adj. soil	31.0_{a}	0.68_{a}	6.5_{a}	13.0_{a}	6.6_{a}	7.2_{a}	8.8_{a}	1.56_{a}
		B. structure	29.7_{a}	0.74_{a}	26.5_{a}	55.0_{a}	28.6_{c}	34.2_{a}	40.8_{a}	6.56_{a}
Ant	*M. indica*	Adj. soil	40.0_{a}	0.75_{a}	14.5_{a}	33.0_{a}	13.6_{ab}	15.2_{a}	20.8_{a}	6.06_{a}
		B. structure	83.9_{a}	0.75_{a}	21.5_{a}	37.0_{a}	15.5_{b}	17.2_{a}	28.8_{a}	11.56_{a}
Ant	*N. leavis*	Adj. Soil	36.2_{a}	0.63_{a}	6.5_{a}	15.0_{a}	8.6_{a}	7.2_{a}	8.8_{a}	1.56_{a}
		B. structure	50.9_{a}	0.77_{a}	16.6_{a}	35.0_{a}	13.6_{ab}	13.7_{a}	30.8_{a}	9.56_{a}
Ant	*P. macrophylla*	Adj. soil	39.9_{a}	0.73_{a}	13.5_{a}	23.0_{a}	9.6_{ab}	11.2_{a}	16.7_{a}	5.56_{a}
		B. structure	53.5_{a}	1.60_{a}	18.5_{a}	32.0_{a}	13.6_{ab}	32.2_{a}	50.8_{a}	8.56_{a}
Termite	Ground	Adj. soil	38.4_{a}	0.72_{a}	11.5_{a}	20.0_{a}	8.6_{ab}	9.2_{a}	13.8_{a}	4.56_{a}
		B. structure	50.8_{a}	0.70_{a}	16.5_{a}	25.0_{a}	8.6_{ab}	12.2_{a}	17.8_{a}	5.56_{a}
		F-value	0.92	2.44	0.68	2.62	3.75	0.55	0.89	2.14
		d.f.	5	5	5	5	5	5	5	5
		P value	0.489	0.066	0.641	0.053	0.013	0.737	0.502	0.099

AWC: available water capacity; DR: dispersion ratio; B. structure: biogenic structure; Adj. soil: adjacent soil.

[1] Results of angular transformed data presented in the original scale.

Values within a column followed by the same letter are not significant different.

Table 4: Main effects of soil engineers' nesting substrate (site) on the mean values of some physicochemical properties of their biogenic structures.

Soil engineer	Nesting site	C^1 (%)	N^1 (%)	SOM^1 (%)	Base^1 Sat. (%)	CEC	Exchangeable bases				pH value		P (mg/kg)	Particle size (%)^1				Textural class
							Ca^{2+}	Mg^{2+}	K^+	Na^+	H_2O	KCl		Clay	Silt	Fine sand	C. Sand	
Ant	*C. nitida*	7.32_b	0.37_{ab}	12.6_b	40.9_c	27.9_a	5.15 + I	5.20_e	0.59_a	0.51_a	6.38_{ab}	6.33_b	53.9_c	12.5_a	11.0_a	17.0_a	59.5_a	SL
Ant	*I. gabonensis*	9.14_b	0.88_b	15.8_{bc}	36.3_{bc}	45.3_a	2.80_a	5.75_f	1.74_b	0.51_a	6.75_{ab}	6.30_b	54.2_c	16.0_a	18.0_a	11.5_a	54.5_a	SL
Ant	*M. indica*	6.98_b	0.46_{ab}	12.0_b	22.7_{ab}	39.2_a	2.15_a	1.95_{bc}	1.69_b	0.46_a	6.28_a	5.68_a	43.0_b	17.5_a	15.0_a	10.2_a	57.2_a	SL
Ant	*N. leavis*	7.01_b	0.41_{ab}	16.5_c	36.2_b	45.5_a	6.08_b	4.50_d	1.03_a	0.54_a	7.28_b	6.35_b	47.0_b	10.5_a	13.5_a	16.8_a	55.5_a	SL
Ant	*P. macrophylla*	8.27_b	1.28_b	14.4_b	20.0_a	36.1_a	2.15_a	2.30_c	1.78_b	0.49_a	6.80_b	6.18_b	42.8_b	15.5_a	12.0_a	19.1_a	53.2_a	SL
Termite	Ground	1.23_a	0.19_a	2.5_a	20.9_a	36.2_a	1.45_a	1.00_a	0.20_a	0.45_a	6.60_{ab}	5.63_a	23.6_a	13.5_a	9.0_a	20.5_a	56.5_a	SL
	F-value	11.94	15.28	9.66	3.83	1.86	38.48	20.05	47.66	2.14	12.99	8.49	5.28	0.92	2.62	0.68	0.55	
	d.f.	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	
	P value	<0.001	<0.001	<0.001	0.012	0.142	<0.001	<0.001	<0.001	0.098	<0.001	<0.001	0.002	0.489	0.053	0.641	0.731	

SOM: soil organic matter and SL: sandy loam; C. Sand: coarse sand; P: phosphorus. C: carbon; N: nitrogen; CEC: cation exchange capacity.

[1] Results of angular transformed data presented in the original scale.

Values within a column followed by the same letter are not significantly different.

K^+ was significantly higher ($F = 47.66$; d.f. = 5; $P < 0.001$) in *Irvingia* (1.74 meq/100 g sample), mango (1.69 meq/100 g sample), and oil bean (1.78 meq/100 g samples) relative to other soil engineer nests. The soil pH in H_2O was lower in kola (6.38), *Irvingia* (6.75), mango (6.28), and termitaria (6.60) compared to other nesting sites. Although SOM, the base saturation, CEC, P, and particle-size distributions did not differ between ant and termite nests, there were clear trends of numerically higher values in the ant nests compared to the termite nests. Based on Black [30] classifications, the values of organic C obtained amongst the ant nests were high (between 6.98 and 9.14%) compared to termite nests (1.23%). Similarly, SOM content of *N. leavis* was significantly higher ($F = 9.66$; d.f. = 5; $P < 0.001$) than other nests, except those from *I. gabonensis* (15.8%). Base saturation of *C. nitida* was significantly ($F = 3.85$; d.f. = 5; $P < 0.012$) higher than those of other nests, except those of Irvingia (36.3%). The N-contents of between 0.37 and 1.28% obtained amongst ant nests were classified as very high compared to 0.19% obtained from termite nests according to Metson [31] classification. Again, the SOM of between 12% and 16.5% from ant nests was considered high compared to SOM of 2.5% obtained from termite nests according to Metson [31]. Similarly, by FAO [32] classification, all the tree-ant nests except those of *P. macrophylla* with base saturations of between 23 and 41% would be regarded as having medium fertility as opposed to ground-termite nests and *P. macrophylla* nests with base saturation of 20% each and classified as belonging to soils of low fertility. Similarly, both the tree-ant nests and ground-termite nests have high phosphorus content (23.6–54.2 mg/kg) judging by Enwezor et al. [33] classification. The exchangeable Ca^{2+} ranged from low to moderately high in tree-ant nest when compared to ground-termite nest with very low Ca^{2+} [30]. Also K^+ was high in tree-ant nests relative to the very low value obtained in the ground-termite nests using the classification of Black [30]. Conversely, Mg^{2+} content of tree-ant nests was moderately high compared to the termite nest which was very low after Black [30] classification. Except for *N. leavis* ant nests with neutral (pH = 7.28) soil reaction, all the ant- and termite-nest soils were slightly acidic with a pH range of between 6.2 and 6.8. The particle-size distribution of the various soil fractions showed that the ecosystem engineers' nests were all of sandy-loamy soil, while their corresponding adjacent soils were predominantly sandy soils.

The result of the soil location effect on chemical compositions showed that biogenic structures contain significantly higher percentages of organic carbon (12.6%), nitrogen (1.10%), organic matter (23.3%), base saturation (33.9%), CEC (51.4%), Ca^{2+} (4.92%), Mg^{2+} (5.2%), K^+ (2.21%), Na^{2+} (0.53%), and phosphorus (44.1%) than their respective adjacent soil nutrient contents of 0.74%, 0.10%, 1.30%, 25.4%, 1.67%, 1.70%, 0.13%, 0.46%, and 16.1% (Table 5). Similarly, both the pH and particle-size distribution of clay-sized (19.20%) and silt-sized (17.9%) particles in the structures were significantly higher for the nest structures compared with those of their adjacent surface soils of 9.3% and 9.7%, respectively. Both the particle sizes of coarse and fine sand fractions as well as the soil reactions in both H_2O and KCl of the nest structures did not differ significantly with those of their adjacent soil.

Differences in the combined effects of the nest substrates of soil engineers and soil locations differed significantly with respect to all the physiochemical properties assessed, except Na^+ content and coarse sand distribution (Table 6). There was a consistent trend of these constituent being higher amongst biogenic structure of ants and termites in the different substrates as opposed to their corresponding adjacent soils. Conversely, in all the chemical properties assessed, the unmodified adjacent soils did not show significant differences amongst the different nest substrates as the nest soils to their microhabitat. Furthermore, the interaction effects of nest sites and soil locations were only significant for C, N, SOM, base saturation. CEC, exchangeable bases (Ca^{2+}, K^+, and Mg^{2+}), soil-pH, clay, and silt contents. This is such that they were significantly higher in the various ant-tree nests (biogenic structures) than in ground-termite mound nest and their corresponding surrounding adjacent soils, except amongst the termitaria (Table 6).

4. Discussion

Soil engineers, notably ants and termites, have been reported to play important roles in the soil fertility in tropical ecosystems because of their impact on the soils they work on [2, 9, 13]. In the present study, however, efforts were made to ascertain whether these modifications significantly differed between biogenic structures of different soil engineers (ants and termites) and also if the modifications within biogenic structures were different for different nesting sites (trees) or locations.

Results of the laboratory assays however showed that the physicochemical properties of the ant biogenic structures were glaringly higher than those of the termites. Tree ants generally are exposed to more diverse range of plant litter diets and foraging materials than ground termites due to their proximity to dense litter falls from tree hosts. There is therefore always an increased resource access associated with ant nest construction relative to termite nest construction. This could therefore be harnessed in biofortifications of our impoverished tropical agricultural soils. Again, not only the soils of nests worked upon by the ecosystem engineers precisely contained higher values of the constituents assessed than their corresponding adjacent soils, but also their nesting sites played a major role in their constituents. Nesting sites differed as to their AWC, DR, and their dispersibilities in both calgon and water but their differences were not significant except for the AWC. Ant nests on *M. indica* consistently had higher AWC relative to other ant plant nests or epigeous termite ground nest. The higher AWC of ant nests from *M. indica* biogenic structures suggest higher tendency of ensuring more water in available form for crop development than those of other soils locations or nesting sites, which makes it still a good promise for biofortification. The process of soil dispersion in either water or calgon which is a function

Table 5: Main effect of soil locations on the mean values of some physicochemical properties of different soils types.

Soil location	C^1 (%)	N^1 (%)	SOM^1 (%)	$Base^1$ sat. (%)	CEC	Exchangeable bases				pH value		P (mg/kg)	Particle size $(\%)^1$				Textural class
						Ca^{2+}	Mg^{2+}	K^+	Na^{2+}	H_2O	KCl		Clay	Silt	Fine sand	Coarse sand	
Adj. soil	0.74_a	0.10_a	1.30_a	25.1_a	25.4_a	1.67_a	1.70_a	0.13_a	0.46_a	6.66_a	5.94_a	16.1_a	9.3_a	9.7_a	20.1_a	60.9_a	LS
B. structure	12.57_b	1.10_b	23.30_b	33.9_b	51.4_b	4.92_b	5.20_b	2.21_b	0.53_b	6.85_b	6.21_b	72.1_b	19.2_b	17.9_i	11.7_a	51.2_a	SL
t-value	321.86	143.75	271.07	6.07	51.52	175.53	96.79	686.77	13.45	7.07	7.40	197.69	16.53	19.31	1.74	3.12	—
d.f.	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	—
P value	<0.001	<0.001	<0.001	0.022	<0.001	<0.001	<0.001	<0.001	0.001	0.014	0.012	<0.001	<0.001	<0.001	0.200	0.091	—

SOM: soil organic matter; LS: loamy soil; SL: sandy loam; B. structure: biogenic structure; Adj. soil: adjacent soil; P: phosphorus. C: carbon; N: nitrogen; CEC: cation exchange capacity.

[1] Results of angular transformed data presented in the original scale.

Values within a column followed by the same letter are not significantly different.

Table 6: Interaction effects of soil engineers' nesting substrates (sites) and soil locations on the mean values of some physicochemical properties of soil engineers' biogenic structures and their adjacent soils.

Soil engineer	Nesting site	Soils locations	C^1 (%)	N^1 (%)	SOM^1 (%)	$Base^1$ sat. (%)	CEC	Exchangeable bases				pH value		P (mg/kg)	Particle size $(\%)^1$				Textural class
								Ca^{2+}	Mg^{2+}	K^+	Na^{2+}	H_2O	KCl		Clay	Silt	Fine sand	Coarse sand	
Ant	*C. nitida*	Adj. soil	0.6_a	0.09_a	1.1_a	36.2_b	12.2_a	1.9_{sb}	1.30_a	0.12_a	0.47_a	6.8_{sb}	6.2_{sb}	17.9_s	6.0_a	6.0_a	33.5_a	54.5_a	S
		B. structure	14.0_b	0.65_a	24.2_b	45.6_b	43.6_c	8.4_c	9.10_e	1.06_b	0.54_a	6.8_{sb}	6.5_b	90.0_b	19.0_b	16.0_{sb}	0.5_a	64.5_a	SL
Ant	*I. gabonensis*	Adj. soil	0.5_a	0.08_a	0.8_a	48.9_b	18.0_a	1.7_{ab}	4.00_c	0.14_a	0.48_a	6.7_{sb}	6.3_b	10.9_a	6.0_a	7.0_a	23.0_a	64.0_a	S
		B. structure	17.8_b	1.69_b	30.7_c	23.6_a	72.6_d	3.9_b	7.50_d	3.33_c	0.54_a	6.8_{sb}	6.4_b	97.5_b	26.0_b	29.0_b	0.0_a	45.0_a	SCL
Ant	*M. indica*	Adj. soil	0.7_a	0.11_a	1.2_a	8.9_a	36.6_{bc}	1.1_a	1.10_a	1.10_b	0.41_a	6.7_{sb}	5.7_{sb}	9.5_a	14.0_a	14.0_{sb}	7.0_a	65.0_a	SL
		B. structure	13.3_b	0.82_a	22.9_b	36.4_b	41.8_c	3.2_{ab}	2.80_b	3.27_c	0.51_a	6.4_{sb}	5.7_{sb}	76.6_b	21.0_b	16.0_{sb}	13.5_a	49.5_a	SCL
Ant	*N. leavis*	Adj. soil	0.7_a	0.08_a	1.4_a	26.2_a	25.0_a	2.5_{ab}	1.70_a	0.17_a	0.51_a	7.4_b	6.4_b	18.8_a	6.0_a	11.0_a	20.0_a	63.0_a	S
		B. structure	13.2_b	0.79_a	31.5_c	46.1_b	66.0_d	9.7_c	7.30_d	1.89_{bc}	0.58_a	7.2_b	6.4_b	75.2_b	15.5_b	21.0_b	14.5_a	49.0_a	SL
Ant	*P. macrophylla*	Adj. soil	1.0_a	0.14_a	1.7_a	16.8_a	28.6_b	1.7_{ab}	1.40_a	0.18_a	0.48_a	6.1_a	5.4_a	13.4_a	13.0_a	10.0_a	22.0_a	55.0_a	SL
		B. structure	15.6_b	2.41_b	27.2_b	23.2_a	43.6_c	2.6_{ab}	3.20_b	3.37_c	0.51_a	7.5_b	7.0_b	72.1_b	18.0_b	14.0_{sb}	16.5_a	51.5_a	SL
Termite	Ground	Adj. soil	1.0_a	0.11_a	1.7_a	13.5_a	31.8_b	1.1_a	0.70_a	0.08_a	0.40_a	6.1_a	5.9_{sb}	25.9_a	11.0_a	10.0_a	15.0_a	64.0_a	LS
		B. structure	1.5_a	0.27_a	3.4_a	28.4_b	40.6_a	1.8_{ab}	1.30_a	0.33_a	0.51_a	6.4_{sb}	5.4_a	21.4_a	16.0_b	9.0_a	26.0_a	49.0_a	SL
		F-value	12.96	14.55	10.31	4.20	4.97	22.20	9.86	44.89	0.34	11.91	9.67	10.45	4.77	9.66	2.62	0.68	—
		d.f.	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	—
		P value	0.001	0.001	0.001	0.008	0.003	0.001	0.001	0.001	0.883	0.001	0.001	0.001	0.004	0.001	0.053	0.641	—

AWC: available water capacity; DR: dispersion ratio; S: sand; SL: sandy loam; SCL: sandy clay loam; LS: loamy sand; B. structure: biogenic structure; P: phosphorus. C: carbon; N: nitrogen; CEC: cation exchange capacity.

[1] Results of angular transformed data presented in the original scale.

Values within a column followed by the same letter are not significantly different.

of the soil organic matter content [34] and an index of nutrient availability to plants did not differ either between the nesting sites or between ant nests and termite nests.

Soil texture on the other hand was not significantly affected in the termite nest compared with the ant nests, but was considerably modified in the biogenic structures compared to their corresponding adjacent unmodified soil. Thus, the nests and their corresponding adjacent soils differed as to their textural classes. The soil engineers ensured greater mineralization of clay and silt which was found to be greatly higher in the biogenic structures than in the adjacent soils resulting in differences in their textural classes. All the soils affected by ants and termites had a greater proportion of clay and silt to the detriment of coarse and fine sand. This finding suggests that the ecosystem engineers prefer the selection of finer materials such as clay and silt for building of its structures, thus supporting the result of the ability of termites and ants to select building materials when presented with different physical size materials but not clay type [2, 35, 36]. Termites have been observed to favour finer particles in their mound constructions which match their ecological, physiological, and behavioural needs [35]. In this study, however, there was a clear distinction between the physical size distribution of soils worked by ants and those by termites. The greater proportion of clay and silt as opposed to sand on soils worked by ant and termites showed the greater impact of clay and silt than sand on soils worked upon by ants and termites in the course of their building activities.

Laboratory analyses of the various samples also showed that both the biota nesting sites and the soil locations richly influenced the SOM, base saturation, CEC, and soil-pH and significantly modified C- and N-contents and their exchangeable bases. It suggests therefore that there was more enrichment of C and N and exchangeable bases (Ca^{2+}, K^{+}, Mg^{2+}, and Na^{+}) in antnests most especially in antnests built on *I. gabonensis* and *P. macrophylla* compared with the termitarium, as nest structures generally were to unaffected adjacent soils. Tree antnests were richer in C, N, SOM, and exchangeable bases (Ca^{2+}, K^{+}, Mg^{2+}, and Na^{+}) compared with the termite nests. This result counteracts our first hypothesis as nesting sites have been shown to influence some of the nest soil properties. Therefore, better nest soil enrichment will be assured when nests are harnessed from *I. gabonensis, N. leavis,* and *P. macrophylla* trees. The ability of ants and termites to work and move through the soil and to build organomineral structures with specific physical, chemical, and microbiological properties has been well documented [15, 37]. The higher mineral contents of the ant-nests relative to the termite nests and the surrounding soils could be explained by (i) the relative intensities with which the two organisms impact on the soil, (ii) the differential efficiencies of the two organisms in the mineralization of the various nutrients, (iii) the quantum of food (organic matter or litter material) available, or their diversity (structural, biochemical, or biological attributes), and (iv) the soil conditions or fertility where the nest soils were formed. That the adjacent soils of the different nest hosts did not differ significantly in this study goes to excluding soil conditions as possible explanation for the differences in the ant and termite nest's chemical content and thus supports the hypothesis that nest soil properties are not a reflection of the initial soil properties when they were unaffected by soil engineers. Jouquet et al. [8, 13] suggests availability of more diversified litter materials at the disposal of the ants than at the disposal of termites as the probable cause of this difference. The quantity of litter materials to be found deposited around trees were likely to be higher than the sparse grassy vegetations reminiscence of a derived savannah ecosystem from where the termite mounds were excavated. Although it has been reported that tropical ant diversity positively correlates with plant structures [38], it was still not clear if litter diversity affects litter nesting assemblages and compositions [39]. From the stand point of this result, ants may be considered to be more efficient in the mineralization of organic nutrients than termites. Enhancement of soil nutrient concentrations according to Wagner [40] may be of general importance in understanding how plants benefit from interaction with ants, especially if ants are more likely to nest near plants bearing extrafloral nectaries.

Also the less abundance of organic matter in soils worked by termites may be attributed to the microenvironment where the mounds are located. Jones et al. [41] observed that termite mounds are usually exposed to intensive sunlight which may reduce the activity of microbes involved in the decompositions of organic matter they contain.

All the ant-nest soils irrespective of tree host contain very significantly higher phosphorus content than termite nests. Also the biogenic structures of either ant or termites irrespective of their nesting sites were found to contain significantly higher P-content than those of their corresponding adjacent surface soils. Ant tree nests were between 81 and 130% richer in P-content than termite ground nests. Similarly, the biogenic structures generally were about 348% richer in P-content than their corresponding adjacent soils. The richer P-content of ant-nested structures of trees relative to the ground termite mounds could still be explained by the higher SOM content of the former as opposed to the latter and the efficient mineralization potential of ants over termites. The rich P-content of the nest soil especially the tree nests could enable them be recommended in the biofortification of acidic tropical soils deficient in phosphorus induced by Fe- and/or Al-toxicity problems.

5. Conclusion

The physicochemical properties of arboreal ant nests, the ground-termite nests, and their corresponding adjacent soils were studied in addition to the influence of nesting sites on nest soil characteristics. Nesting site influenced nest soil characteristics. Ant nests pried from tree tops especially those from *M. indica* were rich in most of the chemical properties assessed compared to those of epigeous ground-termite nests or the adjacent surface soil samples. Holistically, soils altered by soil engineers, notably ants and termites, were also predominantly greater in these basic nutrients relative to their adjacent unmodified soil, whereas soils collected from trees and ground nests were either sandy-loam or sandy-clay-loam in texture; those of their corresponding adjacent surface soils were mainly sandy for soils near trees and loamy-sand for soils near termitaria.

The higher influence of ants than termites on the maintenance of ecosystem heterogeneity through its soil bio-perturbation effects was therefore revealed in this work. Ants in addition to termites have also been seen to influence soil properties by making resources available for other organisms. These findings and more could therefore be harnessed by culturing these organisms and protecting some of these prospective nesting sites like *M. indica, P. macrophylla,* and *I. gabonensis* capable of hosting nests of high mineral content. Such nests could be harnessed for a variety of bio-remediation and biofortification purposes for human use. Purposes where the soil engineers could be utilized include landfills to decompose waste, improvement of soils by composting materials, detoxification of hazardous substances, and the production of biomass of animal feed and biochemical. Besides being fed upon by animals, solid wastes constituting environmental hazards are decomposed and readily converted into useful forms for soil improvement. The soil engineers-mediated chemical changes of soil, commonly represented mainly by a shift in pH towards neutral from acidity and an increase in nutrient content, helps in soil detoxification.

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Psyche
Volume 2012, Article ID 854045, 7 pages
doi:10.1155/2012/854045

Review Article

Abundance of *Sesamia nonagrioides* (Lef.) (Lepidoptera: Noctuidae) on the Edges of the Mediterranean Basin

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Received 5 September 2011; Revised 17 November 2011; Accepted 21 November 2011

Academic Editor: Matilda Savopoulou-Soultani

Organisms inhabiting seasonal environments are able to synchronize their life cycles with seasonal cycles of biotic and abiotic factors. Diapause, a state of low metabolic activity and developmental arrest, is used by many insect species to cope with adverse conditions. *Sesamia nonagrioides* is a serious pest of corn in the Mediterranean regions and Central Africa. It is multivoltine, with two to four generations per year, that overwinters as mature larva in the northern of the Sahara desert. Our purpose was to compare the response of the *S. nonagrioides* populations occurring in the broader circum-Mediterranean area, with particular attention to the diapause period and the different numbers of generations per season. To this end, we tried to determine whether populations in the area differ in their response to photoperiod and whether we can foresee the number of generations in different areas. We present a model for predicting the occurrence of the critical photoperiod according to latitude and temperature and the spread of *S. nonagrioides* in the circum-Mediterranean countries. Responses of populations to short-day length suggest that the spread of the species is associated with a gradual loss of diapause in the southern areas, and that diapause incidence is positively correlated with latitude.

1. Introduction

1.1. Host Plants and Distribution. The corn stalk borer, *Sesamia nonagrioides,* is a polyphagous species with a fairly wide range of host plants, including corn, sorghum, millet, rice, sugar cane, grasses, melon, asparagus, palms, banana, and the ornamental plant *Strelitzia reginae* [1–9]. The population levels of this species, which has considerable potential to establish itself in an area and become abundant, may therefore depend on the abundance of these hosts.

The occurrence of *S. nonagrioides*, including *S. nonagrioides botanephaga,* has been reported in Portugal [10, 11], Spain [12–14], the Canary Islands [15], France [16–18], Italy [19], Greece [20, 21], Cyprus [22], Turkey [23, 24], Morocco [25], Israel [26], Iran [27–29], Syria [30], Ethiopia [6], Ghana [31], and several other African countries [32]. *S. nonagrioides* has been considered the most important pest of maize in Spain since 1929 [12]. Nye [33] observed that *S. nonagrioides* was morphologically very close to one of the new sub-Saharan species that had been described (*Sesamia botanephaga*) and indicated that *Sesamia nonagrioides nonagrioides* and *Sesamia nonagrioides botanephaga* should be regarded as two subspecies distributed to the north and south of the Sahara, respectively. Esfandiari et al. [34] stated that African *S. botanephaga* (or *S. nonagrioides botanephaga*) do not occur in Iran and that it seems that *S. nonagrioides* is native to SW Iran rather than an exotic pest, having adopted sugarcane as a host after it began to be cultivated there about 70 years ago. Leyenaar and Hunter [31] reported that *S. n. botanephaga* can cause 63% loss in maize yield in the coastal savanna of Ghana. In Kenya, *S. nonagrioides* has been commonly recovered in maize fields [35]. The same authors report that these species and other stem borers that are currently restricted to wild hosts may have the potential to shift to cultivated cereals in cases of serious habitat fragmentation. Moyal et al. [36] recently concluded that there is a single species of *S. nonagrioides* but with three different, isolated conspecific populations: one in East Africa, one in West Africa, and a Palearctic one in the circum-Mediterranean countries.

In the circum-Mediterranean countries, *S. nonagrioides* has been designated as the most important pest of corn. Many researchers have attempted to document the economic losses that it causes in Spain, but the results are not clear because the damage is not distinguishable from that caused by *Ostrinia nubilalis*. Arias and Alvez [37] indicated that damage caused by maize borers could range from 5% to 30% of the yield depending on the date of sowing and the cultural cycle of maize. In Greece, the existence of the species was first reported by Stavrakis [38]. The pest increased steadily in the 1980s as a result of the use of new single hybrids and improved culture practices [21]. This increase was followed by problems caused by *S. nonagrioides*, especially in the late-sown crop (sown in early July after the harvest of small cereals) [39]. According to a pilot survey in October 2005, the dominant pest in sweet sorghum, *Sorghum bicolor* (L.) Moench, was *S. nonagrioides* [40].

1.2. Number of Generations and Diapause. The number of generations is marginally governed by the onset of diapause at various latitudes and there are fewer generations in the northern region than in the southern one. Three to four generations are completed per year in Greece [39]. Stavrakis [38] reported that the pupation of the overwintering population in Greece takes place in April-May. It seems that the fourth generation is partial since some of the late progeny of the third generation will not make it through [39].

In Spain and Portugal, the borer completes 2 generations and a partial third one per year [37, 41, 42], with the third one having a low population size in northern Spain [43]. The existence of two generations, in May and July-August, has been reported in France [44]. In Israel, the borer is at least a bivoltine wetland species, flying in March to July and in October [45]. In Iran, it completes 4 generations during the active season, with a partial 5th generation in second plantings [46]. It has also been referred to as multivoltine, with three to four generations per year in southern Portugal [47] and three generations per year in the Izmir area of Turkey [48].

Diapause of this species has been studied extensively [20, 49–52]. Eizaguirre and Albajes [49] and Fantinou et al. [51] reported that larval diapause is induced by the length of photoperiod and that constant temperature modifies the diapause response curve from type III to type I. According to previous studies, the early induction of diapause can be explained by the limited tolerance of insects originating in the tropics to low temperatures, and it could be a mechanism enabling the insect to extend its range into northern regions. It seems that temperature plays a double role in the occurrence of a supplementary generation by increasing the developmental rate and delaying the onset of diapause. Gillyboeuf et al. [53] observed that survival of diapausing larvae at low temperature may be related to the microclimate of the overwintering site and not to their freeze tolerance capacity. However, they argue that the freezing tolerance of *S. nonagrioides* may be a factor favoring northern expansion.

Fantinou et al. [20] and Eizaguirre et al. [54] stated that photoperiods longer than 12:12 h (L : D) terminate diapause and that field-collected larvae complete diapause spontaneously. Under a temperature similar to the natural field temperatures, diapause terminates in approximately 4 months, ensuring that the larvae reach the middle of winter without pupation. When diapause terminates, temperatures in the field are very low and larvae go into quiescence, allowing them to survive and to synchronize their cycle with that of the host plant. The fact that the temperature thresholds for diapause and postdiapause development are 3 or 4 degrees lower than that for continuous development [20, 41] explains the phenological model of *S. nonagrioides* described by López et al. [41]. Moreover, Fantinou and Kagkou [55] reported that under natural conditions the increase in nighttime temperature in late winter and early spring could function as a signal eliciting diapause development. This is ecologically important because in temperate regions insects are exposed to daily photoperiods and thermoperiods in which the long nights coincide with low temperatures. The specific role of low temperature exposure in regulating diapause development is not entirely clear, beyond the fact that exposure to low temperatures is not a prerequisite for diapause termination in this species [20]. The intensity of cold stress reflected in the level of mortality occurring in larvae suggests that the northern boundary of the species' expansion is defined by low temperatures.

2. Key Aspects for the Existence of the Species

2.1. Latitude and Critical Photoperiod. Figure 1 shows the latitude lines of the Mediterranean basin countries. *S. nonagrioides* can be found in northern, mainly European, countries between 35° and 46° N and in southern countries, such as Morocco, Iran, Syria, and Israel, between 31° and 35° N. Spain is located between 36° and 43° N, whereas Greece is located between 35° and 41.5° N. In all the circum-Mediterranean countries where *S. nonagrioides* has been found, including Morocco, the species overwinters as diapausing larvae [2, 21, 44, 56], but there is no evidence of diapause in the populations of warmer and more southern countries. The Sahara desert probably delimits the populations of the borer that diapause in the north from those that complete development without diapause in the south. Masaki [57] suggested that variations in the incidence of diapause might be due to the varying threshold of external stimuli that trigger diapause. If an insect has an extremely low threshold, it will enter diapause in a very wide range of environmental conditions, whereas if its threshold is extremely high, the conditions which induce its diapause might be nonexistent in the ordinary range of environment. Between these extreme thresholds, there is an intergraded series of the reaction thresholds.

According to Eizaguirre and Albajes [49], under laboratory conditions the critical photoperiod (that which induces 50% diapause) is reduced from 13 h 52 min at 18°C to 13 h 15 min at 25°C; this means that a 1°C decrease in temperature corresponds to an increase in the critical photoperiod of about 5.3 minutes. This range of the critical photoperiod corresponds closely to the day length on 15 August in regions where *S. nonagrioides* diapauses. In these regions, the duration of the day on 15 August, from sunrise to

Figure 1: The latitude lines of the Mediterranean basin countries (from Google maps).

sunset, is graduated approximately from 13 h 18 min at 31° N to 13 h 57 at 43° N, an increase in day length of approximately 3.16 minutes for each degree of latitude increase (Figure 2).

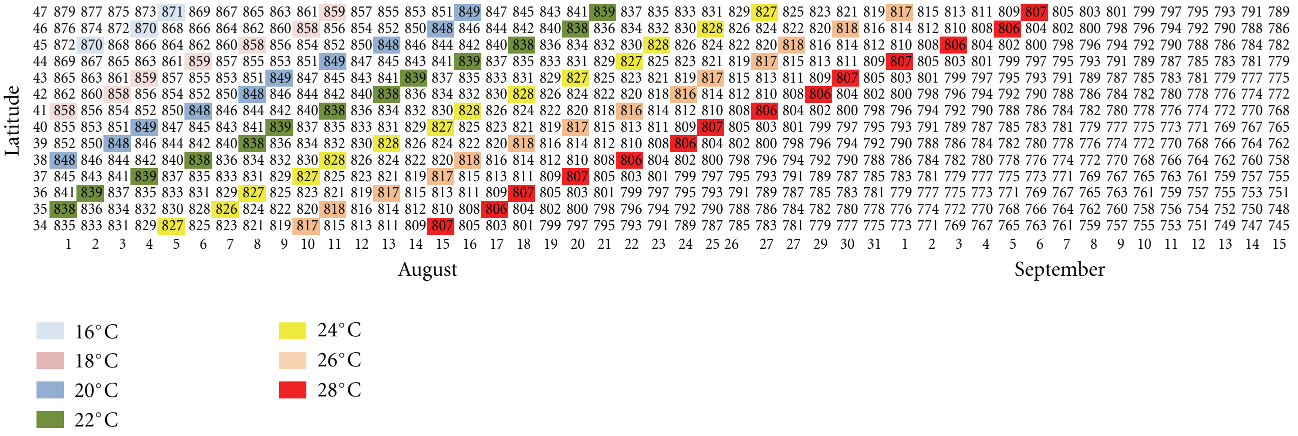
Figure 2 shows the critical photoperiod for each latitude and temperature. In view of this, on 15 August in the northern regions of Europe, the longer photoperiods induce lower percentages of diapause, whilst the shorter ones occurring in southern Europe induce higher percentages. These results may seem contradictory, because in the northern regions *S. nonagrioides* larvae enter diapause earlier than in the southern regions, but the explanation could be that temperature has been reported to play a significant role in diapause induction [20, 50, 55, 58].

Estimation of the critical photoperiod by Eizaguirre and Albajes [49] allows us to design a model that could help to predict the occurrence of the critical photoperiod according to the latitude and the temperature in various countries (Figure 2). This model could help us to estimate the percentage of the live larvae of a generation that will be induced to diapause, the larval proportion that may develop towards adulthood, and therefore the trend of the population density of the next (last) generation.

Figure 3 shows the variation in the climate of 6 cities of the area where *S. nonagrioides* is distributed. The critical photoperiod arrival in these cities based on the data of Figure 2 corresponds to 27 August in Bordeaux, 6-7 September in Teheran, 20 August in Milan, 31 August in Zaragoza, 20 August in Athens, and 6 September in Marrakech. Therefore, the differences in the onset of the critical photoperiods in the various areas do not seem to be significant.

2.2. Freezing Days and Number of Generations Per Year. Although the differences in the critical photoperiod are not very obvious, greater differences can be observed in the range of prevailing temperatures in each region. Milan is the city with most days with a mean minimum temperature below −1°C, whereas Teheran is the city with most days with a mean minimum temperature above 10°C and a mean maximum temperature above 27°C, although temperatures below −1°C may occur on a few days each year. *S. nonagrioides* seems to be to some extent susceptible to high temperatures in summer [56] and the endophytic larval behavior may protect the species from the extreme temperatures of some regions.

Figures 2 and 3 provide data on the factors affecting the number of generations of *S. nonagrioides* in the different regions of the circum-Mediterranean countries. In Northern Italy, *S. nonagrioides* is not present because it is very susceptible to the low winter temperatures [13, 44, 56] and the short period of time with mean minimum temperatures above 10°C (close to the threshold temperatures for the pest [40, 59]). In contrast, in Iran the species completes 4 to 5 generations that can be attributed to the long period of time with prevailing mean minimum temperatures above 10°C (Figure 3) and to the delayed onset of the critical photoperiod in September (Figure 2). Generally, warmer temperatures tend to be associated with a higher number of generations of the insect. The number of generations in a region depends on the early appearance of the first generation derived from overwintering larvae. Galichet [44], Lopez et al. [60], and Fantinou et al. [20] demonstrated that diapause terminates by the end of February, so the occurrence of the first generation will depend on the prevailing temperatures throughout March, taking into account that the threshold temperatures for postdiapause development are lower than those for normal larval development [54]. Once the first generation has occurred, the accumulation of heat units, degree days, will determine the number of generations completed per season before the arrival of the photoperiod that initiates diapause. The degree days (DG) necessary for the completion of one generation in maize are 616 DG according to Hilal [61] and 730 DG according to López et al. [41]. The number of generations will also determine the population size of the pest of the last generation: the population density of the last generation of *S. nonagrioides* is usually higher than that of the previous one because the host crop is available [21, 35].



Latitude																																													
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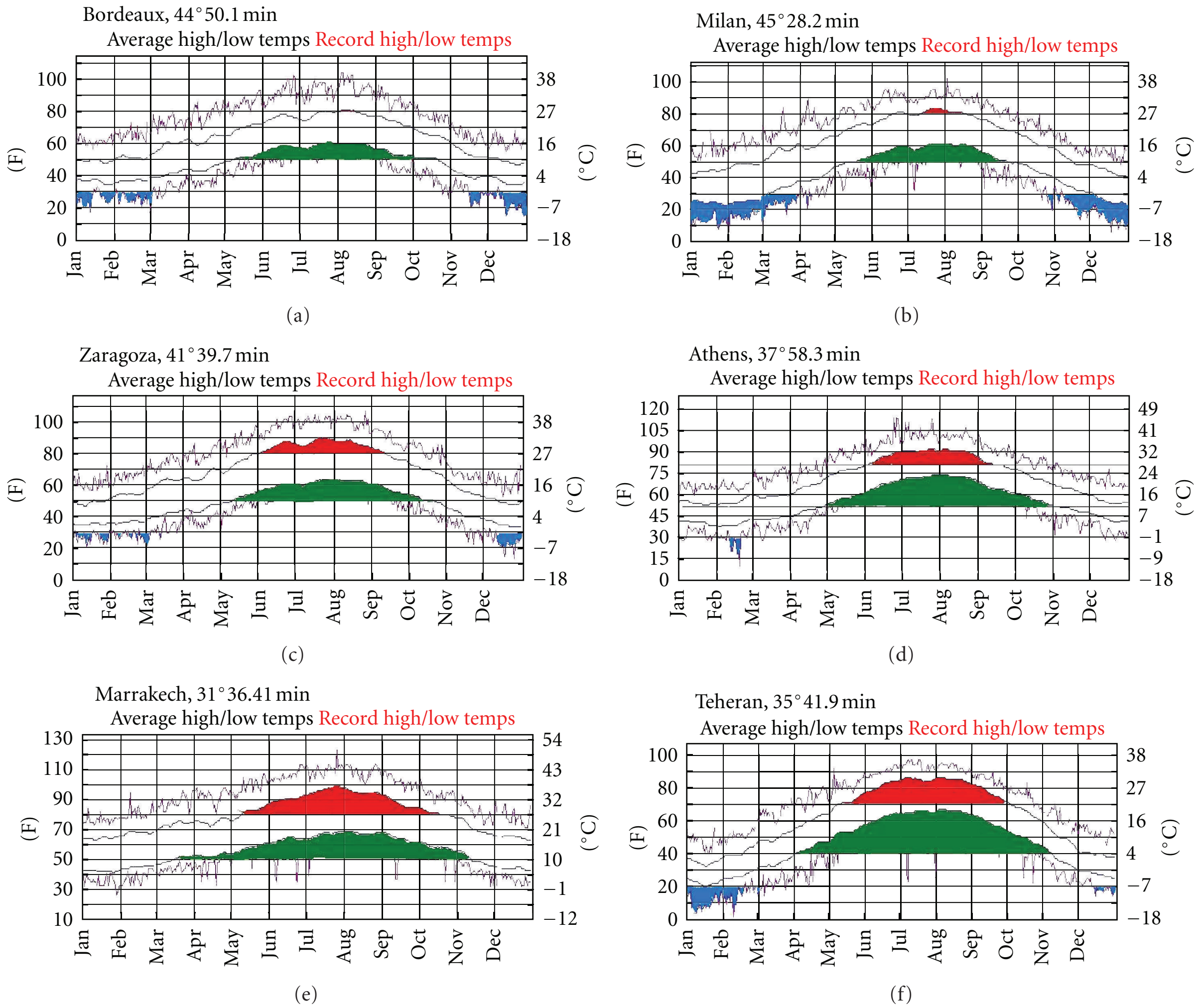
46	876	874	872	870	868	866	864	862	860	858	856	854	852	850	848	846	844	842	840	838	836	834	832	830	828	826	824	822	820	818	816	814	812	810	808	806	804	802	800	798	796	794	792	790	788	786
45	872	870	868	866	864	862	860	858	856	854	852	850	848	846	844	842	840	838	836	834	832	830	828	826	824	822	820	818	816	814	812	810	808	806	804	802	800	798	796	794	792	790	788	786	784	782
44	869	867	865	863	861	859	857	855	853	851	849	847	845	843	841	839	837	835	833	831	829	827	825	823	821	819	817	815	813	811	809	807	805	803	801	799	797	795	793	791	789	787	785	783	781	779
43	865	863	861	859	857	855	853	851	849	847	845	843	841	839	837	835	833	831	829	827	825	823	821	819	817	815	813	811	809	807	805	803	801	799	797	795	793	791	789	787	785	783	781	779	777	775
42	862	860	858	856	854	852	850	848	846	844	842	840	838	836	834	832	830	828	826	824	822	820	818	816	814	812	810	808	806	804	802	800	798	796	794	792	790	788	786	784	782	780	778	776	774	772
41	858	856	854	852	850	848	846	844	842	840	838	836	834	832	830	828	826	824	822	820	818	816	814	812	810	808	806	804	802	800	798	796	794	792	790	788	786	784	782	780	778	776	774	772	770	768
40	855	853	851	849	847	845	843	841	839	837	835	833	831	829	827	825	823	821	819	817	815	813	811	809	807	805	803	801	799	797	795	793	791	789	787	785	783	781	779	777	775	773	771	769	767	765
39	852	850	848	846	844	842	840	838	836	834	832	830	828	826	824	822	820	818	816	814	812	810	808	806	804	802	800	798	796	794	792	790	788	786	784	782	780	778	776	774	772	770	768	766	764	762
38	848	846	844	842	840	838	836	834	832	830	828	826	824	822	820	818	816	814	812	810	808	806	804	802	800	798	796	794	792	790	788	786	784	782	780	778	776	774	772	770	768	766	764	762	760	758
37	845	843	841	839	837	835	833	831	829	827	825	823	821	819	817	815	813	811	809	807	805	803	801	799	797	795	793	791	789	787	785	783	781	779	777	775	773	771	769	767	765	763	761	759	757	755
36	841	839	837	835	833	831	829	827	825	823	821	819	817	815	813	811	809	807	805	803	801	799	797	795	793	791	789	787	785	783	781	779	777	775	773	771	769	767	765	763	761	759	757	755	753	751
35	838	836	834	832	830	828	826	824	822	820	818	816	814	812	810	808	806	804	802	800	798	796	794	792	790	788	786	784	782	780	778	776	774	772	770	768	766	764	762	760	758	756	754	752	750	748
34	835	833	831	829	827	825	823	821	819	817	815	813	811	809	807	805	803	801	799	797	795	793	791	789	787	785	783	781	779	777	775	773	771	769	767	765	763	761	759	757	755	753	751	749	747	745
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	27	29	30	31	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
	August																															September														

Figure 2: Variation in the length of the day, in minutes, from 1 August to 15 September according to latitude. Length of the day in color indicates the day of the critical photoperiod inducing 50% diapause for this temperature and latitude.



Bordeaux, 44°50.1 min
Average high/low temps Record high/low temps

(a)

Milan, 45°28.2 min
Average high/low temps Record high/low temps

(b)

Zaragoza, 41°39.7 min
Average high/low temps Record high/low temps

(c)

Athens, 37°58.3 min
Average high/low temps Record high/low temps

(d)

Marrakech, 31°36.41 min
Average high/low temps Record high/low temps

(e)

Teheran, 35°41.9 min
Average high/low temps Record high/low temps

(f)

Figure 3: Maximum and minimum temperatures of six cities in the area of distribution of *Sesamia nonagrioides*. The curves, from bottom to top, show the record minimum temperatures, the mean minimum temperatures, the mean maximum temperatures, and the record maximum temperatures. Days with mean maximum temperatures higher than 27°C are colored in red, days with mean minimum temperatures higher than 10°C are colored in green, and days with temperatures below −1°C are colored in blue.

Consequently, like many multivoltine species that undergo a state of diapause, *S. nonagrioides* may complete as many generations as temperature and photoperiod conditions will allow, assuming that there is an available food source.

2.3. Winter Mortality. The overwinter mortality of *S. nonagrioides* in the Mediterranean is not only determined by the number of freezing days in winter but may also be associated with the percentage of the larval population that "escape" the critical photoperiod in autumn. If the weather remains warm, it is likely that many larvae will avoid diapause because of the high temperatures. Therefore, a further generation will lay eggs on a suitable green crop if it is available, and the neonate larvae will successfully develop only in those regions where relatively mild autumn temperatures can occur. However, the young larvae that are subsequently exposed to the later winter temperatures are destined to die. Therefore, the higher the percentage of larvae that escape from diapause during autumn, the higher the mortality of the next generation of young larvae.

3. Summary

Field populations of *S. nonagrioides* in the Mediterranean region display winter diapause. Voltinism in this species is a seasonally plastic trait dependent on early emergence of adults of the overwintering generation. The abundance of the species in a given region depends on the number of freezing days of the winter and the heat units accumulated from diapause termination until the arrival of the critical photoperiod for diapause induction in late summer. The species relies on latitudinal gradients in temperature and photoperiod for the induction of diapause, and the effect of environmental cues on diapause and adaptation to local environmental conditions is, therefore, variable.

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Hindawi Publishing Corporation
Psyche
Volume 2012, Article ID 818490, 10 pages
doi:10.1155/2012/818490

Research Article

Gerris spinolae Lethierry and Severin (Hemiptera: Gerridae) and *Brachydeutera longipes* Hendel (Diptera: Ephydridae): Two Effective Insect Bioindicators to Monitor Pollution in Some Tropical Freshwater Ponds under Anthropogenic Stress

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Received 30 July 2011; Accepted 29 October 2011

Academic Editor: Matilda Savopoulou-Soultani

The abundance patterns of two insects, *Gerris spinolae* and *Brachydeutera longipes*, were found to be affected by abiotic aquatic factors including free carbon dioxide, dissolved oxygen, BOD, and phosphate concentrations prevailing in four tropical freshwater ponds, three of which being anthropogenically stressed. Regression analysis between each individual-independent water quality variable and insect abundance demonstrated a significant positive correlation in each case between *B. longipes* abundance and BOD, phosphate, free CO_2, and algae dry weight, while a significant negative correlation of each of these variables was found with *Gerris spinolae* abundance. Moreover, a significant negative correlation of *B. longipes* abundance was calculated with dissolved oxygen concentration, while *G. spinolae* abundance exhibited a positive correlation with the same. Thus, *G. spinolae* appears to be a pollution sensitive, effective bioindicator for healthy unpolluted ponds, while *B. longipes* has potential as a pollution-resistant insect species indicative of pollution occurrence.

1. Introduction

Freshwater bodies in urban ecosystems are under stress due to anthropogenic pressures. Pollution of inland water habitats, both *lotic* (running water) and *lentic* (lakes and ponds), impacts pollution of soil and ground water and thereby affects the essential basic (drinking water supply) and social requirements (aesthetic, religious, etc.) of human societies. Monitoring and maintaining the water quality of wetlands is also important since these recharge the groundwater and also affect the plant diversity in its vicinity. Environmental monitoring of inland freshwater bodies is an essential prerequisite for their management. Biological indication is, therefore, increasingly being advocated. Biological indication or bioindication is the process of using a species or group of species that readily reflects the abiotic and biotic states of an environment, represents the impact of environmental change on a habitat, community, or ecosystem, or is indicative of the diversity of a subset of taxa or of the entire diversity, within an area [1, 2]. Bioindicators or ecological indicators are taxa or groups of animals that show signs that they are affected by environmental pressures due to human activities or the destruction of the biotic system [3]. Bioindicators also provide information about the cumulative impact of the various pollutants in an ecosystem [1, 4–6]. An ideal taxon must respond predictably, in ways that are readily observed and quantified to environmental disturbance [7]. Aquatic bioindicators used so far are plants [8–10] including diatoms [4, 11]; vertebrates, mainly fish [5, 12, 13] and macroinvertebrates [1, 6, 7, 14, 15]. Among invertebrates, insects are good candidates [16–21]. However, not all insects respond in a predictable manner to environmental pollution. Insects widely utilized as bioindicators include larval Chironomids (Diptera: Chironomiidae) [22] and water striders (Hemiptera: Gerridae), the latter being particularly well known for indicating heavy metal pollution, [18, 23–26] which is also characterized by oxygen stress. Insects offer a number of advantages as bioindicators. These include the availability of a wide range of insects from various insect orders which (i) exhibit high sensitivity and the degree of sensitivity gives a series of choice of bioindicators depending upon the needed resolution, (ii) involve the entire trophic levels, thus ecosystems can be monitored from functional point of view, (iii) exhibit high fecundity, greater breeding potential reduces the chances of the potential bioindicator getting destroyed entirely from the ecosystem, and finally (iv) involve less ethical problems.

While some studies have been carried out on bioindicators of *lotic* ecosystems [19, 27–29] studies of potential insect bioindicators of *lentic* ecosystems are scanty [30, 31], especially those of the tropical regions [15]. The present study focuses on assessing the potential of two insect species: the water strider, *Gerris spinolae* (Lethierry and Severin) and the shorefly, a semi-aquatic dipteran, *Brachydeutera longipes* (Hendel). Studies pertaining to the genus *Brachydeutera* are scanty although its occurrence is reported from lentic habitats [32]. While water striders, common in freshwater water bodies of temperate and tropical water bodies, are predaceous [33, 34], the genus, *Brachydeutera,* is documented to include species such as *B. hebes, B. argentata,* and *B. neotropica* the larval stages of which scavenge upon dead and decaying plant and animal tissues and also consume algae [32]. Since *B. longipes* is reported to be an algal feeder [35] and algal blooms are characteristic feature of polluted ponds, this species merits further investigation to examine its potential as a bioindicator. The impact of abiotic aquatic factors on the ecological response of the two focal insect species was investigated and the relationship between the abundance pattern of each species and the degree of pollution was determined.

2. Materials and Methods

2.1. Study Sites. The investigations were carried out from January to March, 2011 (3 months), in Varanasi, Uttar Pradesh, India. Four man-made ponds presently under anthropogenic stress were selected for the present study. While the pond located in the Botanical garden of Banaras Hindu University (not being under any anthropogenic stress) was considered as the control and the three ancient ponds, about 200 years old [36] under anthropogenic stress (due to human activities such as bathing, washing clothes, dumping organic wastes in the form of flowers, and so forth, in the ponds, particularly during religious ceremonies and festivals) located in a thickly populated urban ecosystem, were taken as the experimental.

The Kurukshetra (Krk), Sankuldhara (Skd), Durgakund (Dgk), and Botanical garden (Btg) ponds are located in Assi, Khojwa, Durgakund, and Banaras Hindu University Campus areas, respectively. All the ponds except Btg have 1-2 old temples around them. The dimensions of Krk pond are about 20 m × 25 m × 6 m. Its four banks are bounded by stone tiles from all around. Due to dense human inhabitation around it, there is heavy anthropogenic pressure on it. The dimensions of Skd pond are about 30 m × 30 m × 7 m. Its parapets are also bounded by stone tiles and, in addition it is surrounded by iron grid fencing. The dimensions of Dgk pond are about 40 m × 40 m × 10 m. Its parapets are also bounded by stone tiles and in addition, it is surrounded by an iron grid fencing. Human activities including occasional bathing, washing of clothes, and dumping of organic wastes in the form of flowers, and so forth during religious and social ceremonies occur in all these three ponds. The dimensions of Btg pond are about 10 m × 8 m × 2 m. It was constructed for the purpose of watering garden plants. It is free from all anthropogenic pressures.

2.2. Water Quality Assessment. Transparency was determined for each pond by using the Sechhi disc method while total solids were assessed by the standard dry weight method [37]. All the other physical and chemical parameters were monitored twice a week ($n = 15$) at each study site. DO and BOD (5 days, 20°C) were determined by the modified Winkler's method [37]. Free CO_2 level was assessed by titrating the samples with 0.05 N NaOH solution in the presence of phenolphthalein indicator. Phosphate ion concentration was determined by the standard spectroscopic method [37].

2.3. Insect Diversity of the Ponds and Selection of Insect Species for Investigation of Aquatic Bioindicator Potential. The study revealed that each of the ponds supported a variety of aquatic insects from different orders, including water striders, back swimmers, water bugs (Order: Hemiptera), flies, mosquito larvae (Order: Diptera), and damselfly, dragonfly (Order: Odonata). Among these, two insect species, namely, *Gerris spinolae*, Lethierry and Severin, (Hemiptera: Gerridae; det. NPIB) RRS No. 1116-1117/11 and *Brachydeutera longipes*, Hendel (Diptera: Ephydridae; det. NPIB), and (RRS No. 1118-1124/11), were selected for further studies. These were identified by experts of the Network Project on Insect Biosystematics (NPIB), Division of Entomology, Indian Agricultural Research Institute, New Delhi. These two species were selected to study the impact of specific abiotic factors prevailing in the three anthropogenically stressed ponds, on the basis of the preliminary field observations regarding their differential habitat preferences.

2.4. Abundance of Adult Stages of the Two Insect Species: Gerris spinolae and Brachydeutera longipes. Insect abundance was monitored twice a week ($n = 15$) per pond. Quadrat sampling was done from sixteen different sites of each pond (four sites per side per pond), $n = 240$ quadrats per pond. The following formula was used to calculate the abundance:

$$\text{abundance} = \frac{\text{total number of individuals of the focal species in all the sampling units}}{\text{number of sampling units in which the species occurred}}. \qquad (1)$$

2.5. Life Cycle of B. longipes. *Brachydeutera longipes* was cultured under laboratory conditions by carefully adding about 10 mg of fresh algae, *Microcystis* sp. (which was carefully layered on the water surface), to 1 liter pond water contained in a 5 liter glass jar ($n = 3$). Thereafter, 2 pairs of *B. longipes* were introduced in each jar. Small fractions of the algae were examined daily under the Stereobinocular microscope and the various life cycle stages and feeding behaviour of the larval stages were recorded.

2.6. Statistical Analysis. Variation in the abiotic factors, that is, temperature, pH, free CO_2, dissolved oxygen (DO), biological oxygen demand (BOD), phosphate ion concentration, and a biotic factor-concentration (dry weight/m^2) of the algae, *Microcystis* sp. in each of the four ponds was analysed by using one-way analysis of variance (ANOVA) followed by Dunnett's post hoc test by using SPSS-PC software. Regression analysis for calculation of the correlation between the abundance of each of the two insect species, *Brachydeutera longipes* and *Gerris spinolae* with each of the above-mentioned seven water quality parameters considered individually in each case, was carried out by using SPSS-PC software.

3. Results

3.1. Life Cycle of B. longipes. Examination of the surface of the algal vegetation under laboratory conditions showed the presence of pale brown, cigar-shaped operculated eggs. Three larval instars were recorded, the duration of each stage was found to be approximately 2-3 days with that of the pupal stage being about 3-4 days. The larvae were observed to feed voraciously on *Microcystis* sp. Adults were recorded to have an approximate life span of 2-3 months.

3.2. Water Quality Assessment. A significant variation in water transparency was found in the four ponds: Btg pond (182.5 cm), Krk pond (63.8 cm), Skd pond (52.67 cm), and Dgk pond (29.67 cm). There was also variation in the amount of total solids present in each pond, with Btg pond having least amount of total solids including dissolved (275.8 mg/L) and suspended (3.9 mg/L) in comparison to the solids present in the other three ponds. The amount of dissolved solids were 321.7 mg/L, 537.2 mg/L, and 873.9 mg/L and suspended solids were 4.1 mg/L, 4.6 mg/L, 7.3 mg/L in Krk, Skd, and Dgk ponds, respectively (Figure 1).

Six abiotic parameters, namely, temperature, pH, free CO_2, dissolved oxygen (DO), BOD, phosphate ion concentration, and one biotic parameter, that is, food availability of *B. longipes* larvae in terms of the dry weight of *Microcystis* sp. per square meter, were monitored in all the four ponds. Significant variation was found in case of each parameter except temperature, for all the four ponds: ANOVA-temperature ($F_{3,56} = 0.01$; $P > 0.05$), pH ($F_{3,56} = 9.307$; $P < 0.001$), free CO_2 ($F_{3,56} = 41.667$; $P < 0.001$), dissolved oxygen ($F_{3,56} = 437.235$; $P < 0.001$), biological oxygen demand ($F_{3,56} = 188.284$; $P < 0.001$), concentration of phosphates ($F_{3,56} = 32.839$; $P < 0.001$), and food availability of *B. longipes* larvae in terms of dry weight of *Microcystis* sp. per square meter ($F_{3,56} = 604.686$; $P < 0.001$) Table 1.

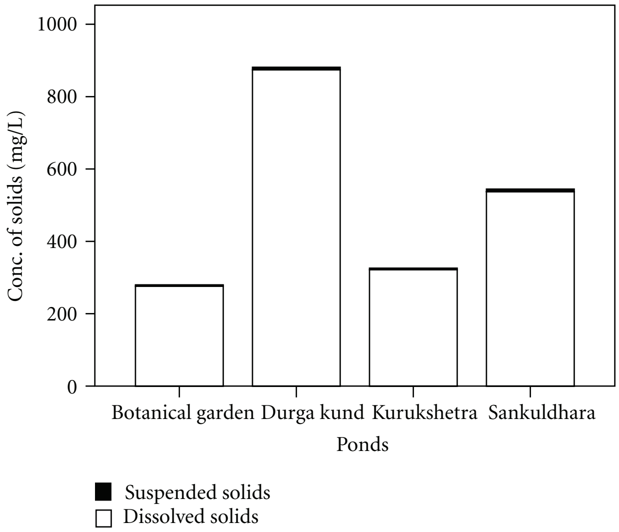


Figure 1: Concentration (mg/L) of total solids, suspended solids and dissolved solids in the control (Botanical garden) and anthropogenically stressed (Kurukshetra, Sankuldhara and Durgakund) ponds.

Post hoc tests revealed significant differences (Dunnett's test, $P < 0.001$) in case of each parameter under study (except free CO_2 level which was not found to be significantly different ($P > 0.05$ in the Krk pond), in all the three experimental ponds in comparison to the control.

3.3. Abundance of Adult Stages of Insects, Gerris spinolae and Brachydeutera longipes, in the Four Ponds. The abundance of adult stages of *Gerris spinolae* and *B. longipes* in the four ponds varied significantly: one-way ANOVA: $F_{3,56} = 11.124$; $P < 0.001$, for *G. spinolae,* and $F_{3,56} = 17.327$; $P < 0.001$, for *B. longipes* (Figures 2(a) and 2(b)).

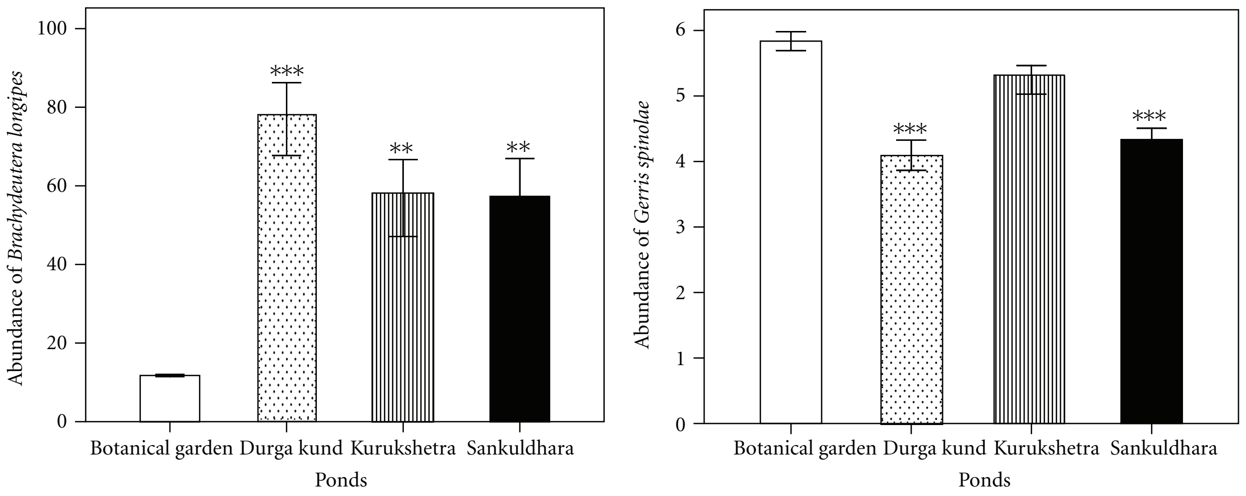
Post hoc tests revealed significant differences in the abundance of *B. longipes* in all the three experimental ponds in comparison to the control pond, the lowest being in Dgk pond (Dunnett's test, $P < 0.001$), with abundance being in the increasing order in Skd and Krk ponds (Dunnett's test, $P < 0.001$, for both). The two experimental ponds Dgk and Skd differed significantly from the control (post hoc test: Dunnett's test, $P < 0.001$, for both) in exhibiting significantly lower abundance of the *G. spinolae*. However, Krk pond did not show significant deviation from the control pond in this respect (Dunnett's test, $P > 0.05$).

Regression analysis between each individual independent water quality variable: temperature, pH, BOD, DO, free CO_2, phosphate, dry weight of algae, with the abundance of adult stage of each of the two insect species, *Brachydeutera longipes* and *Gerris spinolae* (dependent variables) reveals the following: a significant positive correlation ($P < 0.001$) between *B. longipes* abundance and BOD ($r = 0.528$), PO_4 ($r = 0.587$), free CO_2 ($r = 0.473$), and dry weight of algae

Table 1: Physical, chemical, and biological parameters of water quality in the four ponds (Botanical garden—control; Kurukshetra, Sankuldhara and Durgakund—anthropogenically stressed) located in different parts of Varanasi, India.

Water parameters	In Botanical garden pond	In anthropogenically disturbed ponds		
	(Control)	Kurukshetra	Sankuldhara	Durgakund
Temperature (°C) (Mean ± SEM)	16.19 ± 2	16.35 ± 2.01$^{\text{ns}}$	16.53 ± 2.02$^{\text{ns}}$	16.67 ± 2.02$^{\text{ns}}$
pH (Mean ± SEM)	6.89 ± 0.11	9.16 ± 0.015***	8.85 ± 0.013***	6.402 ± 0.016***
Dissolved oxygen (mg/L) (Mean ± SEM)	8.84 ± 0.50	7.61 ± 0.42***	4.98 ± 0.33***	4.13 ± 0.45***
Free CO_2 conc. (mg/L) (Mean ± SEM)	1.8 ± 0.25	1.07 ± 0.16$^{\text{ns}}$	5.18 ± 0.38***	5.38 ± 0.5***
BOD (mg/L) (Mean ± SEM)	5.68 ± 0.42	6.49 ± 0.47***	8.03 ± 0.53***	8.47 ± 0.62***
Phosphate ion conc. (mg/L) (Mean ± SEM)	0.16 ± 0.02	0.43 ± 0.05***	0.47 ± 0.05***	0.63 ± 0.09***
Dry weight of algae, *Microcystis* sp.(g/sq m) (Mean ± SEM)	00.00	10.81 ± 0.35***	10.94 ± 0.29***	30.58 ± 0.36***

Where $^{*}P < 0.05$, $^{**}P < 0.01$, and $^{***}P < 0.001$, ns—not significant.



(a)

(b)

Figure 2: Abundance (No./sq. m) of adults of (a) *Brachydeutera longipes* (Hendel) and (b) *Gerris spinolae* (Lethierry and Severin) in the control (Botanical garden) and anthropogenically stressed (Kurukshetra, Sankuldhara and Durgakund) ponds, where $^{*}P < 0.05$, $^{**}P < 0.01$, and $^{***}P < 0.001$, ns—not significant.

($r = 0.519$) and a significant negative correlation ($P < 0.001$) with DO ($r = 0.527$). On the other hand, *G. spinolae* abundance exhibited a significant positive correlation ($P < 0.001$) with DO ($r = 0.780$) and temperature ($r = 0.60$) and a significant negative correlation ($P < 0.001$) with BOD ($r = 0.686$), PO_4 ($r = 0.604$), free CO_2 ($r = 0.829$), and dry weight of algae ($r = 0.547$) Table 2.

Brachydeutera longipes abundance showed less significant positive correlation with pH ($r = 0.346$, $P < 0.01$) and a negative correlation with temperature ($r = 0.305$, $P < 0.05$) whereas *G. spinolae* abundance demonstrated no significant correlation with pH ($r = 0.115$, $P > 0.05$) Figures 3(a), 3(b); 4(a), 4(b); 5(a), 5(b); 6(a), 6(b); 7(a), 7(b); 8(a), 8(b); and 9(a), 9(b).

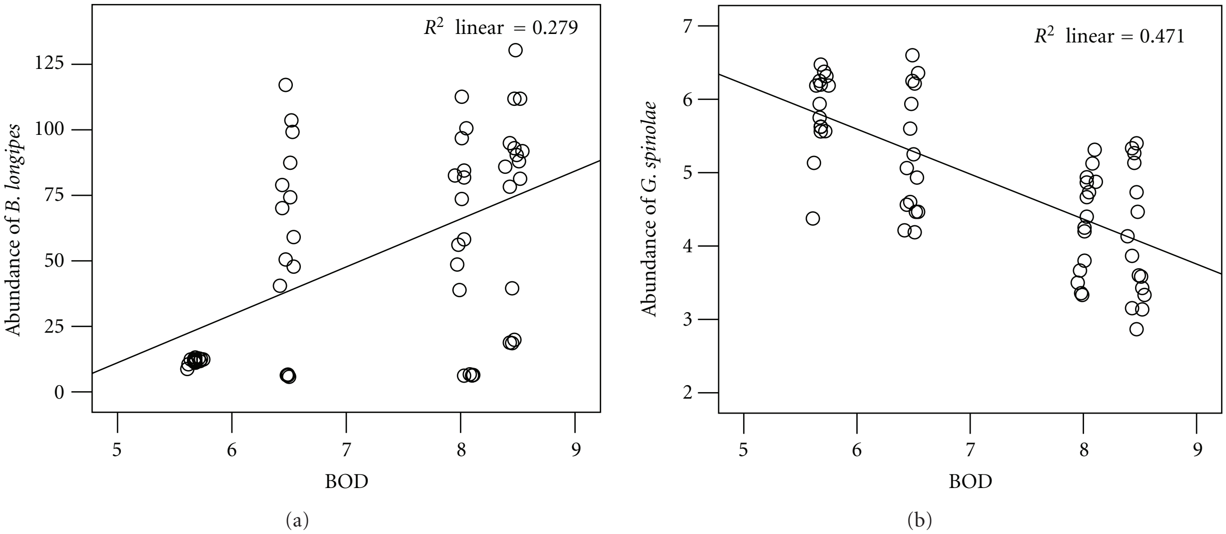
4. Discussion

Our study clearly reveals that the abundance of adult stages of the two insect species, *G. spinolae* and *B. longipes* in the three ponds under anthropogenic stress is affected (although in a contrasting manner) due to differences in the levels of organic pollution and the resulting impacts of abiotic and biotic aquatic components of the ponds. Durgakund, Sankuldhara, and Kurukshetra ponds exhibit pollution in a decreasing order with higher concentrations of total dissolved and suspended solids, free CO_2 levels, phosphate ion concentration, and amount of *Microcystis* sp. being more prevalent in the most polluted Durgakund pond and less in the remaining two anthropogenic stressed ponds.

Table 2: Regression analysis output obtained by corelating each variable (water quality parameter) independently with the abundance of each of the two insect species, *Brachydeutera longipes* and *Gerris spinolae.*

Parameters	Insect species	Regression coefficient (β)	r	Significance
BOD	*Brachydeutera longipes*	18.29	0.528	***
	Gerris spinolae	−0.613	0.686	***
DO	*Brachydeutera longipes*	−10.067	0.527	***
	Gerris spinolae	0.384	0.780	***
PO_4	*Brachydeutera longipes*	134.317	0.587	***
	Gerris spinolae	−3.563	0.604	***
Free CO_2	*Brachydeutera longipes*	7.946	0.473	***
	Gerris spinolae	−0.359	0.829	***
Dry weight of algae	*Brachydeutera longipes*	1.835	0.519	***
	Gerris spinolae	−0.050	0.547	***
Temperature	*Brachydeutera longipes*	−1.584	0.305	*
	Gerris spinolae	0.081	0.602	***
pH	*Brachydeutera longipes*	11.314	0.346	**
	Gerris spinolae	−0.97	0.115	ns

Where $^{*}P < 0.05$, $^{**}P < 0.01$, and $^{***}P < 0.001$, ns—not significant.



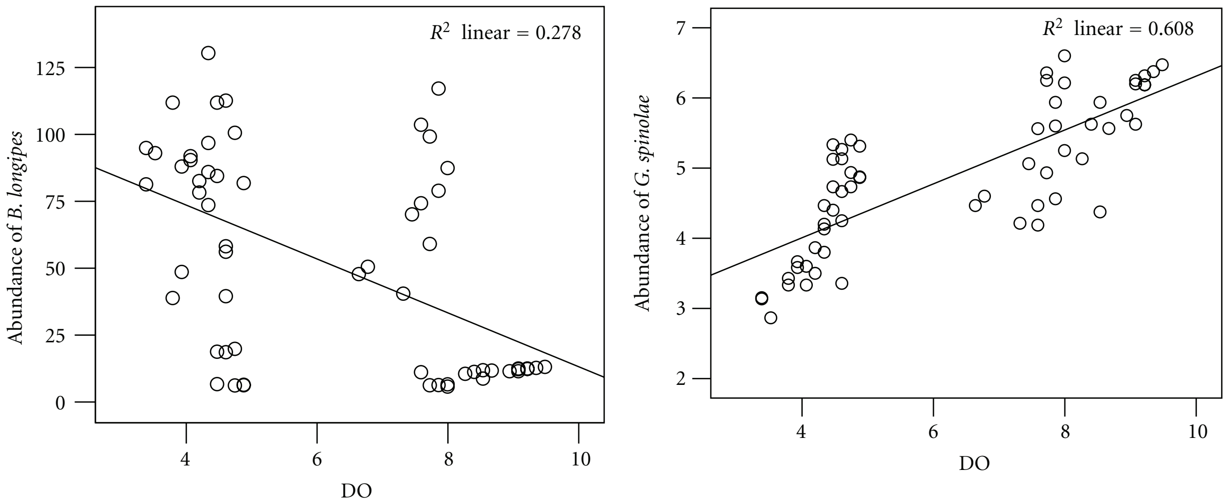
(a)

(b)

Figure 3: Relation between BOD and abundance of (a) *Brachydeutera longipes* (Hendel) and (b) *Gerris spinolae* (Lethierry and Severin) as shown by regression analysis.

Temperature and pH were higher in the polluted ponds in comparison to the control while transparency was much reduced. Thus, the greater the pollution level in the pond, the lesser is the abundance of *G. spinolae* as demonstrated by its low abundance in the Durgakund pond. Regression analysis between each individual independent water quality parameter with the abundance of *B. longipes* revealed a significant positive impact of BOD, free CO_2, phosphate concentration, and dry weight of algae (characteristic of polluted aquatic conditions) and a negative impact of DO concentrations. On the other hand, a significant positive influence of dissolved oxygen concentration (characteristic of unpolluted aquatic conditions) was found on *G. spinolae* abundance with the correlation being negative with BOD, free CO_2, phosphate concentration, and dry weight of algae (characteristic of polluted aquatic conditions). Therefore, higher abundance of *B. longipes* appears to indicate greater aquatic pollution. Since the maintenance of integrity between the physico-chemical and biological components of an ecosystem determines its health status [5, 38], it is abundantly clear that *G. spinolae* prefers unpolluted, while the semiaquatic shore fly prefers polluted *lotic* water bodies.

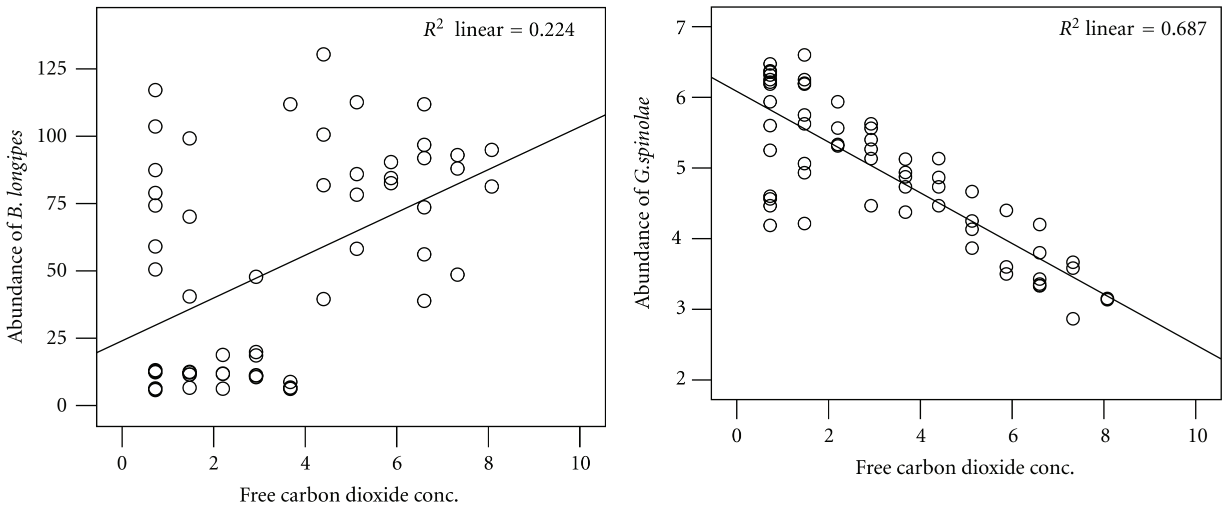
Earlier studies demonstrate that physical, chemical, and biological parameters of an aquatic ecosystem are found to be correlated [39, 40]. Since each parameter in an aquatic ecosystem regulates the others, a freshwater pond supports



(a)

(b)

Figure 4: Relation between DO and abundance of (a) *Brachydeutera longipes* (Hendel) and (b) *Gerris spinolae* (Lethierry and Severin) as shown by regression analysis.

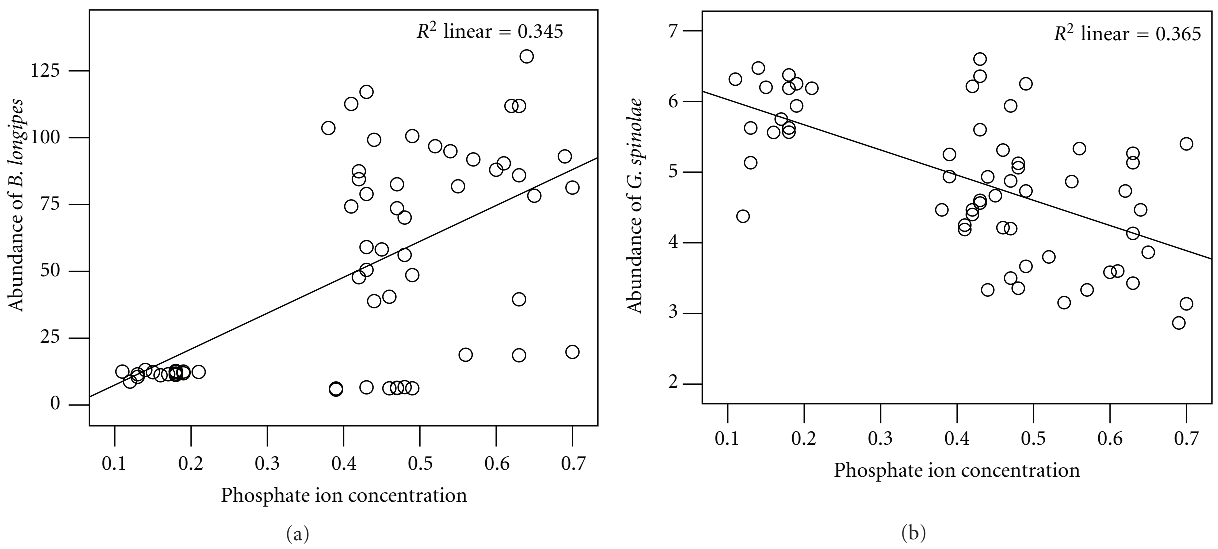


(a)

(b)

Figure 5: Relation between free carbon dioxide and abundance of (a) *Brachydeutera longipes* (Hendel) and (b) *Gerris spinolae* (Lethierry and Severin) as shown by regression analysis.

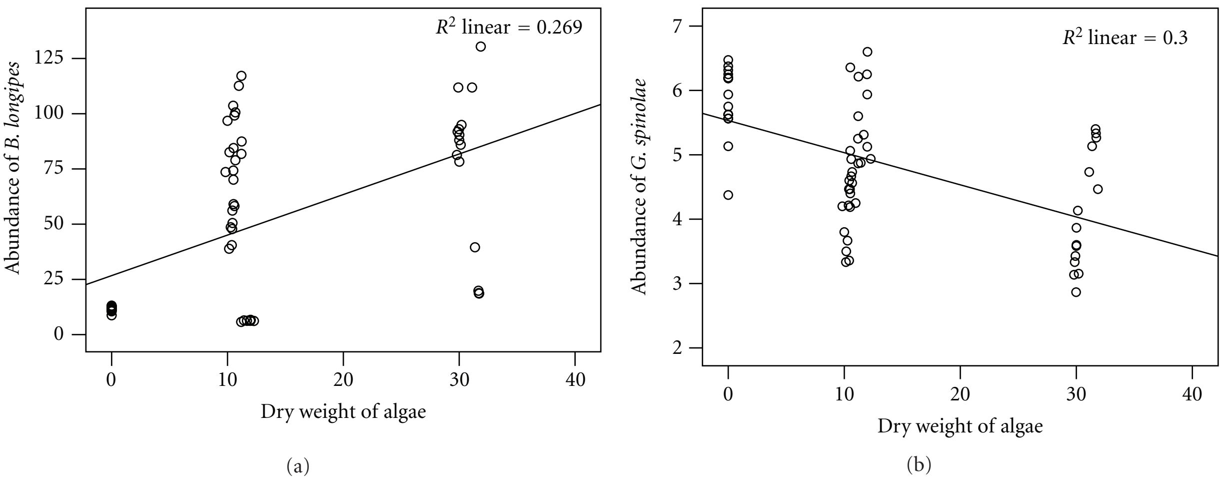
complex dynamics. It has been reported that pH decreases with the increase in temperature [41]. Moreover, increasing turbidity of water increases heat retention capability of water [42]. Hence, ponds having turbid water exhibit relatively high temperature and slightly low pH as is evident in the Durgakund pond. Physical parameters also regulate the concentration of several ions, content of free CO_2, dissolved oxygen, even BOD [43]. However, anthropogenic stress in the three experimental ponds is apparently due to the dumping of organic wastes [44]. Increasing organic degradation initially results in nutrient enrichment and finally in colonization of the various algae and "algal bloom" formation resulting in "eutrophication." The extent of organic pollution in terms of increase in BOD, free CO_2, and heavy oxygen stress can be monitored conveniently by using *G. spinolae* and *B. longipes* as bioindicators. The extent of pollution in ponds can be assessed by the abundance of *B. longipes* which may be predicted to increase and that of *G. spinolae* to decrease with increasing pollution levels. The reason behind the contradictory responses of the two insects under study is due to differences in the habitat requirements of their life-history stages. *Gerris spinolae* lays eggs on the submerged vegetation at depths of 2-3 meters from the surface [14]. This submerged oviposition is regulated by the level of dissolved oxygen and male presence [14]. After emergence, the nymphs respire using dissolved oxygen of the water, though the adults "skate" on the pond surface. This explains the negative correlation of their abundance with parameters indicative



(a)

(b)

Figure 6: Relation between phosphate ion concentration and abundance of (a) *Brachydeutera longipes* (Hendel) and (b) *Gerris spinolae* (Lethierry and Severin) as shown by regression analysis.



(a)

(b)

Figure 7: Relation between dry weight of algae (g/sq. m) and abundance of (a) *Brachydeutera longipes* (Hendel) and (b) *Gerris spinolae* (Lethierry and Severin) as shown by regression analysis.

of higher level of pollution. Consequently, reduction in the abundance of *G. spinolae* may be a good indication of oxygen deficiency of water. Contrastingly, *B. longipes* does not rely on dissolved oxygen for respiration. The surface-living maggots feed on some species of algae like *Microcystis* sp., while the adults are free flying and are reported to feed on particles floating on the pond surface by rapidly extending and retracting their proboscis [32], so their number increases with eutrophication. The study clearly demonstrates that *G. spinolae* and *B. longipes* are good positive and negative indicator taxa for healthy fresh water ponds. We, therefore, conclude that occurrence of higher *G. spinolae* population level indicates a positive correlation with healthy unpolluted pond conditions while enhanced abundance of *B. longipes* indicates higher pollution level of the pond.

Since insects exhibit high fecundity, are fast breeding, easy to sample, and ethical constraints are not involved, *Gerris spinolae* (Lethierry and Severin) and *Brachydeutera longipes* (Hendel) appear to be suitable insect bioindicator candidates for assessing pollution in fresh water bodies. Utilisation of insect bioindicators would be an inexpensive method for monitoring pollution and for carrying out preliminary assessments of the water quality of inland ponds and lakes. This would avoid direct assessment of water quality involving expensive analytical methods, particularly at the preliminary stages. Integration of inexpensive

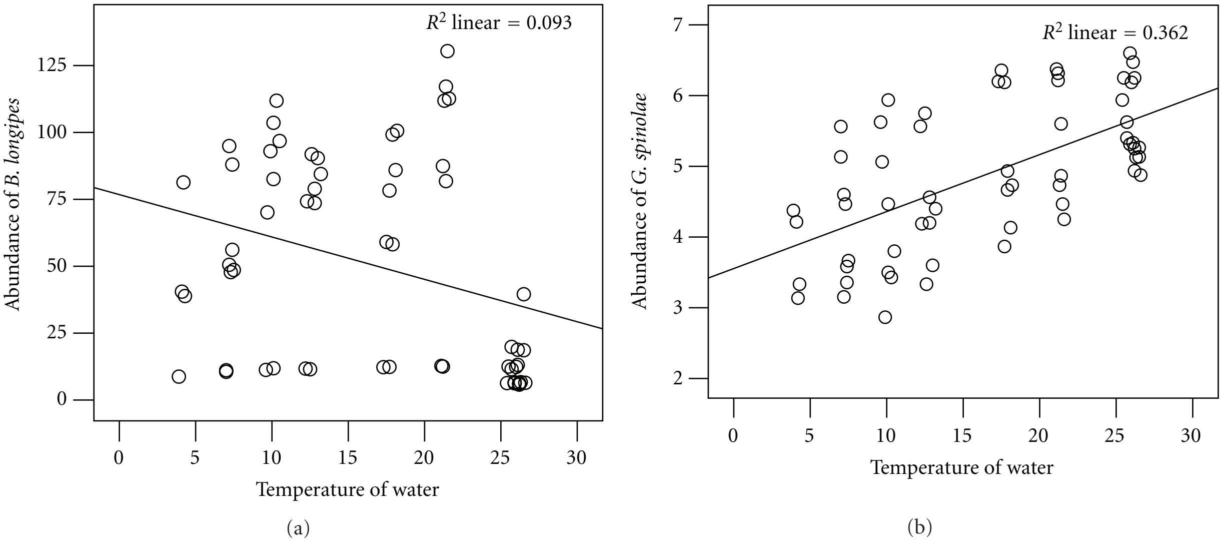


FIGURE 8: Relation between temperature of water and abundance of (a) *Brachydeutera longipes* (Hendel) and (b) *Gerris spinolae* (Lethierry and Severin) as shown by regression analysis.

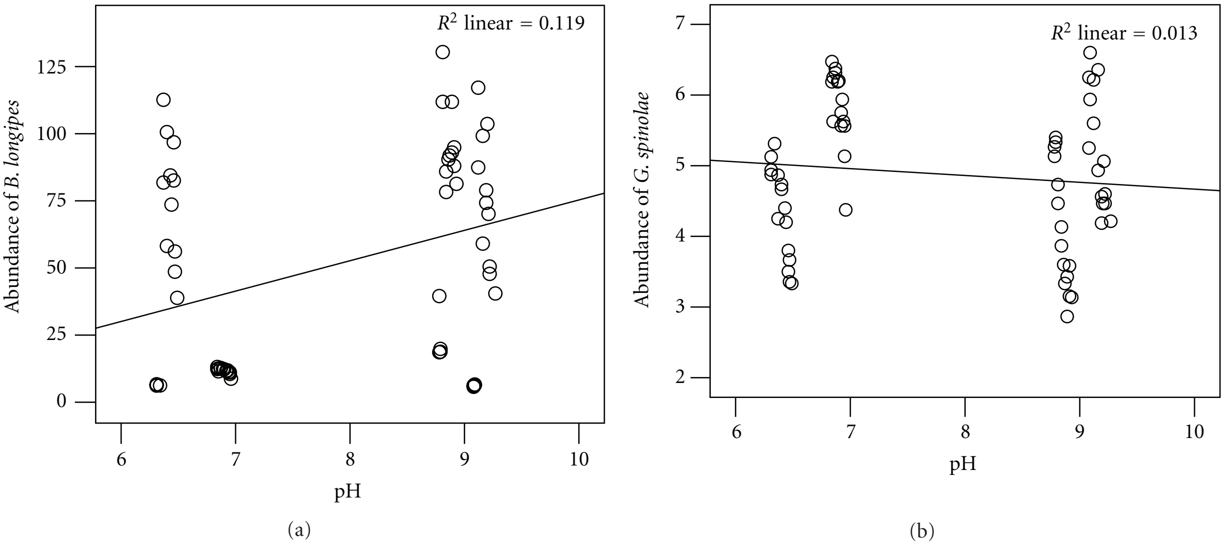


FIGURE 9: Relation between pH of water and abundance of (a) *Brachydeutera longipes* (Hendel) and (b) *Gerris spinolae* (Lethierry and Severin) as shown by regression analysis.

biomonitoring methods with chemical-specific assessment methods would facilitate the restoration of the biological integrity and ecological health of freshwater bodies.

Acknowledgments

A. Pal and D. C. Sinha thank the Head of the Department of Zoology, Banaras Hindu University, for providing laboratory facilities for carrying out the research. The authors appreciate the advice of Dr. B. P. Singh and the help provided by Sudha Kumari for carrying out the statistical analysis. The authors also acknowledge the kind help of Dr. V. V. Ramamurthy, IARI, Pusa, New Delhi, India, for identification of the insect specimens.

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Hindawi Publishing Corporation
Psyche
Volume 2012, Article ID 345932, 7 pages
doi:10.1155/2012/345932

Research Article

Herbivore Larval Development at Low Springtime Temperatures: The Importance of Short Periods of Heating in the Field

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Received 4 July 2011; Revised 14 October 2011; Accepted 29 October 2011

Academic Editor: Panagiotis Milonas

Temperature has been shown to play an important role in the life cycles of insects. Early season feeders in Palaearctic regions profit by the high nutritional quality of their host plants early in the year, but face the problem of having to develop at low average springtime temperatures. This study examines the influence of short periods of heating in the field on larval development and on mortality with the model system *Galeruca tanaceti* L. (Coleoptera: Chrysomelidae), an early season feeder, that hatches at low springtime temperatures. Field and laboratory experiments under different constant and variable temperature regimes were performed. While in the field, the average daily temperature was close to the lower developmental threshold of the species of 10.9°C; maximum temperatures of above 30°C were sometimes reached. Larvae developed significantly faster, and pupae were heavier, in the field and in an assay with short periods of heating than at the same average temperature under constant conditions in the laboratory. We conclude that larvae profit substantially from short periods of heating and temperature variation in the field and that intervals of high temperature enable insect survival and exploitation of nutrient-rich food resources at early times in the season.

1. Introduction

With their early arrival in spring, "early season" or "flush" feeders take advantage of the high nutritional quality of their potential food source, itself the result of a high concentration of nitrogen in growing leaves [1]. Many insects prefer young plants or tissues to old ones and are therefore restricted to feeding at certain times of the season [2]. These herbivores may profit by a fast development and high pupal weight due to the readily assimilated nitrogen at this time of the year [3]. On the other hand, at least in Palaearctic regions, herbivores which appear early in the season are vulnerable to low mean and minimum daily temperatures, which might often drop below the lower developmental threshold of the species in question and severely reduce growth and development.

Insects that specialize in using ephemeral resources (e.g., young leaves) should be especially sensitive when the timing of the availability of those resources is unpredictable. Asynchrony with plant phenology and factors that promote it, such as climate change, have a considerable impact on the dynamics of spring-feeding herbivores [4]. Synchronization between bud burst and egg hatch in a Lepidopteran species varies widely with spring temperatures, while an artificial elevation of temperature prolongs the total period of budburst but shortens the period of egg hatching [5].

Climatic parameters in general have been shown to play an important role in insect life. The most important microclimatic parameters are humidity, solar radiation, and wind, as insects essentially heat up by radiation and lose this heat through convection. Insects, and especially their larvae, are highly sensitive to these variables because of their small size and their relatively large surface area [6]. Temperature plays a major role within the abiotic factors, representing one of the most important environmental factors in the life cycle of insects. In particular, it has been shown to have a considerable influence on their development [7–9]. In general, there is an optimal temperature for the development of a species within a favoured range, where mortality is especially low and development time short. A number of adverse physiological reactions can occur when development takes place at temperatures below this optimum. The chemical reactions of the endocrine system slow down with the cold [10], and growth rate is reduced. Some insects step into a diapause to escape low temperatures [11]. Cold temperatures are also able to change the correlation between body size and the beginning of metamorphosis. Larvae that mature at lower temperatures often produce under- or oversized adults [10].

Below a certain threshold, many insects come to a developmental arrest, but can survive. The temperature at which growth stops is referred to as the "lower developmental threshold." It is specific to each species and is known precisely for only a few. For the wax moth *Galleria mellonella* Linnaeus, for example, the lower developmental threshold is 19°C, while for the Lepidopteran *Xestia C-nigrum* Linnaeus, it is only 5°C [10]—despite their distribution area being very similar. As with growth rate, development time is also related to temperature. Typically, development time decreases exponentially with increasing temperature [12–14].

The influence of temperature upon insect development is related not only to the daily mean average, but also to the rate of temperature change. Likewise, growth is expected to be related to both duration and quantum of temperature above thresholds. Insects have frequently been shown to develop more rapidly, lay more eggs, suffer a lower mortality, or complete their life cycle within a wider temperature range when temperatures are fluctuating, like they predominate in the field, than at constant temperatures, as long as the maximum and minimum of the fluctuating temperature are within the optimal range of development for the organism [15–17]. While the effects of fluctuating versus constant temperatures have already been well studied, little is currently known about the effects of short periods of heating for larval development and for the growth of Palaearctic insect species in the field. This might be achieved for larvae and adults through, for example, their basking behaviour [18], but Richards and Suanraksa [19] have also shown that energy reserves for embryonic development were sufficient for considerable periods spent below the constant temperature threshold, provided that enough time was spent at much higher temperatures beforehand.

The polyphagous leaf beetle *Galeruca tanaceti* Linnaeus was used as the model organism for studying the influence of short periods of heating and temperature variations in the field on the larval development of an early season feeder. The adult females deposit their egg clutches with the beginning of the fall in herbaceous vegetation, preferentially on high and dry blades of grass. While the adult beetles die, the eggs are the overwintering form. Between March and April, at cold springtime temperatures, the larvae emerge and develop while feeding on the first young leaves of their host plants [3]. After approximately four weeks of feeding, the larvae pupate after the fourth larval stage, in the soil.

In this study, we examine the influence of short periods of heating and of temperature variation in the field on herbivore larval development. An adaptation to low temperatures close to the lower developmental threshold is discussed as a prerequisite for early season feeders in Palaearctic regions, so that they are able to exploit the high nutritional quality of their food resource at this time of the year. Larval development was studied under field conditions, and under different temperature regimes in the laboratory, to calculate the lower developmental threshold of the species and to help evaluate the field data.

2. Material and Methods

2.1. Study System. The field experiment was performed on dry grassland in the Hohe Wann Nature Reserve in Lower Frankonia (Northern Bavaria, Germany, 50°03′ N, 10°35′ E). The study site was grazed by sheep until a few years ago. In the two years prior to the study, the site was no longer managed. Randomly picked plots were chosen with the help of GIS and GPS.

The tansy leaf beetle, *Galeruca tanaceti*, is polyphagous and feeds on species of the families Asteraceae, Brassicaceae, Caryophyllaceae, Dipsacaceae, Liliaceae, Lamiaceae, Polygonaceae, and Solanaceae [3]. In the study area, one of the main host plants of *G. tanaceti* is yarrow, *Achillea millefolium* L. (Asterales: Asteraceae) [20], but larvae can also be found feeding on *Centaurea jacea* L. (Asterales: Asteraceae) and *Salvia pratensis* L. (Lamiales: Lamiaceae).

In fall, females of the tansy leaf beetle deposit their egg clutches on vertical structures within the herbaceous vegetation layer, where the egg clutches then hibernate [21]. After hatching in March-April, the larvae seek suitable host plants close to the oviposition site, on which they feed for about four weeks until pupation [3]. After pupation, the adults can be found from early June onwards before they enter reproductive diapause in midsummer.

2.2. Larval Development and Mortality. Prior to the experiments, in fall, egg clutches of *G. tanaceti* were collected from different sites of the reserve and stored over the winter in a closed cage under natural climatic conditions. In spring, egg clutches were transferred to the laboratory and kept at room temperature until hatching of the larvae. Egg clutches were checked daily for hatching larvae. In the field as well as in the climate chambers, the development time of larvae from eclosion to pupation, pupal weight, and mortality rate were all registered. Only larvae that hatched within 24 h of the start of the experiment were used. The larvae of the different egg clutches were mixed prior to use, to ensure a random assignment to treatments.

2.3. Experimental Setup

2.3.1. Field Experiments. After transfer to the field, larvae developed on a dry grassland site in the Hohe Wann Nature Reserve in 40 completely closed gauze cages with a size of 40 × 40 cm. The cages consisted of a wooden frame covered with gauze mesh on all sides, including the top. The mesh width of the gauze was 1.2 mm because of the very small size of the newly hatched larvae. It is possible the gauze may have shaded the larvae and reduced T max; however, the negative effects of closed cages on larval development in comparison to treatments with open cages could not be observed [Müller, unpublished data]. To avoid the escape of the larvae, the cages were placed flush with the soil.

Additionally, the bottom rim was sealed with soil. All cages included the same number of plants of the main host plant of the beetle, *Achillea millefolium* L.. 10 larvae, hatched within 24 hours of the start of the experiment, were positioned on the same host plant in the centre of each cage. The larvae were placed together in groups of 10 larvae per cage to simulate natural conditions as closely as possible, for usually multiple larvae hatch out of the egg clutch at the same time. After 28 days, at the end of the feeding phase, the remaining larvae were counted, collected, kept singly in boxes under natural conditions, and provided with food until pupation. All pupae were weighed immediately after pupation. The experiment was repeated once (1st cycle: 4/22–5/19 and 2nd cycle: 5/19–6/15). Additionally the air temperature was recorded during both cycles of the experiment. For this, a thermobutton (Dallas Semiconductor "DS 1921L-F5X Thermochron iButton") was installed in each cage at a 30 cm height (mean height of egg clutches) and shaded. The temperature was recorded once every hour during both experimental periods.

2.3.2. Laboratory Experiments. Laboratory treatment groups were installed as follows: constant temperatures at 15°C (1) and 23°C (2), variable temperature with short periods of heating at a temperature of 18°C for 22.5 hours, and at 28°C for 1.5 hours (daily mean: 18.6°C) (3). All three climatic chambers received the same daylight conditions, according to the conditions in the field (L/D: 14/10 hours). The experiment began when the larvae, which had hatched within less than 24 hours, were exposed to a certain temperature according to their treatment group. The larvae were kept singly in plastic boxes to exclude interaction influences and were fed with their main host plant, *Achillea millefolium* ad libitum. 17 larvae were kept in each climatic chamber.

2.3.3. Calculation of Lower Developmental Threshold and Degree Days. In this study, for the calculation and graphical definition of the lower developmental threshold, developmental data from two constant temperatures were used (15°C and 23°C), after the line-fitting method of Ikemoto and Takai [22]. A linear regression was calculated of the rate of development (1/D) for the larvae of both chambers and related to the linear degree-day model (e.g., [23, 24]). This is based on the assumption that the rate of development (1/D) increases linearly with incubation temperature T in the range of temperatures usually experienced. The lower developmental threshold results in the intersection of the regression line with the x-axes.

In poikilothermic organisms, it is assumed that the developmental rate depends on temperature in such a way that the product of the duration of development D (days) and the incubation temperature T (degrees) above the species-specific lower developmental threshold t_0 is represented by a constant k (degree days). Thus, a specific number of degree days, the so-called "thermal constant k" (measured in degree days [DD]), are required for an individual to complete development (e.g., [25, 26]). For identification of the development time, the duration in degree days was calculated along with the duration in calendar days for all larvae investigated (field and laboratory).

Degree days are a measuring unit for the amount of heat that acts on animals or plants above a specific developmental threshold temperature. This amount is counted over a period of 24 hours. One degree day is counted for every degree over the specific developmental threshold (lower developmental threshold). Thus, multiple degree days can be accumulated over a period of 24 hours [26]. Different kinds of calculations are possible. If the minimal temperature does not drop below the lower developmental threshold, the so-called "average method" is used (1). This method was used for the climate chamber data.

$$\mathrm{DD} = \left[\frac{(\text{maximal temperature} + \text{minimal temperature})}{2}\right] - \text{base temperature}. \tag{1}$$

If the minimal temperature drops below the lower developmental threshold, the "modified sine wave method" is used. This method takes advantage of the fact that daily temperatures behave similarly to sine functions. The sum of degree days is calculated via the areas under the sine waves. A reference table is available for ease of use, where the degree days can be read off for precise minimal temperatures [26]. The "sine wave method" was used for calculation of the degree days of the field experiment, because the temperatures fluctuated and dropped below the base temperature. For calculation purposes, the maximum and minimum temperature of each cage on each day was noted. Afterwards, the average maximum and the average minimum temperature across all cages were calculated, separately for each run. With these averages, the number of degree days was taken from the reference table for each day.

2.3.4. Statistical Analysis. The calculation of the degree days was performed after Herms [26]. Treatment groups of larval weight, development time, and mortality were compared by a GLM after testing for normal distribution. All statistical analyses were performed with Excel 2003 or SPSS 14 for Microsoft Windows.

3. Results

3.1. Laboratory Experiment. The climate chamber experiment showed a significant difference in the development time of the larvae over all treatment groups ($F = 1911.806$; $P < 0.001$; $n_1 = 5$; $n_2 = 13$; $n_3 = 14$) (Table 1). Mean development time of larvae differed between 24 days (constant temperature group: 23°C) and more than 52 days (constant temperature group: 15°C). In the treatment with variable temperatures and a short period of heating (18°C/28°C; mean daily temperature: 18.6°C) and a mean development time of 32 days until pupation, development was already strongly accelerated when compared to the 15°C group with constant temperatures.

Likewise, the weights of the pupae differed significantly between the treatment groups ($F = 52.483$; $P < 0.001$; $n_1 = 5$; $n_2 = 13$; $n_3 = 14$). The pupae of the 15°C treatment group

Table 1: Comparison of larval development of the different treatment groups in the climate chambers and in the field with a statistics column, showing the differences between all groups. Different letters indicate significant differences between treatment groups, shown with development time, weight, and mortality.

Treatment group	Climate chamber			Field		Statistics
	18°C/28°C	23°C	15°C	(1) run (15.0°C ± 0.3)	(2) run (13.0°C ± 0.2)	
Development time [days] (x ± SD)	32.00 ± 1.03^{a}	24.00 ± 0.75^{b}	52.00 ± 0.89^{c}	31.00 ± 0.0^{a}	31.00 ± 0.00^{a}	$F = 1063.43$; $P < 0.001$
Physiological development time [degree days]	265.64	290.40	221.40	293.00	200.00	
Pupal weight [mg] (x ± SD)	42.00 ± 5.51^{a}	49.00 ± 3.76^{a}	18.00 ± 1.95^{a}	41.00 ± 14.76^{a}	39.00 ± 16.55^{a}	$F = 17.985$; $P < 0.001$
Mortality [%]	18^{a}	23^{a}	70^{b}	90^{b}	90^{b}	$F = 36.442$; $P < 0.001$

were significantly lighter than those of the other treatment groups in spite of their long development time (Table 1). Regarding pupal weight, the pupae of the treatment group with variable temperatures and a short period of heating in the climatic chamber were heavier than those in the constant 15°C group.

Among the laboratory treatment groups, mortality of the 15°C treatment was highest (>70%) and differed significantly from the mortality of the larvae of the two other groups ($F = 6.204$; $P = 0.001$; $n = 17$). At 15°C, 12 larvae died, at 23°C, 4 larvae died, and at 18°C/28°C, 3 larvae did (Table 1). Based on the developmental data of the two chambers with constant temperatures (15°C and 23°C), and an extrapolation after the line-fitting method [22], a "lower developmental threshold" of $T_0 = 10.9$°C was calculated for the development of *Galeruca tanaceti*.

3.2. Field Experiment. In the field experiment, the mean daily temperature differed between the two cycles of the experiment where larvae were exposed. The mean daily temperature of the first cycle (15°C ± 0,33) (4/22–5/19) was higher than that of the second cycle (13°C ± 0.2) (5/19–6/15) (Figure 1). Maximum daily temperatures varied from 15°C to 33°C in the first cycle and from 13°C to 32°C in the second cycle, reaching 30°C and above during several days in each experimental cycle. Regarding the degree days, the first cycle contained more degree days and got a higher physiological development time of $k_1 = 293$°d compared to fewer degree days and lower physiological development time ($k_2 = 200$°d) in the second cycle, caused by lower minimum daily temperatures and more days with a lower mean temperature (Figure 1, Table 1). Nevertheless, all larvae of both groups took 31 days for development. The mean pupal weight was 41 mg ±14.76 ($n = 400$) in the first cycle and 39 mg ±16.55 ($n = 400$) in the second one. The rate of mortality was very high, and 90% of the larvae in both cycles died or disappeared.

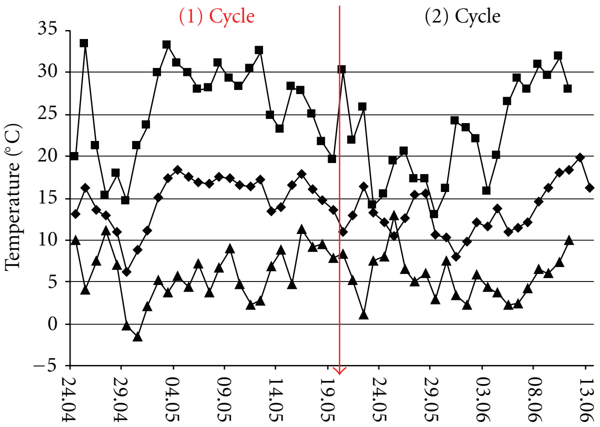

Figure 1: Temperature gradation for both cycles of the field experiment with mean (◆), maximum (■), and minimum (▲) mean daily temperatures measured at 0.3 m height ($n = 40$).

4. Discussion

This study investigates how larvae of an early season feeder, the leaf beetle *G. tanaceti*, manage to develop at relatively low springtime temperatures and profit at the same time by the high nutritional quality of their host plants at that time of the year.

Field and laboratory experiments under different temperature regimes were performed. Mean daily temperatures in the field turned out to exceed the lower developmental threshold of the species (10.9°C) by only a few degrees Celsius. The lower developmental threshold can vary between different Coleopteran species. The Curculionidae species *Cionus latefasciatus* Voss, for example, has a threshold temperature of 7.7°C [27], whereas for the lower developmental threshold of *G. tanaceti*-larvae, a temperature of 10.9°C was determined according to the developmental data of the two chambers with constant temperatures (15°C and 23°C) and an extrapolation after the line-fitting method [22]. Mean daily temperatures during both cycles of the field experiment ((1) cycle: 15°C ± 0.33; (2) cycle: 13°C ± 0.20) therefore exceeded, by two to four degrees on average, the lower developmental threshold of the species, at which no growth or development occurs. Minimum daily temperatures were almost always below the lower developmental threshold, sometimes even dropping to zero degrees Celsius. In general, low temperatures can affect development negatively by causing low pupal weight and prolonged development time and thereby reducing fitness via predation pressure [28], disadvantages in mating [29–31] or fewer and smaller offspring [32].

Mean daily temperatures in the field were therefore either lower than or equal to the constant 15°C climatic chamber. In spite of this, larval development in the field, provided with short periods of heating, differed significantly from that of the larvae in the constant 15°C climatic chamber. Larvae in the field showed an almost twice as fast development and were more than twice as heavy as in the constant 15°C climatic chamber. We assume that larval development at very low temperatures, even if partly below the lower developmental threshold, is possible if there are heating periods with higher temperatures in between and which can be taken advantage of by the larvae. Maximum daily temperatures in the field varied between 15°C and 33°C, reaching values of 30°C and above during several days in each experimental cycle. The use of short periods of high temperature and the regulation of body temperature to maximise radiative gain can be achieved, for example, by basking behaviour [6, 19, 33]. Insects are often found basking on leaves where temperatures are reached that are several degrees higher than the surrounding air, caused by reflected radiation, longwave radiation reradiated from the warm leaf, and possibly convection and heat conducted from the warm leaf [19]. Obviously, basking is especially important during colder weather periods. For adult *G. tanaceti*-beetles, surface temperature was on average 4°C higher while basking in the sun as compared to that of the plant surface on which they were resting (Tearasa, pers. communication).

Beside exposure to short periods of heating, temperature variation in comparison with constant temperatures can also help explain the more rapid development of insects at the same mean daily temperatures [17]. Blanckenhorn [11] has described, using the yellow dung fly, how development time is shorter at variable temperatures in the field than with the same mean constant temperature. The same was found by Sehnal [10] in the context of development at low temperatures. This phenomenon, therefore, seems to be fairly widespread among insects; its underlying mechanisms, however, remain poorly understood. With the field and laboratory data available in this study, it is difficult to discriminate between the two mechanisms. $T\,\max$, however, seems to be a very important factor for larval development at relatively cold average springtime temperatures, as indicated by the climatic data from the field and larval development in the 18/28°C chamber.

The 18/28°C chamber, with a relatively low mean daily temperature (18.6°C), shows that a short time spent heating per day (in the case of the 18/28°C chamber, 1.5 h per day) seems to be sufficient to accelerate larval development and change developmental parameters, such as development time and pupal weight, to values comparable to those in the field. Mortality is much lower than in the field, probably because of the constant conditions in the climatic chamber and the absence of natural enemies or adverse abiotic factors such as rain and wind. The short period of heating per day in the climatic chamber might be equivalent to heating by sunshine or the higher temperatures over midday in the field (Figure 1). In the field, however, larvae may also regulate body temperature independently from ambient temperatures by basking, and this hinders the comparison of field with lab work.

The larvae of the constantly heated 23°C chamber showed, in spite of this, the shortest development time, with 24 days on average and the highest pupal weight compared to the 15°C chamber. This temperature might resemble one close to the temperature optimum of the species. Furthermore, this optimal development demonstrates that the prolonged larval development and high mortality in the 15°C chamber were not due to insufficient conditions in the laboratory, but rather that the chosen temperature regime and progression was responsible for the values obtained. A comparison of the two constant chambers of 15°C and 23°C shows, additionally, that with the chosen temperature regimes, there was neither a positive correlation between body size and development time (calendar days)—as is commonly described in life history theory—nor was there a negative correlation of body size and development time (expressed as degree days), as found by Blanckenhorn [11]. This might be due to extremely unfavourable conditions at constant 15°C which could not be completely compensated for by a longer time of development. In any case, surviving pupae stayed rather small at this low temperature.

The findings of Ratte [12] suggest yet another explanation for the better results of the field study in comparison to the results of the constant 15°C treatment group in the laboratory. He concluded that some insects grow faster if they are also exposed to temperatures below their lower developmental threshold. The larvae of *G. tanaceti* were exposed to temperatures below their lower developmental threshold T_0 in the field, but not in the constantly heated 15°C chamber. The differing development times of 52 days in the climate chamber and only 31 days in the field might also be partly explained by this observation.

The identical development time of all larvae of both field runs is of considerable interest. One explanation could be that the transport from the field to the laboratory after the larvae stopped feeding represented some kind of signal for pupation. Pupation may have been induced by a temperature change, the handling itself, or some alteration of other microclimatic factors.

G. tanaceti is well adapted to its early appearance in March/April at low springtime temperatures. Larvae are black in colour and so absorb the sunlight and use it for movement, feeding, and metabolism. It has been shown that, at least in some instances, specimens from the warmer parts of the range are generally brighter and paler than those from the same taxon collected in cooler areas [6]. Furthermore, overwintering in the egg stage enables larval development at precisely the time of the first bud burst, when the quality of the food resource is especially high. Additionally, these “early season feeders” have only a few feeding competitors at the time of their major growth and development. Finally, the reduced development larvae, suffering from low temperatures close to or below the lower developmental threshold, can be compensated for by short periods of heating or temperature variation. They enable the larvae to develop at almost normal speed even at early springtime conditions in the field. Disadvantages, such as a possible (and possibly worsening) lack of synchronization of hatching with the availability of the host plants due to climate change [4, 5], and slow development at temperatures close to the lower developmental threshold, are at least partly compensated for in the aforementioned ways. As long as the extreme values of thermal conditions are not too high to induce stress in the organisms [34], short periods of heating in the first place enable the exploitation of nutrient-rich food resources at this time of the year.

Acknowledgments

The authors thank H.-J. Poethke for encouraging and hosting this study at the ecological field station Fabrikschleichach, two anonymous reviewers for their valuable comments, and the Council of Lower Frankonia for permission to work in the nature reserve Hohe Wann.

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Hindawi Publishing Corporation
Psyche
Volume 2012, Article ID 497087, 6 pages
doi:10.1155/2012/497087

Research Article

Survival of Wild Adults of *Ceratitis capitata* (Wiedemann) under Natural Winter Conditions in North East Spain

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Received 12 July 2011; Revised 25 September 2011; Accepted 21 October 2011

Academic Editor: Nikos T. Papadopoulos

The overwintering of the Mediterranean fruit fly (medfly), *Ceratitis capitata* (Wiedemann) at the northern limits of its geographic distribution is not yet well known. With the aim of estimating the survival rate of medfly adults in northeast Spain under natural winter conditions, a two-winter-season trial was carried out. A control was carried out in a climatic chamber at 25°C. The results showed that medfly adults were unable to survive the entire winter season in the Girona area. Climatic conditions, including the daily minimum temperature, daily maximum temperature and the high rainfall, appeared to be involved in adult mortality in winter.

1. Introduction

Ceratitis capitata (Wiedemann) (Diptera: Tephritidae) (the Mediterranean fruit fly or medfly) has a worldwide geographic distribution and it is well adapted to the climatic conditions [1], but at the northern border of its distribution the population density is reduced at least once a year by winter temperature [2]. Therefore, in order to design effective control methodologies against this insect, we require knowledge of the strategy that it uses to survive the most hostile winter periods. The northern limits of the medfly distribution include the northeastern part of Spain (the fruit growing area of Girona), where, unlike in more southern latitudes (such as the middle and southern coast of Spain), adults have not been observed during the coldest period of the year [20]. Adults of *C. capitata* are present throughout the year in several areas, including the southern coast of Spain [3] but have not been recorded during the coldest period of the year in the Girona area, north east (NE) Spain [4].

There are two hypotheses on medfly overwintering to explain the appearance of new populations in spring. The first one assumes that infestations are of a temporary nature, originating from infested fruit imported from warmer areas that contain a large quantity of winter hosts [5]. This theory has been questioned in a number of areas, including the central mountains of Israel [5, 6] and the Balearic Islands [2]. The second theory assumes that *C. capitata* adapts to temperate climates because of its ability to withstand low temperatures [7], a fact that enhances successful overwintering for part of the population, as seen in central Italy [8]. In northern Greece, medfly has been observed to overwinter as larvae within infested host fruit even if temperatures fall below zero [9]. These findings were also verified in the region of Tarragona, where medfly larvae were found inside late-ripening varieties of orange [10].

Survival of a small percentage of individuals each winter and regeneration of the entire population from these individuals in spring and early summer probably represents a strong selection pressure in this insect for the evolution of a mechanism to withstand the cold [9].

Studies on medfly population dynamics have shown that the main factor affecting population buildup in the tropics is the abundance and availability of fruit [11–13], whereas in temperate areas, such as northern Greece, low winter temperatures and the absence of host fruits are the two main factors that inhibit overwintering [14–16]. Temperature can also affect the appearance of the population after the winter period, retarding or advancing adult presence, as seen in Girona [4].

Although medfly distribution appears to be ultimately restricted by the severity of the winter, the existence of a variety of microclimates in a particular area implies that other climatic factors may limit or at least regulate the population dynamics of the species [17]. Survival in insects depends on both temperature and duration of exposure [18], and the duration of low temperatures could be used to test the medfly's tolerance to cold [19]. Therefore, the combination of factors such as dry and cold stress [17] and duration of low temperatures could explain the low incidence of the pest in a particular location.

Recent studies performed in Girona support the hypothesis of an overwintering population in this area [4], but the conditions of medfly overwintering are still unknown. Therefore, the aim of this study was to estimate the survival rate of medfly adults in the Girona fruit area, NE Spain under natural winter conditions over a period of two winter seasons and to test the hypothesis that adult medflies survive winter conditions in this area.

2. Material and Methods

The trial was performed over two consecutive winters: from mid-December 2008 to mid-January 2009 and from mid-November 2009 to late December 2009. It was performed on a 962 m^2 north-facing commercial plot of "Golden Delicious" apples, enclosed by a wood structure with walls and a roof made of plastic mesh. The plot was divided into three sealed compartments with the same dimensions, each with its own access door. Climatic conditions in the three compartments, including temperature and relative humidity, sometimes differed slightly. The control treatment was arranged in a chamber maintained at 25°C ± 1°C, 50–80% RH with a photoperiod of 14 h light and 10 h darkness in order to determine the viability and longevity of the population used in the field.

In 2008, 236 five-to-seven-day-old second-generation (F2) adults originally from an autochthonous population reared under controlled conditions in Girona were used, and in the following year 212 six-day-old wild flies were used, with the aim of avoiding any influence from laboratory rearing conditions.

Individuals were placed in cages (61 by 61 by 61 cm) provided with an ad libitum diet composed of 1 : 4 : 5 parts of hydrolysed protein (Biokar Diagnostics, Beauvais, France), sugar, and water. In the second year, a mesh was placed on the base of the cages in order to prevent the flies from sinking into rain water. Each cage was placed on two wooden supports in order to avoid direct contact with the ground. They were also fixed to the soil surface with two 1.5 cm diameter iron pegs to avoid movement caused by the wind.

Three cages (replicates) each containing 45–60 individuals were established on 16 December 2008 and 16 November 2009. The cages were evenly distributed among the compartments of the plot and were maintained under natural winter conditions. In each year a similar control cage was maintained in an environmental chamber at 25°C ± 1°C. Once the cages had been installed, individual mortality was recorded on a daily basis until the death of the last individual.

During both experimental periods, meteorological data were recorded outside the observation orchard at a weather station located 700 m from the survey plot [20]. Moreover, inside each compartment of the observations plot, as well as in the chamber, temperature and relative humidity were recorded hourly using data loggers hung 1.60 m above ground level (Hobo Pro V2-ext. Temp/RH, Onset Company).

The survival analysis was carried out using the Kaplan-Meier estimates of survival and standard error followed by the log-rank test for pairwise comparisons ($P = 0.05$). Hence, the three replicates combined and compared against control. This statistical analysis was carried out using the SPSS v.15 software.

The relationship among the following factors was studied: year of the study, age of adults, daily minimum temperature, daily maximum temperature, daily average temperature, and daily rainfall, using the General Linear Model (Proc GLM) procedure of the Statistical Analysis System (SAS Institute Inc., Cary, NC, USA) to determine significant differences at a level of $P < 0.05$.

3. Results

The results of these observations suggest that adults of *C. capitata* are unable to survive throughout the winter season in the Girona fruit-growing area. Adults subjected to external conditions remained immobile inside field cages, resting on the mesh walls or in the iron-clad corners, but adults inside cages in the environmental chamber were more active.

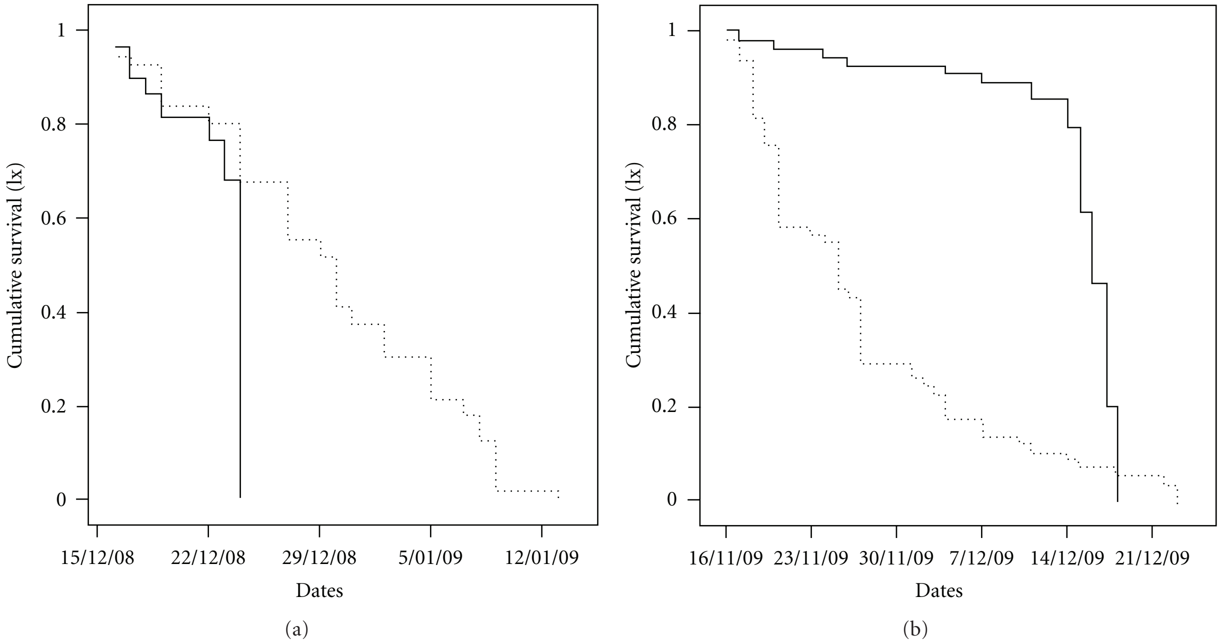
Under natural winter conditions in Girona, adult flies survived an average of 8.43 to 9.88 days in the first study period (starting in mid-December) and 28.45 to 30.24 days in the second (starting in mid-November), but under chamber conditions they survived an average of 15.5 days and 12.87 days, respectively (Table 1). The maximum survival period under natural conditions was 11 days in the first winter and 35 days in the second; under chamber conditions, the figures were 29 and 38 days, respectively. Graphs of cumulative survival rates over the study period are given in Figure 1.

The log-rank test indicated differences in survival rates between field exposed and laboratory-held control individuals ($\chi^2 = 41.02$, $P < 0.5$). Similar results obtained when control was compared against each replicate within the same year. The analysis comparing the survival in the control versus the survival in each replicate provided information related to the possible sources of variability between replicates that are difficult to measure separately in each replicate, such as the wind, normally strong in the study area and usually flowing in NE-SE direction. Due to the orientation of the orchard involved in the study (N-S), each of the replicates could have been differently exposed to it.

The temperature and relative humidity recorded in each cage using data loggers were very similar to those recorded

Table 1: Number of individuals, average survival rates, and maximum survival for Mediterranean fruit fly adults exposed in field conditions in December and November 2008 and 2009, respectively.

Year	Replicate	No. of adults	Survival average ± SE (days)	Maximum life span for the longest lived individual
2008-2009	1	60	8.62 ± 0.47	18
	2	60	9.88 ± 0.33	16
	3	60	8.43 ± 0.44	18
	Control	56	15.5 ± 1.02	34
2009	1	54	30.24 ± 0.85	41
	2	45	29.04 ± 0.78	38
	3	55	28.45 ± 1.11	41
	Control	58	12.87 ± 1.30	43



(a)

(b)

Figure 1: Cumulative survival rates of adult medflies exposed to field conditions on (a) December 16, 2008, and (b) November 16, 2009, and respective controls maintained at 25°C in laboratory conditions (dotted line, control; solid line, average for three replicates).

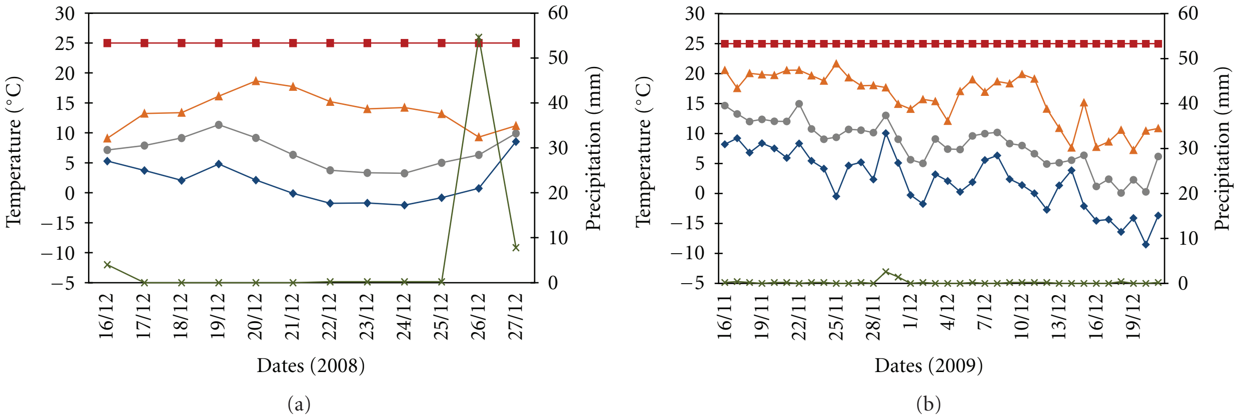
at the nearby meteorological station, with maximum differences of ±1°C. The absolute maximum temperature was 18.8°C in the first year and 22.3°C in the second (Figure 2). The absolute minimum temperature was −2°C in the first year and −8.1°C in the second. The average temperature recorded inside the plot was 6.8°C in the first year and 8.3°C in the second. Relative humidity in the field cage was 47.54% to 100% in 2008 and 40.38% to 62.49% in 2009. Accumulated rainfall in the first year was 67.2 mm, with a maximum daily rainfall of 54.6 mm recorded on 26 December 2008. In the second year, these figures were 7.6 and 2.6 mm, respectively.

In the second year of the study, one day after the absolute minimum temperature (−8.1°C) was recorded, 20.4% and 21.8% of the remaining living individuals from replicates 1 and 3 died, respectively. In the first year, between 16 November and the death of the last individual, the maximum number of cold hours below 9°C tolerated by adults was 173 hours, while in the second year, between 16 October and the end of the trial, this value was 464 hours.

The GLM analysis showed a good fit of the model ($R^2 = 0.6983$) and evidenced significant differences in the following factors: rainfall ($F = 287.26$, $df = 1$, $P < 0.0001$), daily minimum temperature ($F = 9.27$, $df = 1$, $P = 0.0026$), and daily maximum temperature ($F = 11.20$, $df = 1$, $P = 0.001$). The factors year of the study ($F = 0.3$, $df = 1$, $P = 0.5870$), age of adults ($F = 0.14$, $df = 1$, $P = 0.7117$), and daily average temperature ($F = 2.63$, $df = 1$, $P = 0.1067$) were not significant.

4. Discussion

The results showed that medfly adults were unable to survive the entire coldest period of the Girona fruit-growing area. Although adults withstand a high number of cold hours by reducing their movement and keeping still, all of them died



(a)

(b)

Figure 2: Temperature and rainfall recorded within the observation plot and temperature in the control under chamber conditions (line with squares for temperature in the control; line with triangles for daily maximum temperature; line with circles for daily average temperature; line with rhombus for daily minimum temperature; dotted line for rainfall).

after a strong freeze temperature (−8.1°C). It was observed that in semifield conditions the age reached by adults was higher than that of the control. The main factors affecting survival of adult medfly in natural winter conditions of Girona were minimum temperature, maximum temperature, and rainfall. Taking into account these results, the hypothesis that adult medfly may survive the natural winter conditions in the Girona fruit-growing area must be rejected.

Medfly adults are unable to survive low winter temperatures in some Mediterranean areas, including Greece [9]. This was corroborated in the present overwintering study with adults from a population native to Girona. Adults survived winter conditions in this area from mid-November to late December.

The insect's resistance to cold is affected by its microhabitat, which determines the availability of moisture, the developmental temperature, and parameters such as humidity and desiccation tolerance [21]. Other biological factors involved are age, body size during adult development, and feeding. In our study, cold temperature led to a reduction in medfly movements until they kept completely still, at which point they surely did not feed; because they were provided with food ad libitum, we may assume that when they kept still they had enough energy reserves to withstand extreme temperatures. However, it was demonstrated that this process consumed a great amount of energy and that survival is subsequently compromised. On the other hand, Nyamukondiwa and Terblanche [22] showed that the minimum critical thermal limit (Ct_{min}) decreases with age up to 14 days old, after which older flies have less tolerance to low temperatures; these authors also found no interaction between age and feeding in *C. capitata*.

During cold and temperate winters, most species are inactive, leading to a seasonal state of quiescence, dormancy, or even diapause that varies with species and circumstances [21, 23]. It has been shown that, at lower latitudes in temperate regions, populations of certain tephritid species (e.g., *Eurosta solidaginis* (Fitch)) are less cold tolerant than those from higher latitudes [18]. Nevertheless, in some of the southern Mediterranean areas, a small number of medfly adults might be active during winter [15, 24]. In Crete adults survived the whole winter with minimum temperatures between 1°C and 4.5°C [25]. In the present study carried out in Girona, all individuals died during the winter. The temperature threshold for population growth is 12°C to 35°C, [17] and maximum temperatures in both years were always below the upper limit. However, minimum temperatures in the study periods sometimes fell below the lower threshold.

There is high variability in the severity of the minimum temperature and the duration of exposure to low temperatures in the temperate zone [19]. Similar results to those found in the present study were recorded using the fruit fly *Dacus tryoni* at an overwintering site, where mortality was related to the minimum temperatures and mortality rate increased when subzero temperatures occurred [26].

The Ct_{min} for medfly is the temperature at which each individual insect loses coordinated muscle function and consequently the ability to respond to mild stimuli [22]. Adults exposed to this threshold recovered, so it was not immediately lethal. Depending on the age of the flies, Ct_{min} was 5.4°C to 6.6°C [22]. Taking into account these thresholds and the minimum temperatures recorded in Girona during the two study periods (−2°C and −8.2°C), it is possible that the study population lost coordinated muscle function, in which case they would have suffered a rapid demise.

The effect of rainfall on the medfly population has been related to a decrease in adult captures on rainy days and an increase a few days later, because flies are generally inactive during periods of moderate to heavy rainfall [27, 28]. In the current trial, the mortality of adults was observed to be affected by rainfall. In the first year, rain fell for only a few hours, but this had a negative effect on adult survival. The relationship between the accumulated number of cold hours below 9°C and the survival of adults in the first period was also influenced by the high rainfall of 26 December 2008. Therefore, flies in the second year endured more than twice as many cold hours as those in the first year.

Despite the results achieved in the two years of observation, there is a stable population in NE Spain. In the entire Girona fruit-growing area, the first adult medfly captured in the fruit season, using a wide monitoring network (one per orchard) installed from April to January, coincides year by year (mid-June to early July), as does the only population peak (late September to early October) [4]. In some microclimates of the region, medfly larvae may survive inside apples, the only fruit species available for overwintering in the area, as suggested by other authors [9]. It is clear from studies carried out in the area that the previous winter determines the level of the population in the following season. In years with a mild winter, after the capture of the first medfly in the season, the population developed fast and could reach high levels in the peak captures. On the other hand, after cold winters, even if the first medfly is captured on the same date, the population increases slowly, peaking as usual but never reaching the same level as in years following a mild winter [4].

An interesting fact is that, though temperature limits development, it does not necessarily limit the geographic distribution of this species [22]. This could explain why the medfly occurs in southern France, where it is frequently detected [29]. Some studies have developed models for the potential distribution of medfly, and in all of them the Girona area was included [17, 30].

One of the key points to elucidate is the threshold for classifying a winter as mild or cold, from the point of view of the medfly biology of the Girona population. How many cold hours below its $Ct_{\min}$ can the Girona medfly population withstand in order to have enough surviving individuals to quickly develop a new population in the following fruit season? At present we have no answers to this question, and a greater effort must be made to elucidate it. The implications of this knowledge are great, because it would allow us to forecast the development of the population, offering a great advantage for protecting fruit against this pest.

5. Conclusions

Medfly adults were unable to survive the entire winter season in the Girona fruit-growing area in both years studied. Climatic conditions, including low minimum temperatures, maximum temperature, and high rainfall, were responsible for adult mortality in winter. This study makes a contribution to knowledge of the biology of medfly at the northern border of its distribution area, and, jointly with previous findings on the population dynamics of medfly in Girona, it provides a framework for future studies that may answer some of the remaining questions on the biology of the Girona population.

Acknowledgments

The present study was supported by the Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria under Research Project RTA2006-00092-00-00. The authors thank the Serveis Tècnics de Recerca of the University of Girona and Professor Joan Bonany for their statistical support.

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Hindawi Publishing Corporation
Psyche
Volume 2012, Article ID 586491, 8 pages
doi:10.1155/2012/586491

Research Article

Effects of Environmental Temperature on *Capnodis tenebrionis* Adult Phenology

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Received 5 July 2011; Revised 22 September 2011; Accepted 6 October 2011

Academic Editor: Panagiotis Milonas

The phenology of *Capnodis tenebrionis* adults was presented with reference to two different climate conditions. In a temperate moderate-warm climate, adult density showed two separate peaks during the year: one in early summer of the overwintering generation and one with beetles emerging in the late summer. In a warmer semiarid climate, the overwintering adults and the new generation overlapped during summer with a continuous increase of adult density. The difference in the average annual temperature between areas during the study period was almost 3°C, and, in the warmer area, the new generation of *C. tenebrionis* emerged at least one month earlier. To make a prediction of adult presence, a model utilizing degree-days was developed from data collected over a five-year period. Models obtained from equations (Logistic 4-parameter, $y(x) = yo + a/(1 + (x/xo)^b)$) of each year were developed to describe the relationship between degree-day accumulation (with a minimal threshold activity temperature of 14.21°C calculated in the laboratory) and the cumulative percentage of adult presence. According to the overall model, the 50% of overwintering beetles occurred at 726 degree-days (Biofix: 1st March) and the emerging beetles occurred at 801 degree-days (Biofix: 1st July). The results show that a change in temperature is an important aspect that highlights the adaptability of this species.

1. Introduction

Abiotic factors including climate may limit the abundance of poikilothermic species and affect their distribution. In particular, variations in the ambient temperature have a dramatic impact on a range of fundamental biological processes including reproduction [1, 2]. Similarly, the relationship between biological events and temperature may provide useful information for predicting the same events, to define the most appropriate time for pest control using presence simulation and seasonal dynamics in regressive models [3].

The buprestid beetle *Capnodis tenebrionis* L. seriously damages *Prunus* spp. L., especially apricot, cherry, and plum [4–6], and it is capable of constraining the organic cultivation of these tree species [7]. Presence of the beetle has serious effects in orchards, and trees can be rapidly killed by the destructive action of its endophytic larvae. The species is widespread in the Mediterranean region, even in areas where their presence has been considered sporadic [8]. Outbreaks in areas previously not affected by the insect have allowed for the presence of the host, possibly as a consequence of global warming [9]. The adults of this species can live longer than one year and some hibernate twice (C. P. Bonsignore, unpubl. data). The females of *C. tenebrionis* are larger and heavier than males, with a sex ratio of 1 : 1 in the population [10]. During the reproductive phase of their lifecycle, the adults of beetle make male-biased aggregations and mated females lay their eggs at the base of host plants, after which, the larvae penetrate the roots of the tree. When the summer months are cold and wet, the number of eggs laid by one female drastically decreases [11]. The species overwinters in the adult stage or with different larval instars that can be simultaneously present on trees (range: 1–7 cm). The adult is active during day and flies during warm days [12], seriously damaging the plant by feeding on the young bark of shoots, buds, and at the base of the petiole of leaves, which drop off.

The presence of overwintering adults in fields starts in spring and is characterized by a gradual emergence when the temperature rises [7]. The presence of the new generation of adults of the beetle takes place gradually over the summer, with variation in different areas relating to climatic conditions. The timing of adult occurrence is not always predictable, which can make pest control difficult, as measures are generally targeted at the adult stage, eggs, and emerging larvae [13, 14].

Developing models of population phenology can enhance decision-making processes around pest control and provide greater opportunity to control the pest within integrated pest management programs [3, 15]. There are not many references concerning the phenology of *C. tenebrionis*, perhaps due to the cryptic habits of the juveniles and the long life cycle that characterizes the species.

The relationship between temperature and adult beetle activity has been partially explored [12]. In the present study, the movement of the insect has been considered a fundamental feature of the initial activity and presence of the adults in orchards. The objective of this study was to verify the influence of temperature on adult phenology and to describe a development and phenology model able to predict the presence of *C. tenebrionis* adults.

2. Materials and Methods

2.1. Study Site and Experimental Design. Studies on *C. tenebrionis* were conducted on apricot plantations in two different regions of southern Italy. One was in Sicily, in the hilly area of Serradifalco (CL) (37°25′52′′N, 13°52′37′′E 500 m above sea level), and the second was in the coastal area of Gioiosa Ionica (RC) in Calabria (38°11′16′′N, 13°11′56′′E 50 m above sea level).

The climate of the Sicilian orchard, according to the climatic index of De Martonne [16], is defined as "moderate warm," described here as temperate, with an annual mean temperature of 15-16°C [17]. The second site, in Gioiosa Ionica (RC), according to the climatic index of De Martonne, falls into the category of "subhumid" with a tendency towards semiarid, with an annual mean temperature of 17-18°C [18]. Moreover, this is one of Calabria's driest areas, owing to its orographic characteristics. The minimum precipitation is near the coastline as a consequence of the shielding effect of the mountains, because Mediterranean storms usually impact on Calabria from west to east [19, 20].

In the study areas, tree crops are predominantly grown, such as peach, grape, and apricot in Sicily and citrus and olive groves in Calabria. Over the past few decades, *C. tenebrionis* has been abundant in these areas. Observations were conducted in 2005, 2006, and 2007 in Sicily and in 2008 and 2009 in Calabria. The apricot orchards grafted onto Mirabolano (*Prunus cerasifera* Ehrh.) were, respectively, 11 and 9 years old, and the former had been organically managed since planting. No phytoiatric interventions against insects and mites were made in the orchards during the study years. The trees were arranged in a 4 × 4 m layout and grown in the form of a vase 2.5–3.0 m high.

2.2. Sampling of C. tenebrionis. Each year, observations were made weekly, or at least every 10 days. Observations of overwintering adults started in early spring and continued until their disappearance. The new adult generation of *C. tenebrionis* was assumed to start when the adult beetles began to emerge during summer. All insects detected on the sampled trees were manually collected, counted and identified to sex and generation then released back into the tree.

To identify which generation adults belonged to, the mandibles were examined. They were sharp and pointed in the specimens of the newly emerged generation and more blunt in the overwintered generation [6]. To evaluate possible difference between the populations of the two areas, body size measurements were taken for ~60 male and 60 female specimens. At least 24 plants were sampled in the orchard in Sicily and 48 plants in the orchard in Calabria. The observations concerned the number, sex, and generation of adults on each plant.

2.3. Laboratory Experiment. Laboratory trials were carried out in a climatic chamber to investigate the relationship between adult beetle movement and temperature to find the threshold temperature (t0) at which the movement rate was zero. At this thermal threshold, the insect would not be expected to carry out activities and therefore would not be detected in the field. Experimental adults were sourced from the field population by collecting overwintering adults a week before the start of trials. Captured individuals were separated by sex and then provided with *ad libitum* apricot tree shoots. Twelve hours before the observations began, each adult was placed in a cage measuring 25 × 25 × 35 cm. An apricot shoot with at least 12 leaves was placed in the middle of the cage. The base of each shoot was placed in a plastic tube containing water. The cages were kept at 15, 20, 25, 30, 35, 40, or 45 ± 1°C, relative humidity of 50 ± 5% and a photoperiod of 13L : 11D. Seven observations of 60 min each, with an interval of one hour, were carried out at each temperature. Each temperature was replicated eight times. During each observation period, the number of 5-min sequences in which the insect was stationary was recorded.

The rate of movement activity of the insect was calculated using the formula $1/(n+1)$, with n = the number of sequences with no movement for five minutes. This transformation made it possible to use periods of inactivity of any duration with a maximum value of 1, which corresponds with continual movement and also stabilized the variance of the data [21]. The regression method was used to find the threshold temperature (t0) at which the movement rate was zero, estimated by the x-intercept based on linear regression models [22]. The threshold temperature (t0) at which the movement rate was zero was used to calculate degree-day accumulation.

2.4. Data Analysis. The average number of adults per plant was calculated for each monitoring date, and the date of new generation adults emerging was noted for each experimental area and for each year of observation.

Paired t-tests were used to compare the body size of each sex between the two locations. The mean daily temperature was obtained from data loggers (Hobo, Onset Computer Corporation) and was calculated from bihourly data. The daily degree-day was calculated with summation of the difference in mean daily temperature and the minimum temperature threshold of beetle movement. In each year, the biofix starts on the 1st of March for overwintering beetles and 1st of July for new emerging adults. To compare the difference between areas, the annual mean temperatures were calculated.

A Logistic equation (4-parameter) commonly used for phenology modeling [23–25] was applied to the cumulative percentage of overwintering and emerging adult beetles and was fitted for each year of the data:

$$y(x) = yo + \frac{a}{1 + (x/xo)^b}, \tag{1}$$

in which y is the cumulative percentage of adults, x is the accumulated degree-days, and a, b, xo, and yo are the constants. From these, the parameter xo has biological meaning and represents the degree-days of 50% of beetle presence. Moreover, two Logistic overall equations were constructed to find 50% of the cumulative percentage of overwintering and emerging adults considering all years and the two areas. The predicted values of each year and area obtained from overall equations were linearly regressed against the observed cumulative percentages of the adult to verify the fit between observed and predicted data [26].

The values of degree-days at 50% of cumulative percentage obtained with the nonlinear regression were also compared with values obtained from the ordinary least square (OLS) method, where the cumulative percentage of the observed beetle was used as independent variable versus degree-days.

For each year, the time between the appearing and subsequent increase of adults in each generation was calculated using degree-days. This was defined as time between the onset of generations (TBG). For each area, this was calculated by the average of TBG. All analyses were performed with SigmaPlot and SPSS software.

3. Results

3.1. Laboratory Results. Using data from the movement activity of the beetle, a minimum threshold temperature for movement was calculated. The increase in temperature in relation to the rate of insect movement followed a sigmoidal function (Figure 1). Given the average daily temperature trend in the experimental areas is long periods under 25°C, we considered the first three temperatures used (up to 25°C). The movement rate was almost linear, and the linear regression method ($y = a + bx$) calculated the temperature threshold to be 14.21°C. From this temperature, the value of the accumulated degree-days was calculated for overwintering and emerging adults.

The different thermal conditions of the two areas are shown in Figure 2. In the warmer area (Calabria), the temperature is higher in the first and last months of the year. The average annual temperature estimates were 15.81 ± 0.34°C for the temperate area and 18.79 ± 0.33°C for the semiarid area. These temperatures are consistent with the reported data available for the two areas [17, 18]. Usually, females were larger than males, but paired t-test found no difference in the size of each sex between the two experimental areas: male $t = 1.221$, $n = 61$, $P = 0.227$ or female $t = 1.111$, $n = 64$, $P = 0.271$.

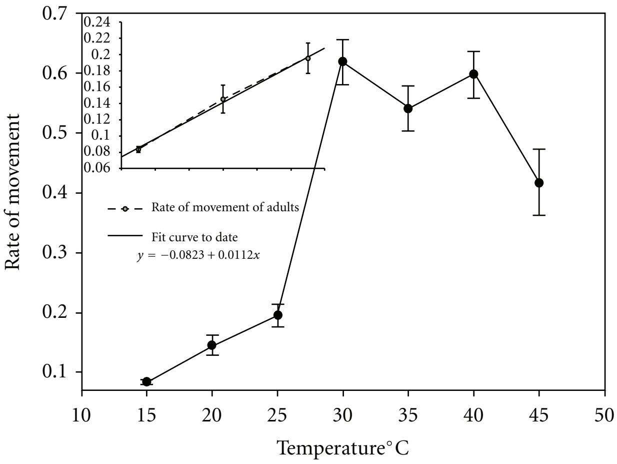


FIGURE 1: Rate of movement of *Capnodis tenebrionis* adults at different temperatures. Linear rate of movement at the first three temperatures can be observed ($R^2 = 0.996$; $F = 302.37$; df = 1, 2; $P = 0.037$).

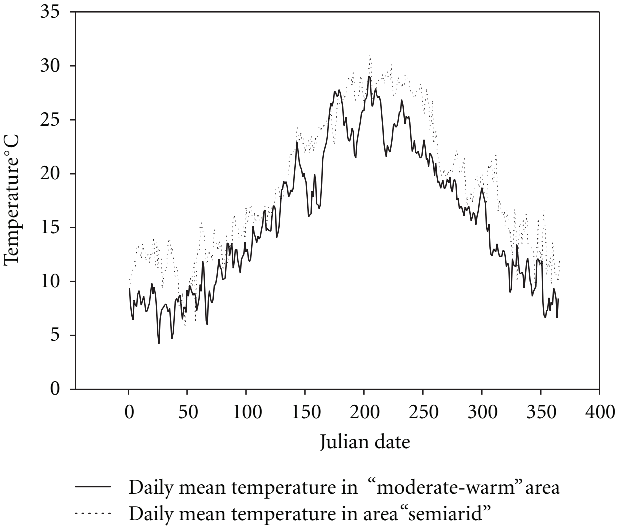
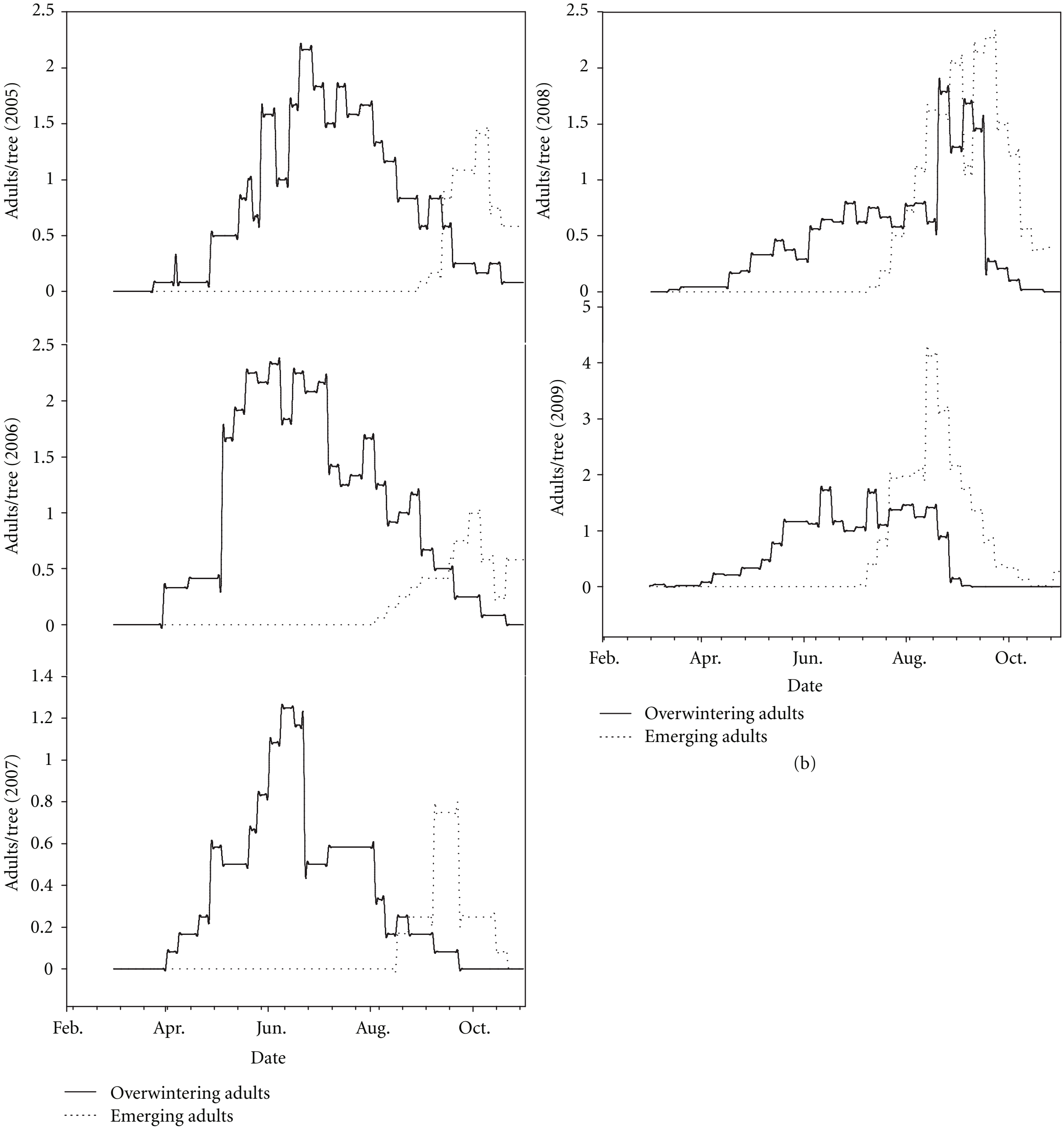


FIGURE 2: Daily mean temperature of temperate climate (Sicily), years 2005, 2006, and 2007; daily mean temperature of semiarid climate (Calabria), years 2008 and 2009.

3.2. Beetle Phenology. The presence of *C. tenebrionis* adults, although it has shown some variation in density over the years, has been widely documented in the two areas of investigation.

In the temperate area, the maximum density of adults in the field is reached with the overwintering generation,



(a)

(b)

Figure 3: Adult presence of *Capnodis tenebrionis* in a temperate area (*a*) and in a semiarid area (*b*). The early onset and the overlapping of generations of adults are evident in the warmer area.

and the lowest density of adults was found in 2007 (1.25 adults per tree), which was connected with the disappearance of plant resources due to *C. tenebrionis* attacks. The first adult maximum density in the temperate climate was reached in the middle of June in 2005 and in the first 10 days in June in 2006 and 2007. In the semiarid area of investigation in 2008 and 2009, the adult maximum density was reached in the middle of August (Figure 3), at which time the overwintering generation overlapped with the newly emerged adults. Research in the Calabrian orchard was suspended in 2010 due to the disappearance of the host resource and, subsequently, the disappearance of beetles. The overwintering generation appeared in open fields from late March and gradually spread as temperatures rose.

The appearance of adult beetles in 2005, 2006, and 2007 varied slightly in the temperate area, with the new adults emerging in August. In 2008 and 2009, the new generation emerged in the first 20 days of July, in accordance with the more elevated temperatures of this area. The emergence of adults in the two areas differed by around one month (Figure 4).

The analysis of the parameters obtained with logistic equations for overwintering gave the value of the parameter *xo* (time of 50% adult emergence), which ranged from 320

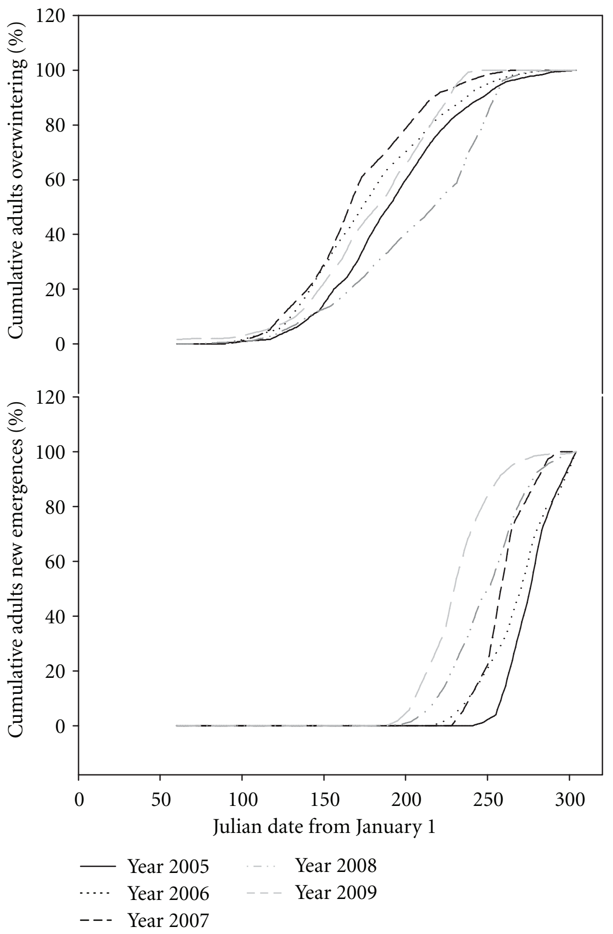


Figure 4: Cumulative percentage of *Capnodis tenebrionis* (overwintering and emerging) adults. The grey line refers to semiarid climate, and the black line refers to temperate area.

degree-days (DD) (2007) to 930 DD (2005) for the temperate area. In the semiarid climate, *xo* ranged from 1163 DD (2008) to 768 DD (2009) (Table 1). The overall equation for the analysis of data allowed us to obtain a value of 726 DD for 50% of cumulative adults. It should be noted that, for 2008, the logistic equation of the data was not adjusted to the programmed iterations of the software, so the Boltzmann equation was utilized.

For the emerging generation of *C. tenebrionis* whose onset is in midsummer, the values obtained were a minimum of 812 DD (2005) and a maximum of 1199 DD (2006). In the semiarid climate, the values were 1385 (2008) and 722 DD (2009). The overall analysis of data allowed us to obtain the figure of 801 DD for 50% accumulation of adults emerging (Table 1).

The comparison with the linear regression for each year of the observed cumulative percentage (overwintering and emerging adults) versus the predicted values with the overall logistic equation showed a close fit between the model and observed data (Table 1). The comparison of the DDs at 50% of cumulative adults obtained with the nonlinear regression with values from the OLS method has been highlighted in Table 1. In this case, only the overall values of DDs are similar, and, in general, the value for this linear method is lower, with differences reduced between years in the OLS method.

The average time between the appearance of each generation (TBG) and calculated degree-days showed in the temperate area that for the three years (2005–2007), the TBG value was greater (DD = 858 ± 51 SE, $n = 3$), while in the semiarid area, the value remained the lowest (DD = 631 ± 46 SE, $n = 2$).

4. Discussion

This study of *C. tenebrionis* showed the crucial role of temperature in the emergence of adult beetles. The thermal differences between the two different locations affected the development of species and caused the early onset of the new generation in the summer in the semiarid area. In contrast, overwintering adults emerged in spring in both areas, though the timing appeared to be more uniform in the temperate area. Interestingly, initial emergence of *C. tenebrionis* at both sites coincided with the opening of the earliest flowers at each site; however, the increase of adults at each location was slow, and the maximum density occurred when plants were fully vegetative. Thus, the emergence of beetles in spring appears not to be bound by the phenology of the plant, perhaps because its feeding is independent of the flowering plant.

The temperature seems to be responsible for spring adult appearance, and this strong dependence was expected, because the average daily temperatures for the first four months often remain below the threshold calculated (see Figure 2). It is necessary to obtain more years of monitoring dates of appearance to verify whether climatic fluctuations are primarily responsible for the interannual variability in spring appearance phenology. An early onset brought about by increasing temperature is seen in other species of insects, such as *Apis mellifera* (L.) and *Pieris rapae* (L.) [27]. However, other factors may influence the phenology of *C. tenebrionis* and their subsequent appearance in orchards. For these, we can refer to the microhabitats of orchards, which can influence the activity of adults. For example, in some orchards, tillage of the soil is not carried out, leaving a ground layer of grassy vegetation. In this case, the heating process of the basal part of the plant is reduced, which may result in retardation of the emergence of overwintering adults and formation of new adults. The effects of the grass, as discussed by Snyder et al. [28], could explain the delayed appearance of the overwintering adults in the semiarid orchard compared with the temperate orchard. Although during winter in the semiarid area specimens were rarely present at the base of the plants, they would be unable to feed due to the absence of plant resources.

The difference of recorded temperature in the two study areas was nearly 3°C, and this made it possible to identify the effects of temperature on the phenology of the species in the field, but a manipulation of temperature in the laboratory is desirable for further investigation. *Capnodis tenebrionis* can be reared in the laboratory, although certain technical issues make it a difficult species to culture [29].

Table 1: The parameter estimate of a nonlinear model describing *Capnodis tenebrionis* adult phenology. The comparison with the linear regression for each year of the observed cumulative percentage versus the predicted values with the global logistic equation. Degree-day values at 50% of cumulative adults calculated with ordinary least squares regression for *Capnodis tenebrionis* adults (overwintering and emerging adults of the year) for two different Mediterranean areas (S: Sicily; C: Calabria).

Parameter estimates (SE) with logistic equations and regression statistics											
	Overwintering adult						Emerging adult				
	Log. equat. parameter		Log. regression values versus observed cumulative		OLS regression		Log. equat. parameter		Log. regression values versus observed cumulative		OLS regression
2005 (S)	a	167.99 (1.7)	$y = 0.91x + 2.22$	$R^2 = 0.997$		**2005 (S)**	a	109.70 (1.21)	$y = 0.831x + 6.33$	$R^2 = 0.922$	
	b	−1.22 (0.01)		($N = 245$)			b	−24.75 (0.48)		($N = 123$)	
	$x0$	**930.95** (15.22)			**560.73**		$x0$	**832.96** (0.98)			**727.41**
	$y0$	0.49 (0.07)			($r^2 = 0.9829$)		$y0$	0.06 (0.1)			($r^2 = 0.5147$)
	R^2	0.9998					R^2	0.9984			
2006 (S)	a	161.56 (4.04)	$y = 0.93x - 2.49$	$R^2 = 0.991$		**2006 (S)**	a	571.93 (180.13)	$y = 0.942x + 0.31$	$R^2 = 0.978$	
	b	−0.92 (0.02)		($N = 245$)			b	−6.21 (0.23)		($N = 123$)	
	$x0$	**753.58** (41.16)			**517.23**		$x0$	**1198.71** (83.18)			**725.70**
	$y0$	−0.83 (0.27)			($r^2 = 0.9360$)		$y0$	0.11 (0.14)			($r^2 = 0.7166$)
	R^2	0.9982					R^2	0.9970			
2007 (S)	a	117.52 (1.35)	$y = 1.01x - 4.00$	$R^2 = 0.973$		**2007 (S)**	a	108.88 (1.13)	$y = 0.876x + 1.52$	$R^2 = 0.997$	
	b	−1.22 (0.02)		($N = 245$)			b	−13.22 (0.31)		($N = 123$)	
	$x0$	**319.92** (7.12)			**488.05**		$x0$	**812.03** (1.93)			**690.76**
	$y0$	0.511 (0.29)			($r^2 = 0.8845$)		$y0$	0.13 (0.14)			($r^2 = 0.7416$)
	R^2	0.9974					R^2	0.9979			
2008 (C)	a	120.79 (2.67)	$y = 1.007x+13.90$	$R^2 = 0.904$		**2008 (C)**	a	228.14 (23.74)	$y = 1.074x + 2.60$	$R^2 = 0.896$	
	b	402.77 (11.41)		($N = 245$)			b	−3.28 (0.14)		($N = 123$)	
	$x0$	**1163.03**			**923.60**		$x0$	**1385.63** (79.62)			**842.25**
	$y0$	*			($r^2 = 0.9908$)		$y0$	0.044 (0.24)			($r^2 = 0.9213$)
	R^2	0.9847					R^2	0.9945			
2009 (C)	a	123.01 (2.05)	$y = 0.991x + 3.89$	$R^2 = 0.985$		**2009 (C)**	a	114.20 (1.00)	$y = 1.066x - 13.13$	$R^2 = 0.926$	
	b	−1.67 (0.04)		($N = 245$)			b	−3.53 (0.06)		($N = 123$)	
	$x0$	**768.28** (17.47)			**736.34**		$x0$	**721.70** (4.91)			**682.0**
	$y0$	3.33 (0.30)			($r^2 = 0.9582$)		$y0$	0.22 (0.13)			($r^2 = 0.9731$)
	R^2	0.9965					R^2	0.9984			
2005–2009	a	137.42 (6.72)				**2005–2009**	a	93.65 (1.27)			
	b	−1.18 (0.06)					b	−12.94 (0.66)			
	$x0$	**726.74** (63.03)			**636.55**		$x0$	**801.08** (3.49)			**754.64**
	$y0$	0.8499 (0.71)			($r^2 = 0.8608$)		$y0$	1.06 (0.38)			($r^2 = 0.7807$)
	R^2	0.9231					R^2	0.9176			

*Boltzmann equation $Y(x) = a/1 + e^{((-x-xo)/b)}$.

As in other agroecosystems, in the cultivation of stone fruits, the joint action of different factors (variety, agricultural choices, fertilizer, etc.) can influence the development rates and population dynamics of pests. Among other climatic factors that may affect the adaptability of pests, it is possible to consider photoperiod, but in this case, the difference of this factor between the areas was very low. Moreover, factors such as moisture availability, competition, and extreme weather events could affect phenology, potentially modulating the effects of cumulative heat units. Even the effect of heat on development rate might be nonlinear [30, 31] or can vary according to the life stage of the insect [23].

In early July, the new generation of adults causes more adverse effects on vegetation (decrease of photosynthetic activity and disorders) in accordance with the negative action of the beetle on leaves and buds. As these effects are added, the opportunity for adults to reach sexual maturity before winter is reduced (C. P. Bonsignore, unpubl. data). This advantage of early onset, however, may be accompanied by the inability to survive a second winter, as for some individuals in a temperate climate. In fact, emergence of the new generation in late summer could lead to a second overwintering (C. P. Bonsignore, pers. observation). Also, the average time between the appearances of each generation (TBG) showed in the temperate area for the three years yielded a greater value (DD = 858), while the semiarid area yielded the lowest value (DD = 631). This difference showed a shorter interval between the two generations and a greater overlap of generations in the semiarid area. In confirmation of this species' thermophilic preferences, other activities (e.g., egg laying, egg hatching, and feeding activity) require high thermal optimal condition [12, 32], and some of these events also need to be associated with drought conditions, such as low soil humidity being preferable for newly hatched larvae to reach plant roots [14].

The information collected here suggests new possibilities for the pest to expand its range of distribution under drought and warmer conditions. The various reports of the presence of the species, in areas such as the south of France [8], are generally not considered preferential for the presence of *C. tenebrionis*, which suggests that its expansion may be linked to global warming. In these new areas, the simple, single-parameter degree-day models of phenology may not fit well and could have little power to predict phenology under new conditions. Greater understanding of these possible complexities should permit better forecasting of the phenology of species.

The possibility to recognize, in the orchard, the susceptible stages of the pest and their seasonal predictability is crucial for the application of control measures. This may be even more important if the natural antagonist is unable to exert, either individually or together, a satisfactory control of root-borer populations [33–35].

The values in degree-days calculated for each generation in the five years of study show a close correspondence with the values observed annually for the adoption of a defense strategy that takes into account the emergence of adults. Given the length of adult life of *C. tenebrionis*, it is necessary to take the first action against adults of the overwintering generation when the DD reaches 50% of the value calculated with the equation. Generally, half of this value coincides with the first peaks of the presence of adults, and the first treatment would reduce the number of eggs laid in the field. Understanding the life history of *C. tenebrionis* and its population will be necessary for improving its management and further understanding the spread of this beetle, which is heavily influenced by abiotic climatic factors.

Acknowledgments

The authors sincerely thank the growers Franco Fragomeni and Lelio Lunetta. This research was partially funded by the Mediterranean University.

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Hindawi Publishing Corporation
Psyche
Volume 2012, Article ID 746342, 11 pages
doi:10.1155/2012/746342

Research Article

The Influence of Abiotic Factors on an Invasive Pest of Pulse Crops, *Sitona lineatus* (L.) (Coleoptera: Curculionidae), in North America

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Received 15 July 2011; Revised 23 September 2011; Accepted 27 September 2011

Academic Editor: Nikos T. Papadopoulos

Pea leaf weevil, *Sitona lineatus* (L.), native to Europe and North Africa, has been introduced into many other countries around the world, including the USA and Canada. Adults are oligophagous pests on leguminaceous plants. *Sitona lineatus* was first recorded in Canada in 1997, near Lethbridge, Alberta. Since then, it has spread north in Alberta and west into Saskatchewan in 2007. Bioclimatic simulation models were used to predict the distribution and extent of establishment of *S. lineatus* in Canada based on its current geographic range, phenology, relative abundance, and empirical data. The study identified areas in Canada that are at risk for future establishment of *S. lineatus* and developed a better understanding of climate effects. Climate change projections (General Circulation Models) were then imposed on the bioclimatic model of *S. lineatus*. Bioclimatic model output varied for each of the three General Circulation Models. In terms of suitability for pest establishment (Ecoclimatic Index), the NCAR273 CCSM climate data resulted in the most significant shift northward.

1. Introduction

Pea leaf weevil, *Sitona lineatus* (L.), native to Europe and North Africa, has been introduced into many other countries around the world, including North America. Adults are oligophagous pests on leguminaceous plants. *Sitona lineatus* was first recorded in Canada in 1997, near Lethbridge, Alberta. [1–3]. The adults are oligophagous pests on leguminaceous plants but prefer and maximize their reproductive potential on peas and faba beans [4]. The species has one generation per year [5]. Adults overwinter in a variety of locations, particularly sites containing perennial legumes and weeds. In spring, adults leave overwintering sites in search of pea fields. Eggs are laid in the soil, near developing pea plants. Larvae feed on root nodules and develop through five instars. Pupation occurs in the soil. In late summer adults leave pea fields in search of late season pulse crops before overwintering [6]. Adults feed on leaf margins of legume seedlings. Larval feeding on nodules can result in partial or complete inhibition of nitrogen fixation [7].

Sitona lineatus was first collected in Canada in 1997, near Lethbridge, Alberta [4]. Since then, it has spread northward in Alberta and east into Saskatchewan in 2007 [8, 9]. The introduction of *S. lineatus* into this region presents a risk to pea production in Northern Great Plains of Canada and USA [10, 11].

Abiotic factors, primarily climate, constrain population growth and survival that ultimately affect species distribution and abundance [12]. Bioclimatic simulation models have been used successfully to predict the distribution and extent of insect establishment in new environments [13–17]. Bioclimatic modelling software, such as CLIMEX [14], enables the development of models that describe the potential distribution and seasonal abundance of a species based on climate. Inferential models infer a species response to climate, based on its geographic range, phenology, seasonal abundance, and empirical data. CLIMEX models allow researchers to develop an overview of climatic factors that affect species distribution and abundance and permit identification of nonclimatic factors that limit species distribution [14]. Sensitivity analysis can be used to test hypotheses related to the effect of varying climate variables (i.e., warmer/cooler or wetter/dryer than normal conditions) on the species distribution and abundance [14].

The objectives of the study were to develop a bioclimatic model to predict potential range and relative abundance of *S. lineatus*, to identify areas in Canada that are at risk for future establishment of the pea leaf weevil, and to use the model to develop a better understanding of how a changing climate might potentially influence *S. lineatus* populations across North America.

2. Methods

The bioclimatic modeling process has been previously described [15, 18, 19]. CLIMEX models derive Ecoclimatic Index (EI) values that describe the climatic suitability, in terms of insect survival and reproduction, of specific locations. The respective Growth Indices and Stress Indices (with related parameters) are illustrated in Table 1. The EI value integrates annual growth (GI) with annual stress (heat, cold, dry, wet) to produce a single value (between 1 and 100) for each location. Ecoclimatic Index values near zero indicate that the location's climate is not suitable for long-term establishment of the species. An EI value greater than 20 indicates a "Very Favourable" climate.

Initial model parameter values were based on published data that resulted from laboratory and field studies [3, 6, 20–24] and are defined in Table 1. Climatic requirements were inferred from known distributions of pea leaf weevil in Europe. The model for *S. lineatus*, using CLIMEX 3.0 [14], was developed by iteratively adjusting parameter values to produce mapped results that closely approximated observed distribution for *S. lineatus* in Europe [1–3]. Model parameterization was conducted for Britain, Denmark, France, Germany, Switzerland, Norway, and The Netherlands. The remaining European countries were treated as an independent dataset and used for model validation. Once the European distribution was defined, based on a visual comparison of model output with observed distribution, EI values were compared to reported data on relative abundance. Published results related to abundance were used to refine parameter values so that highest EI values occurred where *S. lineatus* was known to cause damage and lower values occurred when the species was less prevalent.

The model was validated by comparing output to reported distributions and seasonal phenology and tested for consistency with empirical data. Three methods were used to validate the model. The model was then applied to predict the population distribution of *S. lineatus* in eastern Europe (Bulgaria, Czech Republic, Hungary, Poland, Romania, Slovakia, Ukraine, and Yugoslavia), Asia, Washington, Oregon, and Idaho. Model output for these regions was compared to known distributions as reported by Schotzko and Quisenberry [25], Fauna Europaea Web Service [1], and Hoebeke and Wheeler Jr. [3]. Second, model output for phenology and life history was compared to published reports for Europe [22, 26]. Third, model results which related to insect phenology were based on weather data and insect population data collected from southern Alberta [27].

The CLIMEX model required five meteorological inputs: temperature (maximum and minimum), precipitation, and relative humidity (09:00 and 15:00 hours). The *Compare Locations* function required monthly long-term average climatic variables. Climate data was used as an input for the Compare Locations function. The dataset represents a splined 0.5° world grid dataset [28]. Models were run for Europe ($n = 6416$ grids) and Canada (south of 65°N latitude, $n = 4472$ grids). The moisture index (MI) is based on a calculated soil moisture value. CLIMEX used a hydrological submodel to compute a weekly soil moisture balance. Soil moisture balance was based on soil moisture from the previous week, current week values for precipitation and evapotranspiration. CLIMEX used a degree-day model, based on the algorithm published by Baskerville and Emin [29], to compute the temperature index (TI) and the potential number of generations per year.

Climate change projections were obtained from the Intergovernmental Panel on Climate Change [30] as monthly means for three General Circulation Models (GCMs), based on current climate, 30-year average (1961–1990) dataset (A1B emission scenario) (CRU: Climate Research Unit, East Anglia, UK). The GCMs used were CSIRO Mark 3.0 (CSIRO, Australia), NCAR273 CCSM (National Centre for Atmospheric Research, USA), and MIROC-H (Centre for Climate Research, Japan). All three had the requisite climatic variables at a temporal resolution appropriate for CLIMEX and were pattern-scaled to develop individual change scenarios relative to the base climatology [31]. The GCMs cover a range of climate sensitivity, defined as the amount of global warming for a doubling of the atmospheric CO_2 concentration compared with 1990 levels [32]. The respective sensitivities are CSIRO Mark 3.0 (2.11°C), NCAR-CCSM (2.47°C), and MIROC-H (4.13°C).

In order to query the resulting database at a regional scale, a geographic rectangle, 4° latitude by 7° longitude, was used to delineate a regional template consisting of 112 grid cells. Specific regions, based on latitude and longitude coordinates, were defined and output (averaged across the region) was generated for detailed analysis. The datasets permitted comparison of variables, both spatially and temporally (weekly intervals). Analyses were based on values centered on six locations including Peace River, Alberta (56.25°N; 117.25°W), Lethbridge, Alberta (49.75°N; 112.75°W), Red Deer, Alberta (52.25°N; 113.75°W), Saskatoon, Saskatchewan (52.25°N; 106.75°W), Regina, Saskatchewan (50.25°N; 104.75°W), and Winnipeg, Manitoba (49.75°N; 97.25°W).

Sensitivity analysis was conducted to quantify the response of *S. lineatus* to changes in precipitation and temperature. Incremental scenarios were developed to reflect the possible range of temperature and precipitation values that could be expected to occur in Europe and Canada, based on current climate. Scenarios were selected, based on potential variation of present climate. EI values, based on current climate, were compared to scenarios that differed by −2, −1, +1, and +2°C from current temperatures (maximum

Table 1: Descriptions of CLIMEX parameters and parameter values used to predict the potential distribution and relative abundance of *Sitona lineatus* in North America.

Index	Parameter	Description	Value
Temperature	DV0	Limiting low temperature	7.0°C
	DV1	Lower optimal temperature	16.0°C
	DV2	Upper optimal temperature	25.0°C
	DV3	Limiting high temperature	32.0°C
Moisture	SM0	Limiting low soil moisture	0.10
	SM1	Lower optimal soil moisture	0.40
	SM2	Upper optimal soil moisture	1.00
	SM3	Limiting high moisture	1.50
Diapause	DPD0	Diapause induction day length	14 h
	DPT0	Diapause induction temperature	11.0°C
	DPT1	Diapause termination temperature	3.0°C
	DPD	Diapause development days	120
	DPSW	Diapause indicator for winter diapause	0
Cold Stress	TTCS	Cold stress threshold	−14.0°C
	THCS	Cold stress temperature rate	−0.00025
Heat Stress	TTHS	Heat stress temperature threshold	34.0°C
	THHS	Heat stress temperature rate	0.002
Dry Stress	SMDS	Dry stress threshold	0.02
	HDS	Dry stress rate	−0.003
Wet Stress	SMWS	Wet stress threshold	2.0
	HWS	Wet stress rate	0.01
Day-degree accumulation above DV0			
	DV0		7.0
	DV3		32.0
Day-degree accumulation above DV3			
	DV3		32.0
	DV4		100
Day-degree accumulation above DVCS			
	DVCS		8.0
	DV4		100
Degree-days per generation			
	PDD	Minimum degree days above DV0 to complete generation	450

and minimum monthly values) and precipitation values (monthly total) that were −40, −20, +20, and +40% of current values. The comparison was conducted for five locations within the major pulse crop production region of western Canada (Table 2). The locations were selected to provide a range of EI values (EI = 22–36).

Contour maps were generated by importing CLIMEX output into ArcView 8.1 [33]. Ecoclimatic Index values were displayed in five categories: “Unfavourable” (0–5), “Suitable” (5–10), “Marginal” (5–10)”Favourable” (15–20), and “Very Favourable” (>20). The “Suitable” and higher categories represent areas that may experience pest outbreaks of *S. lineatus.* Actual densities will be dependent on meteorological conditions that differ from long-term climate normals. The “Favourable” and “Very Favourable” categories describe meteorological conditions, similar to long-term climate normals, in which outbreaks resulting in crop damage may occur.

3. Results and Discussion

3.1. Model Development. In Europe, Hans [23] reported that overwintered *S. lineatus* adults become active when temperatures exceed 4.5°C. Flight was found to occur when temperatures were greater than 12.5°C [6]. In North America, Prescott and Reeher [22] observed that overwintered adults began spring flight in March, when maximum temperatures were 57°F (13.9°C) or greater. In Idaho, USA, Fisher [21] reported that adult flight occurred between April 25 and May 19 and adult flights, out of the host crop, occurred in late July and August.

Table 2: Effect of changes in mean annual precipitation (−40% to +40%) and temperature (−2 to +2) from current values on Ecoclimatic Indices for *Sitona lineatus* at five locations.

			Current	Change in mean precipitation (%)				Change in mean temperature (C)			
Location	Latitude	Longitude	Climate	−40	−20	+20	+40	−2	−1	+1	+2
Lethbridge, Alberta	49.69°	−112.83°	11	3	7	16	19	10	11	11	10
Red Deer, Alberta	52.27°	−113.80°	21	10	17	22	22	14	18	24	26
Regina, Saskatchewan	50.44°	−104.61°	11	3	7	15	19	10	11	10	9
Saskatoon, Saskatchewan	52.15°	−106.65°	10	2	6	14	19	10	9	9	8
Winnipeg, Manitoba	49.89°	−97.15°	20	8	14	22	22	18	20	20	18

In Europe, oviposition was found to occur when the daily mean temperature is 12°C and the daily temperature must rise above 13°C for some hours [34]. In Idaho, USA, oviposition occurred during May [21]. Prescott and Reeher [22] reported that in the Pacific Coastal region of North America oviposition can occur between February and May. Lerin [26] reported that it took 70 days for eggs to hatch at 8°C and 6.2 days at 29°C. Development was linear up to 25°C and only one day difference between 25 and 30.5°C. Egg mortality was negligible at 30°C, 26% at 32°C, and 100% at 33°C. In England, larvae were collected on May 21 and in Scotland larvae were collected as late as July 24 [24]. In Idaho, USA, pupae required 14–18 days to complete development and pupae occurred from early July to early August [21]. In England, late summer flights began soon after adults emerged from pupal cells during late July, with flights continuing until mid-October [6].

The model was developed to produce output that fitted with reported results, based on phenology and distribution for Britain, Denmark, France, Germany, Switzerland, Norway, and The Netherlands. Limiting lower temperature (DV0) values between 4 and 12°C were iteratively tested and a value of 7°C provided the best fit with distributions and phenologies in Europe. Similarly, values for optimal and limiting high temperatures (DV1, DV2, DV3) were incrementally adjusted in order to develop a model that matched reported distributions and phenologies for Europe (Table 1).

Soil moisture indices (SM0, SM1, SM2, SM3) reflected the assumption that soil moisture is a significant factor that is related to plant moisture content and microclimatic conditions [14]. The moisture index was based on computed weekly soil moisture levels. This species, particularly larval stages, appears to prefer moist conditions. High temperatures and dry soil resulted in mortality rates of eggs and larvae reaching 85% [21]. Andersen [34] reported that survival of first instar larvae was 5.5 days at 100% RH and 9°C but dropped to 1.5 days at 100% RH and 26°C. When relative humidity dropped below 90% (15°C), all larvae died within 5 hours. Limiting low soil moisture (SM0) was set at 0.1. The lower optimal moisture was increased to 0.4 from 0.3 and the upper optimal moisture level (SM2) was set at 1.0 and SM3 was set at 1.5 to permit saturation that may occur in irrigated fields (Table 1).

CLIMEX uses both photoperiod and temperature as inputs for determination of induction and temperature for termination of diapause. Simulations indicated that an induction day length of 14 hours provided the best fit to results reported for Britain, Denmark, Germany, and Idaho (USA) [21, 23, 24]. Final diapause values for induction day length (DPDO), diapause induction temperature (DPTO), diapause termination temperature (DPT1), and required days for diapause development (DPD) were set at 14, 11, 3, and 120, respectively. The known distribution of *S. lineatus* seemed to indicate a greater diversity of diapause behaviour than could be accounted for with the model parameters. As a result, the parameters were adjusted to reflect the weevil's patterns in its core distribution (i.e., north of 45° latitude in Europe) (Table 1).

Stress values, related to the ability of the species to survive adverse conditions, were set to limit geographical distributions. Cold stress limits were assigned at a level to reflect the occurrence of *S. lineatus* in northern countries such as Denmark, Finland, and Sweden. Selected values were similar to values for the pollen beetle, *Meligethes viridescens* (Fabricius) [19]. *Sitona lineatus* occurs across southern Europe, central Asia, and Africa. The rate of heat stress accumulation (THHS) was set in order to permit distribution across these regions.

3.2. Model Validation. Lower limiting temperature (DV0) values between 4 and 12°C were iteratively tested and a value of 7°C provided the best fit with distribution and growing season phenology in Europe. Similarly values for DV1, DV2, and DV3 were incrementally adjusted in order to develop a model that matched reported distributions and phenologies for Europe.

Predicted distribution of *S. lineatus* in Europe (Figure 1) agreed with the extensive distribution data reported from Fauna Europaea Web Service [1], Botha et al. [2], and Hoebeke and Wheeler Jr. [3]. The model did not predict that *S. lineatus* would occur in Egypt or Saudi Arabia. Output suggested that soil moistures were too dry and that diapause would not occur, resulting in EI = 0. Application of irrigation scenarios indicated that soil moisture values could be raised to suitable values. Diapause (based on day length) still proved to be limiting. The model predicted that some locations with climates where *S. lineatus* does not currently occur are suitable for establishment of this species. For example, the model predicted that climates in Australia, New Zealand, China, Ethiopia, Kenya, and Tanzania could support *S. lineatus* populations.

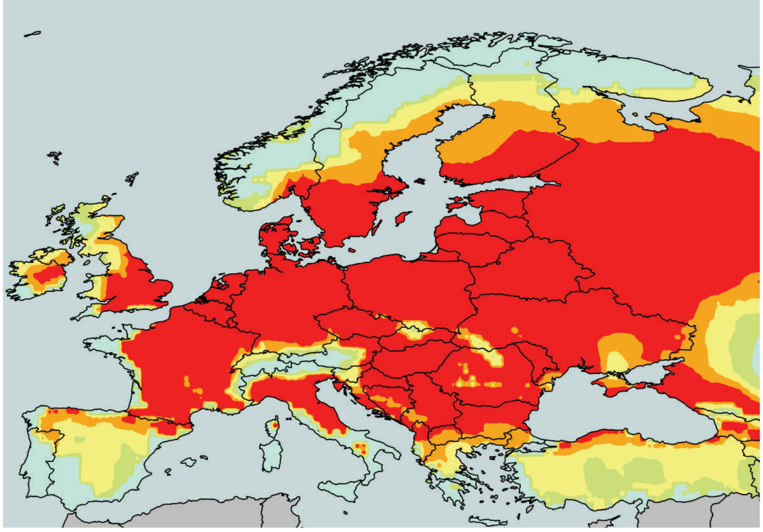


Figure 1: Potential distribution and relative abundance of *Sitona lineatus* in Europe as predicted by CLIMEX. Light blue: "Unfavourable" (EI = 0–5); Green: "Marginal" (EI = 5–10); Yellow: "Suitable" (EI = 10–15); Tan: "Favourable" (EI = 15–20); Red: "Very Favourable" (EI > 20).

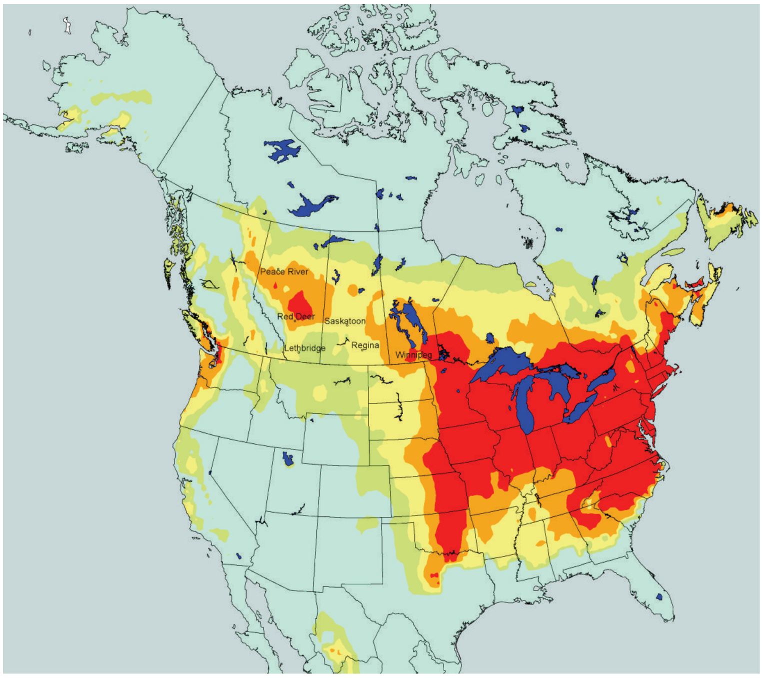


Figure 2: Potential distribution and relative abundance of *Sitona lineatus* in North America as predicted by CLIMEX under current climate conditions. Dark blue: lakes; Light blue: "Unfavourable" (EI = 0–5); Green: "Marginal" (EI = 5–10); Yellow: "Suitable" (EI = 10–15); Tan: "Favourable" (EI = 15–20); Red: "Very Favourable" (EI > 20).

In North America, predicted distributions (Figure 2) in the province of British Columbia, Canada, and the States of Washington, Oregon, Idaho, California, and Virginia in the USA agree with reported distributions [3]. Model output also predicted that *S. lineatus* could become established in the Prairie Ecozone of western Canada and agreed with population surveys in Alberta and Saskatchewan that have been conducted since 2001 [27]. Further, the model indicated that EI values would be greater in regions north of the current geographic range of *S. lineatus*. Moisture Index (MI) values were shown to be less than optimal, indicating that precipitation in southern Alberta was less than optimal. Rainfall, between late June and August, was minimal, relative to the species requirements. Ecoclimatic Index values near Red Deer were higher. The increased EI values were associated with higher MI values. Rainfall amounts for the period of June to August were greater than those that were reported for Lethbridge. Dry moisture conditions could have a negative impact on both larval and pupal survival [4].

Model predictions for phenology agreed with published reports. Early season activity of *S. lineatus* is of particular interest. At Rothamsted, England, adults were first collected from late March until mid-April [6]. Our model predicted that first flights would occur in early April. In Kent, England adults were observed in peas in late March [24] and these dates were similar to the model prediction of March 22. Jackson [24] also stated that adult appearance was delayed by two weeks (April 8) during a cool spring. The model was run with a scenario in which the temperature was reduced by 1°C and adults were predicted to first become active on April 12. In Denmark, the model predicted that adults would become active in mid-April. This result was in agreement with data presented by Nielson and Jensen [20]. In Canada, adults first appeared in pea fields in June of 2007, and peak larval counts occurred on June 8 at Lethbridge, Alberta. [8]. It is likely that adults were active before this time. The weekly growth index suggested that *S. lineatus* would be highest in early to mid-June.

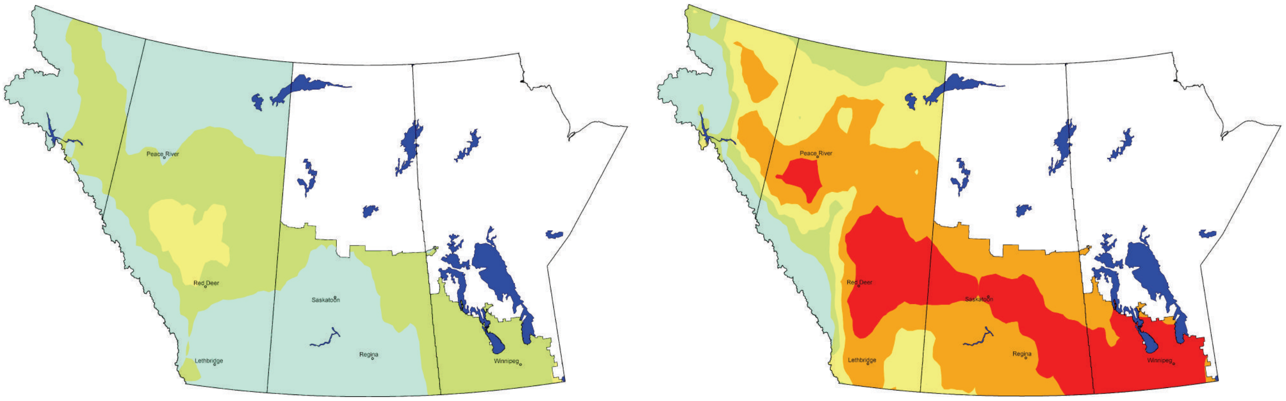
The model predicted that the potential range of *S. lineatus* could extend well beyond current distributions along western and eastern seaboards in North America. Areas in southern Ontario, Quebec, and eastern USA were also predicted to be at risk. Current areas of Canadian pulse production include Quebec and Ontario (a wide selection of coloured beans and the white navy bean), Manitoba (white and coloured beans, pea, and lentil), Saskatchewan (pea, lentil, and chickpea and some bean), and Alberta (beans, pea, lentil, and chickpea) [35].

3.3. Sensitivity Analysis. Sensitivity analyses were conducted to measure EI response to changes in temperature and precipitation. Model output indicated that *S. lineatus* was more sensitive to changes in precipitation (Figure 3) than temperature, indicating that the five locations (climate) were dryer than optimal moistures and temperatures within the Prairie Ecosystem were generally suitable for this species. The model also indicated that sensitivity was location specific. Varying temperatures from −2 to +2°C from current long-term normals revealed that the Lethbridge, Regina, Saskatoon, and Winnipeg locations were not sensitive to temperature changes (Table 2). That is, EI values showed marginal changes. Temperatures at these locations are between lower and upper optimal temperature parameters (DV1 and DV2). Ecoclimatic Index values at Red Deer did show a linear effect with increasing temperatures, increasing from EI = 14 to EI = 26 with incremental temperature increases. The results suggest that *S. lineatus* populations may increase, in areas north of Calgary, in warmer growing seasons. The *S. lineatus* model also demonstrated a linear response in EI values to increased precipitation amounts (Table 3). The model predicted that EI values near Saskatoon would increase from EI = 2 (40% less than long-term normal climate data) to EI = 19 with wetter than average weather (+ 40%).

Sensitivity analysis was also conducted to compare spatial response of EI values to variations in temperature and precipitation. For current climate, EI values were relatively low. Categories were set for EI = 10 (low), 15, and 20. This analysis was conducted for all five locations within the Prairie Ecosystem ($n = 3420$ grid cells) and also specifically for areas in central and southern Alberta ($n = 456$ grid cells). Responses were similar across both scales and agreed with location specific trends (Tables 3 and 4). Ecoclimatic Index values increased from temperatures that were 2°C below long-term normals back up to long-term normal levels. Temperatures warmer than long-term normals appeared to have little effect on EI values. Results suggest that moist conditions would be conducive to large populations (i.e., compared to cool or dry conditions). Under climate conditions that were 40% wetter than long-term normals, the model predicted that 47% (Prairie Ecosystem) and 39% (Alberta) of the spatial area could expect to have EI = 20 or greater (Tables 3 and 4; Figure 3). Across southern Saskatchewan and Alberta, the model predicted that EI values would be reduced for dryer than normal conditions (Figure 3(a)).

Compared to climate data (long-term normals), sensitivity analysis results suggest that *S. lineatus* should respond less favourably in dry seasons and more favourably in wetter seasons. This conclusion may be based on conditions that occurred in the previous summer. That is, late May to July rainfall may be an important factor that determines mid-summer survival and potential number of adults available for the following season. For example, the number of notches per plant (>27) from locations near Lethbridge was greatest in 2006 [8]. Though the 2006 growing season (April–August) was dry, April and May were wetter than normal [36]. Also, the 2005 growing season was much wetter than normal. The model would predict that these conditions would be conducive for population increase. Across most of Alberta, numbers declined dramatically between 2007 and 2008 [37, 38]. This may have been due to exceptionally dry periods during June, July, and August in 2007. In 2008, April and early May were exceptionally dry near Lethbridge [36]. Dry conditions may have reduced larval and pupal survival. Though *S. lineatus* was first collected in fields around Lethbridge in 1997, only sporadic damage was reported in the early 2000s. The region experienced a severe drought between 2001 and 2003 [36]. Increasing outbreak levels and geographic expansion throughout southern Alberta were experienced in 2006 and 2007 (reported in Saskatchewan as well) when several thousands of hectares of field peas were sprayed [8]. Low densities and associated sporadic damage may have been associated with the hot dry conditions and increased damage/range expansion may be explained by increased moisture levels experienced between 2004 and 2008.

3.4. General Circulation Model Analyses. Bioclimatic model output varied for each of the three GCMs (Figures 4, 5 and 6). In terms of EI values, the NCAR273 CCSM climate data resulted in the most significant increase in northern regions. Application of this GCM predicted that *S. lineatus* would



(a)

(b)

FIGURE 3: Predicted Ecoclimatic Index (EI) values with precipitation 40% less (a) and 40% greater (b) than current climate. Dark blue: lakes; Light blue: "Unfavourable" (EI = 0–5); Green: "Marginal" (EI = 5–10); Yellow: "Suitable" (EI = 10–15); Tan: "Favourable" (EI = 15–20); Red: "Very Favourable" (EI > 20).

TABLE 3: Effect of changes in temperature and precipitation from current climate on Ecoclimatic Index (EI) values for *Sitona lineatus* across all locations within the Prairie Ecosystem ($n = 3420$ grid cells). The values are expressed as a percentage of total geographic area.

Variable	Scenario	EI ≥ 10	EI ≥ 15	EI ≥ 20
	Current climate	**85.7%**	**51.1%**	**13.5%**
Temperature	−2°C	79.9%	20.5%	0.1%
Temperature	−1°C	86.3%	37.9%	3.9%
Temperature	+1°C	82.3%	54.7%	17.0%
Temperature	+2°C	78.8%	51.2%	15.8%
Precipitation	−40%	2.8%	0.0%	0.0%
Precipitation	−20%	52.3%	10.4%	0.2%
Precipitation	+20%	98.4%	81.5%	32.4%
Precipitation	+40%	99.8%	93.7%	47.4%

TABLE 4: Effect of changes in temperature and precipitation from current climate on Ecoclimatic Indices (EIs) for *Sitona lineatus* in southern and central Alberta ($n = 456$ grid cells). Values are % of total area. The values are expressed as a percentage of total geographic area in this region.

Variable	Scenario	EI ≥ 10	EI ≥ 15	EI ≥ 20
	Current climate	**56.6%**	**15.1%**	**2.2%**
Temperature	−2°C	49.1%	2.6%	0.0%
Temperature	−1°C	57.0%	9.0%	0.0%
Temperature	+1°C	53.1%	17.5%	2.6%
Temperature	+2°C	48.2%	15.1%	3.3%
Precipitation	−40%	0.9%	0.0%	0.0%
Precipitation	−20%	15.6%	1.8%	0.0%
Precipitation	+20%	92.8%	51.3%	11.4%
Precipitation	+40%	99.6%	82.0%	39.0%

be very abundant north of 53°N. Similar, though slightly lower, EI values were predicted for the CSIRO MARK 3.0 and MIROC-H GCM climates. The three GCMs also resulted in varying output across the Prairie Ecosystem. NCAR273 climate data resulted in suitable to very favourable EI values while the CSIRO MARK 3.0 data resulted in some areas being categorized as marginal to suitable. The model predicted that south eastern Alberta and a large area of southern Saskatchewan would be marginal when the MIROC-H GCM was applied. Results of this study suggest that species responses are specific not only to GCM but also to specific regions across North America. Olfert et al. [39] assessed the impact of GCMs on *Melanoplus sanguinipes* (Fabricius) distribution and abundance. Their study was based on

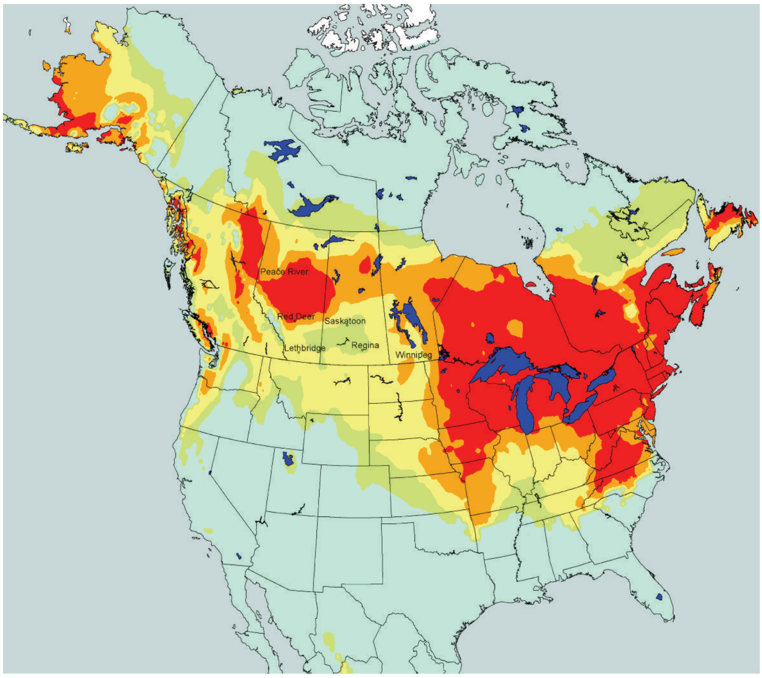


FIGURE 4: Potential distribution and relative abundance of *Sitona lineatus* in North America for 2080 as predicted by CLIMEX and the CSIRO Mark 3.0 climate change projection. Dark blue: lakes; Light blue: "Unfavourable" (EI = 0–5); Green: "Marginal" (EI = 5–10); Yellow: "Suitable" (EI = 10–15); Tan: "Favourable" (EI = 15–20); Red: "Very Favourable" (EI > 20).

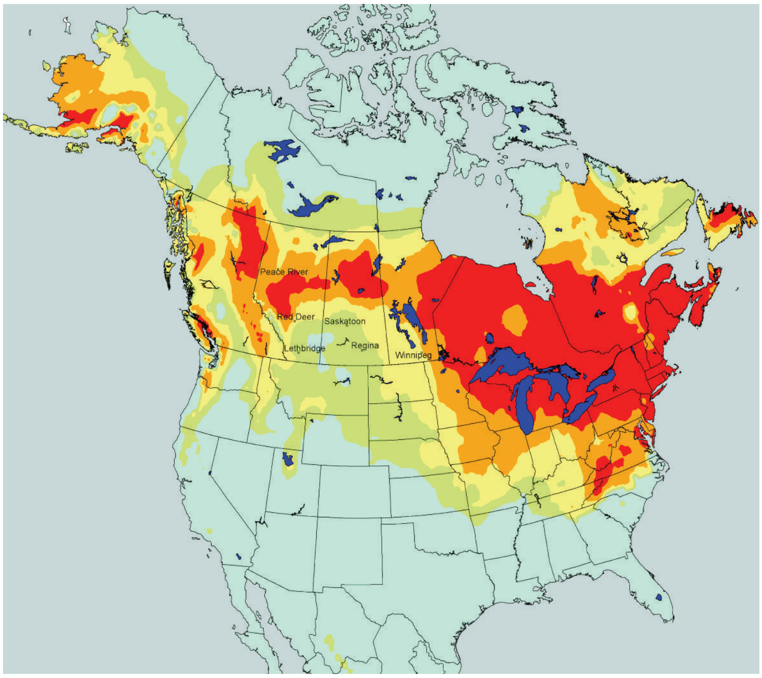


FIGURE 5: Potential distribution and relative abundance of *Sitona lineatus* in North America for 2080 as predicted by CLIMEX and the MIROC-H climate change projection. Dark blue: lakes; Light blue = "Unfavourable" (EI = 0–5); Green: "Marginal" (EI = 5–10); Yellow: "Suitable" (EI = 10–15); Tan: "Favourable" (EI = 15–20); Red: "Very Favourable" (EI > 20).

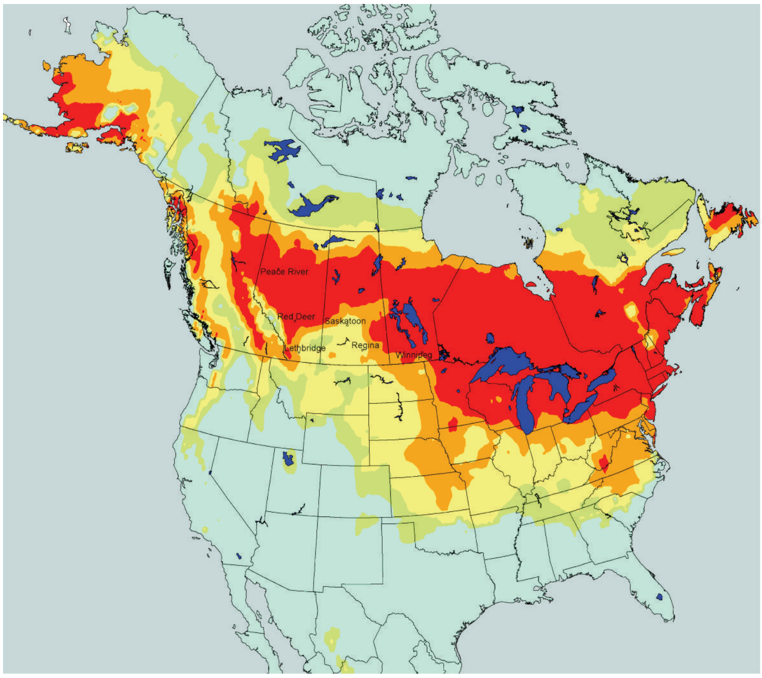


Figure 6: Potential distribution and relative abundance of *Sitona lineatus* in North America for 2080 as predicted by CLIMEX and the NCAR273 CCSM climate change projection. Dark blue: lakes; Light blue: "Unfavourable" (EI = 0–5); Green: "Marginal" (EI = 5–10); Yellow: "Suitable" (EI = 10–15); Tan: "Favourable" (EI = 15–20); Red: "Very Favourable" (EI > 20).

Table 5: Baseline (Current climate: CRU) and General Circulation Model scenarios (CSIRO MARK 3.0, MIROC-H, NCAR273 CCSM) and resulting changes to mean Ecoclimatic Index (EI) values for *Sitona lineatus* at six defined regions (geographic rectangle, 4° latitude by 7° longitude) in western Canada.

Location	Latitude	Longitude	Current climate (CRU)	CSIRO Mark 3.0	MIROC-H	NCAR273 CCSM
Lethbridge Alberta	49.75°	−112.75°	9	13	6	13
Peace River Alberta	56.25°	−117.25°	13	14	13	21
Red Deer Alberta	52.25°	−113.75°	20	21	13	28
Regina Saskatchewan	50.25°	−104.75°	10	8	6	12
Saskatoon Saskatchewan	52.25°	−106.75°	11	8	6	11
Winnipeg Manitoba	49.75°	−97.25°	20	14	14	22

the three GCMs that were used in the current study and they found that response of *M. sanguinipes* not only varied by GCM but also was region specific. Mika et al. [13] reported that effect of climate change differed strongly between GCMs and that EI differences for *Contarinia nasturtii* were greatest for regions that were categorized as "very favourable" (EI = 30).

The relational database was queried to analyze the impact of climate change for six locations in western Canada (Table 5). Model output based on NCAR273 CCSM resulted in EI increases at each of the locations with the greatest increases at Red Deer and Peace River. The CSIRO MARK 3.0 resulted in EI increases for Lethbridge, Red Deer, and Peace River and decreased EI values for the remaining three locations. Model output based on MIROC-H climate data resulted in reduced EI values for five of the six locations. Peace River was predicted to have an EI value that was the same as for current climate.

Table 6: Effect of changes in precipitation (expressed as a percentage of total geographic area) from current values on Ecoclimatic Indices for *Sitona lineatus* across North America for CRU (current climate) and general circulation model (CSIRO MARK 3.0, MIROC-H, NCAR273 CCSM) scenarios.

Scenario	EI ≥ 10	EI ≥ 15	EI ≥ 20
Current climate (CRU)	25.2%	17.1%	9.8%
CSIRO Mark 3.0	37.5%	25.5%	15.2%
MIROC-H	34.6%	22.9%	13.1%
NCAR273 CCSM	37.4%	26.2%	17.3%

Analysis was conducted to compare changes in EI values, as a result of climate change, across North America (Table 6). Compared to current climate, model output indicates that the area of the continent that will have EI values greater than 10 will increase by 37–48%. Model runs showed that areas with EI >20 could increase by 33% (MIROC-H), 54% (CSIRO MARK 3.0), and 76% (NCAR273 CCSM). These results were similar to values reported by Olfert and Weiss [40] who indicated that a + 3°C increase in temperature would result in 19.7% to 47.1% increase in areas with EI >20 for *Ceutorhynchus obstrictus* (Marsham), *Oulema melanopus* L., and *Meligethes viridescens* (Fabricius).

4. Conclusions

Some cautions have been expressed regarding the utilization of bioclimatic models for investigating the potential impact of climate on insect populations. For example, adaptation is likely to occur with the result that biotic interactions may not remain the same over time, and genetic and phenotypic composition of populations may change [41]. In addition, most insect species have some limitation to dispersal [42]. In the instance of *S. lineatus*, the impact of biotic factors such as natural enemies (e.g., diseases, parasites, predators) and host plant resistance and other abiotic factors, such as intercropping and chemical insecticides, must also be considered [4]. So even though model results suggest conditions in some regions to be conducive to *S. lineatus* populations under climate change, these additional biotic and abiotic factors could result in population decline. In these instances, bioclimate and GCMs may not account for changes in population and may overestimate populations.

To address these naturally occurring phenomena, bioclimatic modeling of *S. lineatus* populations would benefit from multitrophic studies (host plants—*S. lineatus*—natural enemies). For example, Cárcamo et al. [9] suggested that when adults lay eggs on plants past the 5th node stage, larval recruitment was lower compared to oviposition at the 2nd node stage. As a result, cooler growing conditions in the spring may delay *S. lineatus* invasions into fields until the crops are more advanced. Warmer temperatures may improve the synchrony between insect and plant.

Sitona lineatus is expected to continue to expand its range; as a result Vankosky et al. [4] suggested that an integrated approach of intercropping, host plant resistance, predators, parasitoids, pathogens, and chemical insecticides would be required to successfully manage this recently introduced pest species. In an effort to provide advance warnings of continued range expansion a region wide monitoring program has been initiated across western Canada [43].

Acknowledgments

The authors would like to acknowledge C. Herle and S. Barkley for their technical support and D. Giffen for preparation of the maps.

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Hindawi Publishing Corporation
Psyche
Volume 2012, Article ID 123405, 13 pages
doi:10.1155/2012/123405

Review Article

Temperature-Driven Models for Insect Development and Vital Thermal Requirements

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Received 15 July 2011; Revised 9 September 2011; Accepted 11 September 2011

Academic Editor: Nikos T. Papadopoulos

Since 1730 when Reaumut introduced the concept of heat units, many methods of calculating thermal physiological time heat have been used to simulate the phenology of poikilothermic organisms in biological and agricultural sciences. Most of these models are grounded on the concept of the "*law of total effective temperatures*", which abstracts the temperature responses of a particular species, in which a specific amount of thermal units should be accumulated above a temperature threshold, to complete a certain developmental event. However, the above temperature summation rule is valid within the species-specific temperature range of development and therefore several empirical linear and nonlinear regression models, including the derivation of the biophysical models as well, have been proposed to define these critical temperatures for development. Additionally, several statistical measures based on ordinary least squares instead of likelihoods, have been also proposed for parameter estimation and model comparison. Given the importance of predicting distribution of insects, for insect ecology and pest management, this article reviews representative temperature-driven models, heat accumulation systems and statistical model evaluation criteria, in an attempt to describe continuous and progressive improvement of the physiological time concept in current entomological science and to infer the ecological consequences for insect spatiotemporal arrangements.

1. Introduction

Climate has a profound effect on the distribution and abundance of invertebrates such as insects, and the mathematical description of the climatic influence on insect development has been of considerable interest among entomologists. Additionally, as temperature exerts great influence among the climate variables, by directly affecting insect phenology and distribution, most of the models that describe insect development are temperature driven [1–5].

This first effort for a formal description of the relation between temperature and developmental rate was taken by botanists, to model the effect of temperature on plant growth and development [6–10]. However, similar modeling procedures extended to most of the poikilothermic organisms, including insects as well [1–3]. To date, the earliest experiment that related the velocity of insect development and heat, was made by Bonnet (1779) [11] on the study of the reproduction rate of *Aphis evonymi*, F. [12], while the major assumption and principles that have been brought out by these earlier works, constituted the basis for all future research. Nevertheless, since then, several theoretical and experimental works have been carried out and current progress in entomology, mathematics and computation offers new means in describing the relation of temperature to insect development [13–20].

Thus, although simple predictive models have been developed during the last century, the development and broader availability of personal computers in the 70s and 80s resulted in the rapid development of computer-based models to predict responses of insects in relation to climate [21, 22].

Insects are adapted to particular temperature ranges and temperature is often the most detrimental environmental factor influencing their populations and distribution. In general, within optimum ranges of development and as environmental temperature decreases, their rates of development slow and cease at the lowest (base) temperature, while as temperature rises, developmental rates increase up to an optimum temperature, above which they again decrease and eventually cease at their temperature maximum [4, 5, 15, 23, 24].

It is proposed that this effect of temperature on poikilothermic organism functioning is related to the effect on enzymatic activities. For instance, the conformation of enzymes is the essential step in the enzymatic reaction and this conformation depends on temperature [22, 25, 26].

One common approach to model temperature effects on insect development is to convert the duration of development to their reciprocals. This simple transformation is used to reveal the relationship type, as it will be shown later close to linear, between temperature and rate of development and permits the determination of two vital parameters of development namely, the thermal constant (K) and the base or lower temperature of development ($T_{\min}$). The thermal constant is expressed as the number of degree-days (in °C) and provides an alternative measure of the physiological time required for the completion of a process or a particular developmental event [4, 5, 21, 27].

Attempts to quantify the influence of temperature on insect development rates, growth, and fecundity have been carried out by several studies for species of economic significance [16, 27–32]. Entomologists have strong interest on this kind of relationships, since they are prerequisite to predicting timing and phenology of insect life cycle events and to initiating management actions [33–35], while application of temperature driven models are also essential in epidemiology modeling, development of effective vector control programmes [36] and prediction of biological invasions [37, 38]. From an agronomical standpoint, empirical models are often used to predict specific population events and provide means for precisely applied control methods, reducing costs as well as insecticide use [39, 40]. Furthermore, the determination of insect-specific vital thermal requirements provides evidence to infer on observed geographical distributions and predict future dynamics [8, 41].

The current review highlights the importance of the relationship between insect development and its vital thermal requirements and outlines important constraint and challenges regarded to model selection and applicability in pest management and insect ecology. Within our aims, building on preview reviews, was to provide a simple account for applied entomologists and field ecologists by avoiding complex and technical details. Furthermore, efforts are also made to present a short example of the linear model and to propose a simple three parameter non-linear equation for modeling temperature effects on insect developmental rates.

The rest of this article is structured as follows. The first section describes and explains the concept of the *law of total effective temperatures* and how it is related to the linear models of insect development. A paradigm of the *x-intercept* method is presented in defining lower developmental threshold for *Grapholitha molesta* (Lepidoptera: Gelechiidae). This threshold is vital in applying phenology models in field, and to our knowledge estimated for first time in a laboratory trial. The next section summarises the most common non-linear regression models, including the derivation of the biophysical ones, which have been proposed by researchers in order to estimate cardinal temperatures of insect development. Additionally, among the given functions, a new 3-parameter equation is proposed and its general shape is also presented. Section 3 lists principal statistics that are used for parameter estimation in regression analysis and criteria for model selection among candidate equations. Section 4 briefly outlines the major heat accumulation systems for estimating species-specific heat energy in field during the growth season. Finally, there is extensive discussion regarding constraints and challenges of the models for pest management while efforts have been made to discuss how the estimated insects vital thermal requirement are related to the species environmental adaptation and field distribution.

2. Mathematical Models and Insect Development

Mathematical models represent a language for formalizing the knowledge on live systems obtained after experimental observation and hypothesis testing. An empirical model, if successful, determines result and cause and can be further used to describe the behavior of the system under different conditions [39, 40, 42].

Since temperature is considered as the most critical factor affecting insect development, numerous efforts have been made by researchers to propose models to describe such relations either in laboratory or field [6, 16, 22, 28, 29, 39, 40, 43–45]. Moreover, several of these models have been constructed in the view to be applicable for pest management [1, 21, 23, 27, 39, 42, 43, 46–48].

The term model emphasises some qualitative and quantitative characteristics of the process, which are actually abstracted, idealized, and described mathematically rather than the system itself.

Most of these approaches are based on the empirical detection of relationships and the construction of relative models that in brief capture all information about the response variable in relation to temperature. It should be noted that the presented temperature relationships can be judged as deterministic or empirical, by the sense that they consist of descriptions in which processes are not known, but where relations are established. However, all regression procedures that are followed, for parameter estimation, are purely probabilistic.

In applied entomology, empirical approaches are often used in the construction of developmental models. In general, the procedures include the delimitation of all the factors that affect development to the most limiting one, which is further chosen (i.e., temperature), in order to reveal empirical dependence of the developmental variable upon the limiting factor. A function which describes the data with higher accuracy is plugged to this relation, and its prediction power is further evaluated by using new datasets.

2.1. The Law of Total Effective Temperatures and the Linear Model.

2.1. The Law of Total Effective Temperatures and the Linear Model. All poikilothermic organisms are related to a species-specific thermal constant that corresponds to time units that must be accumulated to complete a particular developmental event. The above principle forms the basis for all modeling approaches that have been developed since the first introduction of the heat units concept by Reaumut on 1730 and the following initiation of the temperature summation rule [20, 49]. This rule, which was first proposed by Candolle [6] and characterized the development of all poikilothermic species, is referred to as the *law of total effective temperatures* and consists of the first effort in modeling temperature-dependent developmental rates instead of developmental times [7, 31, 50].

The model is characterized by universality, since development of all species is addressed by a thermal constant which corresponds to the accumulated degree-days that are needed to complete a particular developmental stage. This principle is further related to most other cumulative degree-day approaches.

According to the *law of total effective temperatures*, it is possible to estimate the emergence and number of generations for a given duration, of the organism of interest, according to the following fundamental equation:

$$K = D(T - T_0), \tag{1}$$

where K is the species (or stage-specific) thermal constant of the poikilothermic organism, T temperature, and T_0 developmental zero temperature. This thermal constant provides a measure of the physiological time required for the completion of a developmental process and is measured in degree-days (DD).

One popular method of estimating the above parameters is to use a linearizing transformation of the above function by calculating the rate of development $y = 1/D$ for the day variable resulting to the following equation [44]:

$$\frac{1}{D} = -\frac{T_0}{K} + \frac{1}{K}T. \tag{2}$$

Equation (2) is often referred to as the linear degree-day model or as the *x-intercept* method [24, 51], which is simply derived after growth rate fitting to a simple linear equation and then extrapolated to zero:

$$y = a + bT. \tag{3}$$

The lower theoretical temperature threshold (i.e., base temperature) is derived from the linear function as $T_b = -a/b$ whereas 1/slope is again the average duration in degree days or thermal constant K.

Equation (3) simply means that the thermal constant is a product of time and the degrees of temperature above the threshold temperature.

2.2. Lower Developmental Threshold for Grapholitha Molesta (Lepidoptera: Gelechiidae). Figure 1, for instance, describes a typical temperature effect on the developmental time of the pupae of *G. molesta* as well as the respective linear relationship between temperature and developmental rate according to (3). To reveal the above relations, larvae were reared in the laboratory at the Aristotle University of Thessaloniki and respective pupae were incubated at different constant temperatures at constant laboratory conditions (15, 20, 25, and 30°C, and 65 ± 5% R.H., 16:8 h L : D).

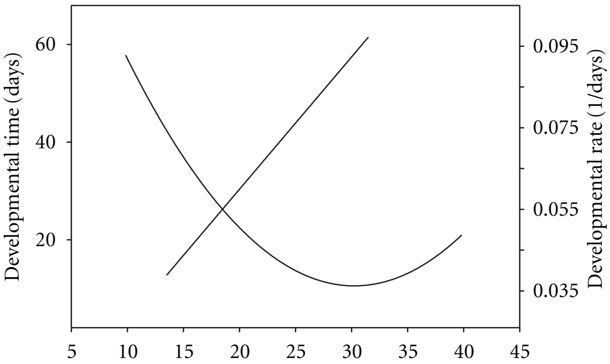


Figure 1: Typical response and temperature effect on the developmental time ($y = 115.5 - 6.9x + 0.1134x^2$) of an insect (i.e., pupal stage of *G. molesta*) and respective linear relationship between temperature and developmental rate according to the linear model ($y = 0.041x - 0.0412$, $T_{\min} = 10°\text{C}$).

The need for inverse regression, as also displayed in the above paradigm, arises most often when the observed variable (developmental time) is the result of the major factorial cause variable (temperature) which is not subjected to error. Thus, in order to measure the predicted variable with negligible error and avoid bias, such kind of "physical problems" should be treated as inverse even if causality is not known or not considered [21, 27, 39, 52, 53].

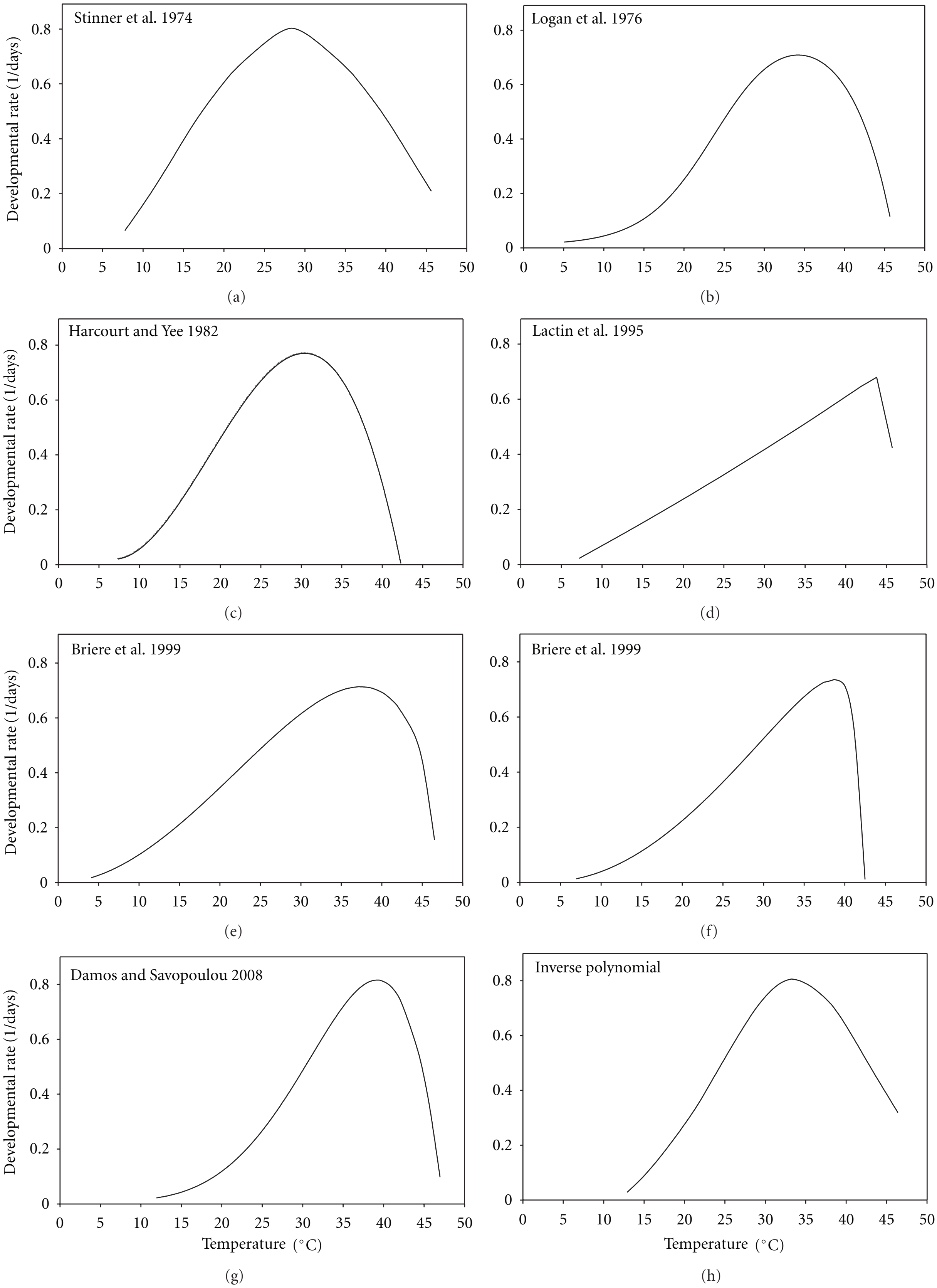
However, if the dependent variable is measured with negligible error (relative to error in the measurement of the factorial variable), or is much smaller than that of the response variable, the direct prediction will involve bias, unless the two variables are perfectly correlated [53]. Therefore, regressions in which both variables are subjected to error have been also proposed [12] and are applied to insect temperature-dependent development to improve prediction precision [21, 27]:

$$DT = K + T_b D, \tag{4}$$

where D is development time (days) and T is temperature.

One of the major advantages of this equation, as in the case of the *x-intercept* method, is simplicity and the existence of biological interpretation over the estimated parameters: thermal constant and lower temperature threshold. Its added value, however, is increased precision in parameter estimation and the detection of outliers that reside on the non linear response curve and should be eliminated by the regression [44].

2.3. Nonlinear Regression Models. Although in practice the linear models are quite adequate over a range of favourable temperatures, they proved unsecure in predicting development in extreme conditions and temperatures in which the relationship becomes non linear [21, 27, 48, 55, 57]. Hence, ideally one should know the response of the organism



(a) (b) (c) (d) (e) (f) (g) (h)

Figure 2: Typical relationships between temperature and insect developmental rates according to several representative non-linear models.

Table 1: Some representative regression models that have been created for the description of temperature-dependent development of insects and related arthropods.

Non-linear model	Equation	Description	Reference
$1/D = c/(1+e^{(a+b\cdot T)}), \quad \text{if } T \leq T_{\text{opt}}$ $1/D = c/(1+e^{[(a+b\cdot(2\cdot T_{\text{opt}}-T)]}), \quad \text{if } T > T_{\text{opt}}$	(1)	"Stinner" (non-linear)	Stinner et al. 1974 [54]
$1/D = \psi \cdot [1/(1+k\cdot e^{-\rho\cdot T})\cdot e^{-((T_{\max}-T)/\Delta)}]$	(2)	"Logan 10"	Logan et al. 1976 [55]
$1/D = a\cdot T^3 + b\cdot T^2 + c\cdot T + d$	(3)	"3rd-order polynomial" (non-linear)	Harcourt and Yee 1982 [56]
$1/D = e^{\rho\cdot T} - e^{(\rho\cdot T_{\max}-(T_{\max}-T/\Delta))} + \lambda$	(4)	"Lactin" (non-linear)	Lactin et al. 1995 [57]
$1/D = a\cdot T\cdot(T-T_{\min})\cdot(\sqrt{T_{\max}-T})$	(5)	"Briere 1" (non-linear)	Briere et al. 1999 [29]
$1/D = a\cdot T\cdot(T-T_{\min})\cdot(\sqrt{T_{\max}-T})^{(1/m)}$	(6)	"Briere 2" (non-linear)	Briere et al. 1999 [29]
$1/D = \rho\cdot(a-T/10)\cdot(T/10)^{\beta}$	(7)	"Simplified beta type" (non-linear)	Damos and Savopoulou-Soultani 2008 [27]
$1/D = a/(1+bT+cT^2)$	(8)	"Inverse second-order polynomial 1"	This study

over the entire range of temperatures to compute accurately developmental rates over all temperature range.

Several non linear models have been proposed to describe developmental rate response curves over the full range of temperatures, aimed either to build general insect phenology models, or to be used as forecasting tools for pest management [4, 5, 20, 21, 27, 29, 31, 34, 45, 50, 57–60]. Although the procedure can be easily generated using several different softwares, one important limitation is that the optimization procedure is performed only for the dependent variable and assumes that the residual errors of the independent variable are negligible.

Table 1 presents some of the most common non-linear models that have been developed to describe insect development rates over the whole range of temperature. Figure 2 depicts typical temperature response curves according to some common non-linear equations that are presented in Table 1. The models have been abstracted by the respective references and are additionally generated for representative selected empirical data.

Typically, and according to all models, there is no growth below the lower temperature threshold, while developmental rate increases and reaches a maximum at optimal temperature and declines rapidly approaching zero at the higher temperature threshold that is often considered as lethal temperature.

2.4. Biophysical Models. Biophysical models predict the behavior of insect developmental rate in physical terms. Since "*temperature rate biophysical models*" are representations of temperature-depended development and based on the primitive rules of temperature dependence of reaction rates narrowed by biophysics, they are differentiated to all the other non-linear models.

The conformation of enzymes is the essential step in the enzymatic reaction and this conformation depends on temperature. Because poikilothermic development can be considered as a macroscopic revelation of enzyme reactions, in which temperature exerts a catalytic effect at a molecular level, these equations have been applied in modeling microorganism growth and in describing temperature-dependent development of arthropods.

Traditionally, such kinds of relations are based on the empirical equations of *Van't Hoff's law* [7], Arrhenius [46], and Eyring [50, 60–62]; and these relationships provided the principal foundation of later works.

Van't Hoff, based upon the experimental results of the botanist and pharmacist Pfeffer (who first measured osmotic pressure in 1877), concluded that the osmotic pressure π of a sugar solution in relation to its volume is constant and directly related to the absolute temperature T:

$$\pi = kT, \tag{5}$$

where k is a constant of analogy. Furthermore, by applying the ideal gas state equation to describe the osmotic pressure, as in the case of ideal gas, results in

$$\pi = RT\Sigma c_i, \tag{6}$$

where R is the universal gas constant, T is the absolute temperature, and c_i is the molar concentration of solute i. Interpretation of (5) and (6) simple states that the rate of chemical reactions increases between two- and threefold for each 10°C rise in temperature. This conclusion, according to *Van't Hoff's law,* that an increase in temperature will cause an increase in the rate of an endothermic reaction had a huge impact in chemistry, biochemistry, and physiology.

The Arrhenius equation relates the chemical reaction rate constant to temperature T (in Kelvins or degrees Rankin) and the activation energy of the reaction E_α as follows:

$$k = k_0 e^{-E_a/RT}, \tag{7}$$

where K_0 is the rate coefficient, E_a the activation energy, R the universal gas constant, and T absolute temperature. According to the Eyring function [61] any biochemical reaction rate (without prior enzyme activation) increases exponentially while in the equation parameterized by Schoolfield et al. [60] the reaction rate $r(T)$ is given as a modification of a reference reaction rate to a respective reference temperature:

$$r(T) = \rho \frac{T}{T_{\text{ref}}} e^{[H_\alpha/R\ (1/T_{\text{ref}}\ -1/T)]}. \tag{8}$$

In (8), ρ is considered as *1/time* (reference rate) and H_α corresponds to the temperature sensitivity coefficient (or activation enthalpy in J/mol) and R is the universal gas constant ($8.314\,\mathrm{J\,K^{-1}\,mol^{-1}}$). The above equation can be applied to any intended temperature sensitive rates including developmental rates as well.

However, when dealing with biological rates, exponential increase is observable on a limited range and not throughout all temperature regimes. Sharp and DeMichele [63] considered activation process of the two extreme temperatures as independent and proposed a modification of the Arrhenius equation. This result to an equation having two components in the denominator, each for the description of the reversible inactivation of the rate-controlling enzyme considering both low and high temperatures and including “linearity” at middle temperatures:

$$r(T)=\left[\frac{T\cdot\exp\left[\left(\Phi-\Delta H_A^{\neq}/T\right)/R\right]}{1+\exp[(\Delta S_L-\Delta H_L/T)/R]+\exp[(\Delta S_H-\Delta H_H/T)/R]}\right], \tag{9}$$

where $r(T)$ is the mean developmental rate at temperature T (1/time), T is the temperature in K, R is the universal gas constant ($1.987\,\mathrm{cal\,deg^{-1}\,mol^{-1}}$), while the other parameters are associated with the rate-controlling enzyme reaction: ΔH_A is the activation enthalpy of the enzyme reaction while ΔH_H is the change in enthalpy associated with high-temperature inactivation of the enzyme ($\mathrm{cal\,mol^{-1}}$), ΔS_L is the change in entropy associated with low-temperature inactivation of the enzyme ($\mathrm{cal\,deg^{-1}\,mol^{-1}}$), and Φ is a conversion factor having no thermodynamic meaning.

Figure 3 gives the biophysical model (9) for representative datasets as well as the respective Arrhenius plot. The biological interpretation of the above function has analogies to those of the Arrhenius function in which the dominator represents the fraction of rate-controlling enzyme that is in the active state. Derivation of the above mathematical function as well as the basic assumptions and modifications of the original formula are covered in details in [60, 63].

3. Statistics for Parameter Estimation and Model Comparison

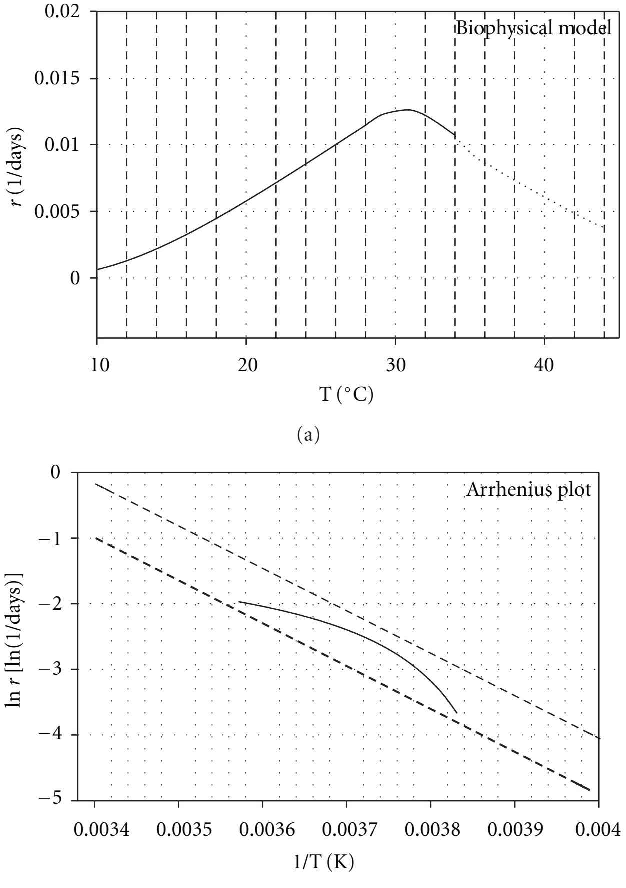
3.1. Parameter Estimation. Numerous procedures have been developed for parameter estimation and inference in regression analysis.

Campbell et al., 1974 [43, 64], provide statistics for the Standard error (SE) of the lower developmental threshold ($T_{\min}$) and the thermal constant K for the linear model based on “principal-manually” derived statistics:

$$\mathrm{SE}_{T_{\min}}=\frac{\bar{r}}{b}\sqrt{\frac{s^2}{N\cdot\bar{r}^2}+\left[\frac{\mathrm{SE}_b}{b}\right]^2}, \tag{10}$$

where s^2 is the residual mean square of r, $\bar{r}$ is the sample mean, and N is the sample. Additionally, the size of the SE_K for the thermal constant K for the linear model having slope b is, respectively [64],

$$\mathrm{SE}_K=\frac{\mathrm{SE}_b}{b^2}. \tag{11}$$



(a)

(b)

Figure 3: Curve shape of the biophysical model of sharp and DeMichelle [63] as modified by Schoolfield et al. [20] (a) and the respective Arrhenius plot (b).

However, several other procedures are also proposed for parameter estimation and relative statistics. The most common are the maximum likelihood (ML) and the ordinary least square (OLS) estimation, and they are used for both linear and non linear models [65].

Point and interval estimation using ML relies on distributional assumptions (here a specific probability function for error dispersion must be specified), in contrast to OLS point estimates, which generally do not require hidebound distributional assumptions, are unbiased, and have minimum variance.

The OLS minimise the sum of square residuals of the regression function of interest. Additionally, most statistical packages of parameter estimation are based on the Levenberg-Marquardt algorithm (LMA) which provides a numerical-iterative solution of curve fitting over a space of parameters of the function.

The Marquardt algorithm [66] is a least squares method based on successive iterations for parameter optimization. Thus, if $(x_i,\ y_i)$ is the given set of n empirical observation pairs of the independent (temperature) and dependent (developmental times) variables, the algorithm optimizes the parameters p of the model curve $f(x, p)$ so that the sum of the squares of the deviations is minimum:

$$g(p) = \sum_{i=1}^{n} \left[y_i - f(x_i, p) \right]^2 \tag{12}$$

The method is that the analyst has to provide an initial starting guess for final parameter estimation. This is an important constrain of the method and especially in curves with multiple minima the initial guess must already to be closed to the final solution. Furthermore, problems can arise in the case of observational data (i.e., time series) in which covariates can exist between observed and response variables.

The methods described above for calculating standard error and confidence intervals for a parameter relay on the assumption that the statistic of interest is assumed to be normal distributed. Thus, there is no need whatsoever for bootstrapping in regression analysis if the OLS assumptions are met. However, in the case of estimating population values in the absence of any information (i.e., variables in which sampling distributions and variances are unknown due to limited data), or in the case in which the variable is the final result of several observations (as in the case of life table statistics), parameter estimation and standard errors can be based on resampling methods such as the Bootstrap and/or the Jackknife method, or even based on Bayesian inference estimation.

For more details on resampling the reader should consider the references cited [67, 68].

3.2. Model Comparison. Since several regression models are available it is convenient to provide criteria or goodness of fit tests for model comparison. For instance, a common question that applied entomologists are facing is how to compare two different models for a given species and/or how to compare two different species with a given model.

Generally, several criteria have been proposed to evaluate model performance including the root mean square error (RMSE), the Pearson x^2, the deviance (G^2) statistics, regular and adjusted to the parameter numbers regression coefficients, and information criteria such as the *Akaikes* and *Bayes-Schwarz* information criteria [21, 27, 39, 69].

The idea behind most of these criteria is to measure the "range" of which the predicted values of a given model match the observed and can be applied in evaluating prediction capability for a particular dataset (i.e., one species-several models). Some of them are described in brief.

The Pearson x^2 statistic is based on observed (O) and expected fitted or predicted (e) observations and has similarities to the Root Mean Square Error [27, 65]:

$$x^2 = \sum_{i=1}^{n} \frac{(o-e)^2}{e} = \sum_{i=1}^{n} \frac{(y_i - n\hat{\pi}_i)^2}{n\hat{\pi}_i(1-\hat{\pi}_i)} \tag{13}$$

Where y_i is the observed value of Y, $\hat{\pi}_i$ is the predicted or fitted value of x_i and n is the number of observations. Additionally, based on the same concept a "prediction capability" index d can be addressed to be used to compare candidate models and rank them according to the degree to which the predictions are error-free:

$$d = 1 - \frac{\left[\sum (P_i - O_i)^2\right]}{\sum\left[\left(\left|P_i - \overline{O_i}\right|\right) + \left(\left|O_i - \overline{O_i}\right|\right)\right]^2}, \tag{14}$$

where $\overline{O_i}$ is the average of the observed values [27, 70].

For a comparison of only two models, an efficacy ratio can be calculated as follows [27, 70]:

$$E_{1,2} = \frac{\mathrm{MSE}_1}{\mathrm{MSE}_2}. \tag{15}$$

Where the respective to the models efficacy ratio E is based on the mean square errors (MSE) and can be used as evaluation index [70]. Values close to 1 indicating very low differences between the selected models in predicting a particular dataset [21, 27].

Considering that there are cases in which different datasets (i.e., two different species) are described with a particular model and cases in which there is model selection among equations that differ on the number of parameters, model performance comparisons can be made according to the adjusted coefficient of determination ($\mathrm{Adj} \cdot r^2$) and on the Akaike's information criteria [71].

The $\mathrm{Adj} \cdot r^2$ is a modification of r^2 that adjust for the number of explanatory terms in a model. Unlike r^2, $\mathrm{Adj} \cdot r^2$ increases only if an additional new term improves the model more than would be expected by change [21, 39]. The $\mathrm{Adj} \cdot r^2$ is defined as

$$\mathrm{Adj} \cdot r^2 = 1 - \frac{\mathrm{RSS}/(n - (\vartheta + 1))}{\mathrm{SS}/(n-1)}. \tag{16}$$

Akaike's information criterion (AIC) developed and proposed by Akaike in 1974 [39] is

$$\mathrm{AIC} = n \cdot [\ln(\mathrm{RSS})] - [n - 2 \cdot (\theta + 1)] - n \cdot \ln(n) \tag{17}$$

and the Bayesian-Schwartz information criterion (BIC or SIC) was proposed on 1978 and is [39]

$$\mathrm{BIC} = n \cdot [\ln(\mathrm{RSS})] + (\theta + 1) \cdot \ln(n) - n \cdot \ln(n), \tag{18}$$

where RSS is the residual sum of squares and SS total sum of squares, θ number of parameters and n observation number. These criteria permit to infer on how the different number of parameters add to the explanatory power of the candidate model.

4. Physiological Time and Heat Unit's Accumulation Systems

Considering the above models in defining cardinal temperatures of development in the laboratory, as well as the respective for each stage and species thermal constants, the interest is to apply this knowledge in order to make field predictions of temperature effects on insect phenology in time and space, according to the physiological time and related heat accumulation systems [50, 72–75].

Often referred to also as thermal time, the progress of the development of an organism is viewed as a biological clock that measures time units. Thus, although physiological time accelerates or slows according to prevailing temperatures, the time units to complete a particular developmental event in field should be the same as defined in the laboratory and equals the species specific thermal constant.

Thus, since the *law of effective temperatures* suggest that the completion of a given stage in development requires an accumulation of a definite amount of heat energy, similar approaches can be followed in which effective accumulated temperatures are estimated by the respective heat energy in field during the growth season.

According to this approach the amount of age or development accumulated from time 0 to t, and for discrete time intervals is

$$\Delta\alpha = \sum f\ [T(t)]\Delta t, \qquad [T(t)] > 0. \tag{19}$$

According to this function the species integrate temperature effects according to some function, f, peculiar to their species. This function, $f[T(t)]$, can be either linear or non-linear. If $f[T(t)]$ is assumed to be linear, then the developmental rate is proportional to temperatures above threshold (as defined according to the *x-intercept* method and apart from the linearity check of the rate-temperature curve), on the other hand, several non linear relations exist such as the logistic curve. However, in order to be effective, heat summation takes into account only the active temperatures within the species-specific range of development [24, 51].

Several methods have been proposed in calculating degree days accumulated in field, as well as related software. However, for the sake of brevity, in this review, the following three widely applied methods the average method, the modified average method, and the modified sine wave method, are briefly discussed.

4.1. Average Method. According to the average method developed by Baskerville and Emin [14], which is the simplest one, the number of daily degree-days is calculated by subtracting the base temperature from the average daily temperature as follows:

$$DD = \left[\frac{\min T + \max T}{2}\right] - T_{\min}. \tag{20}$$

Among the disadvantages of the above approach is that it does not take into account those daily minimum temperatures that can fall below the species lower temperature thresholds. This situation is very common in spring and results in bias and underestimation of degree-days accumulated by the insect since not all hourly temperatures during a day are above the threshold level. Thus, during this short period, development proceeds but is not taken into account by the proposed heat accumulation system.

4.2. Modified Average Method. In order to avoid the above-mentioned disadvantage it is convenient to modify the first component of (20) by substituting minimum temperature with lower temperature threshold, thereby approximating closer reality by calculating the daily temperature accumulation that corresponds to the interval between maximum temperature and that which is higher than the lower threshold of the species, or

$$DD = \left[\frac{T_{\min} + \max T}{2}\right] - T_{\min}. \tag{21}$$

This approach will result in a higher number of degree-days by taking into account development during the short periods in which temperature is slightly above the lower developmental threshold.

4.3. Modified Sine Wave Method. In principle mathematical relationships for this technique were given by Baskerville and Emin [14], Allen, and Watanabe [2]. Arnold [24, 51, 76] showed that the area under the temperature curve, the amplitude of which has been adjusted to the daily maximum and minimum temperatures for a given day, can be approximated according to sine curve.

Thus, according to the modified sine wave method, proposed by Allen [51], a trigonometric sine function is being used to describe this kind of daily temperature fluctuations. Based on the same principle as previously stated, heat accumulations during a day correspond to the area above the species lower temperature threshold. It is also noteworthy to state that this method leads to similar results as the modified average method in the case where minimum temperature is higher than the base temperature.

All these methods that are briefly described are based on the principle that the specimen is accumulating climate temperatures that are limited within its thresholds. Heat units are expressed as accumulated degree-days that correspond to a 24-hours daily interval that is limited between minimum and maximum temperature range and the predetermined species-specific thresholds.

5. Discussion

Among the scopes of this article was the description of representative models that have been proposed to model insect temperature dependent development either in the laboratory or field. However, a tremendous amount of prior work has been done in the field of insect temperature modelling since the first defined principles and the reader should consider the work of Ludwig [18], Uvarov [49], Powsner [19], Wigglesworth [26], Laudien [25] and Wagner et al. 1984 [20] for additional information.

Nevertheless, among the purposes of this review was to popularise prior studies. Several statistical criteria for model comparison are also gathered in order to integrate and familiarise most current approaches and tools for modelling the effect of temperature on insect development. This is an essential step to be made in order to draw inference upon the species ecology, spatiotemporal arrangement, and abundance.

According to selected linear and non linear models, that are presented in brief, developmental responses can be summarized in terms of the three critical, or cardinal, temperatures of development. In addition, since calculation of physiological time by temperature-driven field models is related to the area summated by the chosen heat-accumulation system, the definition of these temperatures is a prerequisite for accurate phenology prediction. Thus, apart from the ecological concerns, the importance of finding a mathematical/statistical model which describes and then simulates the phenology of individuals under field conditions is a prior constraint for further successful timing of pest management practices in field.

Depending on their parameters, the presented models can be judged more or less complex and several algorithms for least squares estimation have been proposed for nonlinear parameters [66, 77]. By incorporating several more factors-parameters on the equations, the authors search to gain higher accuracy on data description. However, complexity does not assure more accuracy in all cases. Prior comparative approaches should be followed to choose among most appropriate models that are available. To put forward, since most model shapes are quite similar, comparative differences of model performances can be only indicated by detailed statistical measures [39].

Hence, not all models display the same fit behaviour when carefully observed while very few provide a detailed biological interpretation of the estimated parameters. For instance, the advantage of the models proposed by Logan and Lactin over the other equations is due to the fact that they incorporate parameters that have direct biological interpretation and this is a major asset. In addition, the models proposed by Sharpe and DeMichele [63] and Schoolfield et al. [60], based on enzyme kinetic reactions, display a radical departure from those based on empirical fits to data. Nevertheless, it is common that temperature affects not only the rate of chemical reactions, but also induces conformational changes in biological systems [49].

Moreover, one disadvantage of complexity in models is that it strongly influences parameters estimation [39]. For example, although most of the polynomial models do not have any biological interpretation, probably the most important advantage they have is that parameter estimation can be easily done [56].

One other characteristic, among the presented models, is that not all of them are able to make predictions that are matched over, the experimentally derived, observed values. Unfortunately, there are instances in which optimum and upper threshold temperature predictions are quite overestimated when compared to real data [21, 27]. For instance the lower temperature threshold for *G. molesta*, as estimated in the current laboratory trial, slightly deviates from that estimated by prior field studies [47]. Nevertheless, differences in respect to insect stage can also exist so it is important to model all development of *G. molesta* for safer interpretations. Thus, a good fit for a respective model has no utility if it predicts temperature thresholds that have no biological meaning. Such false predictions can result in bias on the estimation of cardinal temperatures. In most cases overestimation of optimum and maximum temperature thresholds is the result of skewed curve, although coefficients of determination are quite high but can be the result of a good data fit on the intermediate temperature range. In other words, a good fit is not always a guarantee for biologically significant model performance and a reliable and accurate data description over all temperature range [21, 27, 44].

On the other hand, not all models can predict lower temperature thresholds, since there is no intersection with the temperature axis, when rate of development is zero [27], while in some cases cardinal temperatures are derived graphically and not numerically. In addition, the assumption of a base temperature close to 0°C, in the cases in which the curve approximates origin may seem unreasonable, considering that it is well accepted that lower temperature thresholds for most arthropods are well above 0°C, usually around 6–10°C, or higher. This is also displayed for the dataset used to model *G. molesta* in the current study. Thus, the most currently used non-linear temperature models describe only part of the whole picture of insect temperature-dependent development. The equation of Logan et al. [55], as modified by Lactin et al. [57], due to the constant factor that intersects with the temperature axis, as well as the equation proposed by Hilbert and Logan [16], proposes a lower threshold as well, although proved rigid in describing particular datasets [27].

The above reasons, as well as the species and stage-specific plasticity on temperature responses, give important reasons that should be taken into account to choose among several available formulas. These trends have been pointed out by several researchers and are probably the major cause that resulted to the development of plethora of non-linear models in the literature [27, 31, 55–57, 78, 79].

Another important constraint is that most of these models are directly related to temperature and do not take into account other climatic variables. For insects in particular, temperature is probably the most critical abiotic factor that influences their developmental rates and their life cycles, although other factors such as photoperiod, humidity, and nutrition should not be excluded, as well as crowding or density and competition [13, 40, 44].

Furthermore, in most cases it is virtually impossible to measure the temperature that an insect experiences in its original microenvironment. For example, most plant-feeding insects display a species-specific behavior in relation to their host (i.e., crawling inside of shoots or barks at the larval stage) while others exert some control over their body temperature through their behavior (i.e., they rest at shadowed and cool places when temperature is high) [21, 40].

Considering that the existence of alternating temperatures is more probable in reality [80], there are cases in which models displayed considerable inaccuracy in predicting insect development and phenology under field conditions [21, 39, 42, 44, 58, 81, 82, 82, 83].

Hence there is no perfect model, but we rely on the available ones that best describe our datasets, under certain conditions, and even though most models are oversimplifications, they are acceptable for empirical predictions in some defined ranges and instances.

Thus, if the model is proved reliable after seedily experimental evaluation, heat accumulations of a phenological event that occurs in field should reflect that which have been estimated by the model and thereby provide means of accurate timing of pesticides and initiation of pest management tactics. Therefore, it is not risky to claim that temperature has a prominent role in insect biology and by understanding the temperature effects on insect development we are able to describe and predict the distribution and abundance of insect species in any locality [83–85].

From an ecological standpoint, insect vital thermal requirements, as described in this article (i.e., thermal constant and temperature thresholds) provide ecologically and practically useful information [34, 66, 86]. For instance, as the thermal constant differs among genera, species or even stages, their study reveals various aspects of temperature adaptation and in particular the adaptation of each to its environment. On the other hand, species specific thermal requirements can also be used as indicators of the distribution and abundance of insect populations [32].

The effect of a climatic factor, such as temperature for instance, sets the tolerance limits for a species, and this has been acknowledged by earlier studies (i.e., Shelfold, 1913: The Law of Tolerance). Later studies [13, 87, 87, 88, 88] discuss how the species-specific "environmental boundaries" are determined by the ultimate tolerance factor (i.e., temperature) which may further restrict geographic distribution [8, 37, 41, 89].

Moreover, is it though for species whose geographical distributions ultimately are determined by temperature, global warming should result in spatial range shift [33]. Thus, the speculations on the effects of climatic change on the spatial dynamics of insect species have been quite general and populations are expected to extend their ranges to higher latitudes and elevations [37, 38, 90–94].

However, contrasting results concerning future projecting of species distribution have been also reported [90, 95], and one cannot exclude a progressive temperature selection of individuals that are adapted to the new temperature environment and especially for species with high reproductive potential [96–98] and host alternatives. Furthermore, the rate of temperature change affects species acclimation potential which further results in different conclusions regarding the responses of the species to acclimation [38, 99] and that thermal tolerances of many organisms to be proportional to the magnitude of temperature variation they experience.

Since genetic variation and potential response to selection should be positively correlated with population size, species with restricted ranges, or smaller populations, are predicted to have reduced capacity to adapt to environmental change [96, 97, 100]. On the other hand, it is more likely that temperature alteration can affect the reproductive potential of a species (i.e., abundance) and its life cycle, since additional generations or/and outbreaks are possible during the growth season [101] when not limited by photoperiod [48].

For a particular species, there is an inverse relation between the thermal constant and the lower developmental threshold and it is suggested that this trade modifies the fitness of the species and finally influences the outcome of competition between related species and their distributions [85, 88, 102–104]. Moreover, tropical species and warm-adapted species tend to have higher values on their lower temperature thresholds when compared to cold-adapted species that had greater *DD* requirements and much lower temperature ranges [85, 88, 102, 104].

Based on such linear relationships, between thermal constants and lower temperature thresholds, for several cold-blood species, it is suggested that there is an inverse relationship between lower temperature thresholds and the thermal constant associated with latitude and/or habitat that adapts each species to its thermal environment [85, 103]. Thermal constant and respective *DD* requirements are also based on the particular morphology and size of the species. For example, size at maturity is a function of the rate and duration of growth, and large size at maturity implies a long generation time and a correspondingly large *DD* requirements [17, 102, 105].

Hence, insect thermal requirements have a strong physiological and ecological interpretation since they modify species-specific ecological strategy which is adapted to a particular thermal environment [26, 49, 74, 84, 104, 106].

Thus, any model which provides biologically important parameters is useful in modeling population dynamics under several temperature regime alterations. In addition, by incorporating more factors in the equations, climate-driven models have the potential to describe the general ecological behaviour, abundance, distribution, and outbreaks of insects on a regional or even global scale, with important practical applications.

Finally, future research must be carried out in the direction of insect thermal adaptation in order to assess the species reproduction potential and related evolutionary properties as they respond to short- and long-term temperature alterations. The development of more sophisticated models, such as demographic system models and ecological niche models, that incorporate species-specific vital thermal requirements as well, is also an urgent necessity to improve and complete all current models. Thus models that are based on weather and other factors can more realistically estimate the spatiotemporal population evolution and invasive potential of native and nonindigenous species in new areas.

Acknowledgment

Part of this work was supported by IKY (Greek Scholarship Foundation) through a postdoctorate scholarship awarded to P. Damos.

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Hindawi Publishing Corporation
Psyche
Volume 2012, Article ID 879715, 12 pages
doi:10.1155/2012/879715

Research Article

Effects of Habitat and Human Activities on Species Richness and Assemblages of Staphylinidae (Coleoptera) in the Baltic Sea Coast

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Received 15 June 2011; Accepted 6 August 2011

Academic Editor: Panagiotis Milonas

In 2009, the staphylind fauna was studied in six habitats of the Baltic Sea coast of Schleswig-Holstein (northern Germany). The following habitats lagoon, sandy beach, shingle beach, primary dune, wooded cliff, and woodless cliff were significantly separated by their species composition. Vegetation and soil moisture were the most important factors separating the assemblages. Lagoons exhibited the most species-rich habitat. Sandy beaches provided the highest number of endangered species. Both sandy beaches and woodless cliffs showed the highest number of exclusive species. A loss of species was determined in the gradient from sandy to shingle beaches. Few species preferred shingle beaches; abundance of *Cafius xantholoma* increased with the increasing amount of shingle. More species preferred the sandy conditions, for example, *Polystomota grisea*, *P. punctatella*, and *Phytosus spinifer*. *Anotylus insecatus* and *Bledius defensus* require distinct mixtures of sand and silt on woodless cliffs. Tourist impact on sandy beaches accounts for approximately 50% loss of species.

1. Introduction

In general, staphylind beetles are rarely taken into consideration in ecological investigations [1, 2]. This is due to the fact that the identification is difficult, and little information is available on species ecology. Moreover, in several investigations, the differentiated assemblages corresponded only weakly to environmental parameters [3, 4]. Nevertheless, Staphylinidae are one of the most species-rich coleopteran families and, thus, might give more information about biodiversity than any other arthropod group. This is particularly relevant as many species are associated with other animals, for example, with birds, mammals, or as parasitoids of flies. Staphylinid diversity not only informs about the abiotic heterogeneity of the habitat, but also about the heterogeneity produced by animal species.

Very few studies are available concerning the biodiversity of coastal habitats along the Baltic Sea. More is needed since activity by tourists on beaches has increased dramatically in the last decades [5] and coastal habitats are included in the list of endangered habitats in the Fauna-Flora-Habitat (FFH) directive of the European Union (EU). Coastal lagoons are listed in a priority class [6]. Most information exists concerning salt marshes which also include studies on Staphylinidae [7–9].

Even though the fauna of beaches is well known in general in many European countries (e.g., [10, 11]), there is very little information about the fauna of other coastal habitats and the influence of environmental parameters from the coasts of the Baltic Sea. In particular, little knowledge is available about sandy beaches and cliffs. In contrast to tidal coasts, the Baltic Sea coast has little or no tides. This is reflected by a wide distribution of terrestrial organisms towards the sea line.

Thus, the following study mainly focuses on sandy and shingle beaches and cliffs. In the present study, the relationships between staphylinid assemblages and habitat factors, the relationships between individual species and soil factors, and the effect of tourism on species richness are highlighted. We address the following questions in this study: (i) which environmental parameters control the composition of staphylinid assemblages at the coast? (ii) are soil parameters responsible for the occurrence of different staphylinid species? and (iii) where are the most species-rich coastal habitats and are they influenced by beach tourism?

2. Sites and Methods

The investigation was performed in 2009, from April 9 to August 20 at nine locations along the Baltic Sea coast in Schleswig-Holstein, northern Germany, having an extremely low tidal range of less than 10 cm (Figure 1). At these 9 locations, different sites were selected representing the following habitat types: woodless and wooded cliffs, sandy and shingle beaches, primary dunes, and lagoons (Table 1). Six sandy beaches were selected in contrast to three or four sites of the other habitat types since beaches were the focus of the investigation. Two of the six beaches were open to tourists. Staphylinidae were collected by means of pitfall traps. Up to eight replicate pitfall traps were installed at each site to compensate loss by tourist damage. Only four pitfall traps were included in the final analysis in order to have equal numbers of traps for the different sites. Pitfall traps with an opening of 5.6 cm diameter were filled with 10% vinegar and a tension-reducing agent and covered by a transparent shelter to shield against direct precipitation.

To compare the environmental conditions between the habitat types, the following environmental parameters were determined: soil moisture by difference between wet weight and dry weight of soil as mean of 11 sampling intervals; pH in deionised water using a WTW pH-Meter; organic matter after combustion of a dried soil sample; shingle content by sieving a larger soil sample in the field; sand content by sieving using a 0.063 mm sieve after oxidising the organic matter by H_2O_2; finer silt and clay material was determined by subtracting sand content [12].

The statistical analysis was performed using the program STATISTICA [13]. Data were tested according to parametric or nonparametric distribution using the Kolmogorov-Smirnov test. The data of environmental factors of assemblages and species richness (normal distribution) were compared using ANOVA with subsequent LSD post hoc test. Differences between two habitats were tested by U test or t-test, correlations by Pearson correlation. To get an idea of total species richness in the habitats, Jackknife II species richness was calculated using the program PAST version 2.04 [14]. The second order of Jackknife estimator seems to be most accurate to estimate total species richness [15]. Detrended correspondence analysis (DCA) and canonical correspondence analysis (CCA) were executed using the program CANOCO [16]. According to ter Braak [17], a distinct ordination of assemblages can be expected at eigenvalues higher than 0.5. Monte Carlo Permutation test was performed to find the significance of environmental parameters.

In the beach habitats, sand and shingle contents were closely correlated: sand content = 97 + 0.96* shingle content ($r = 0.99$; $P < 0.001$). Therefore, either sand content or shingle content was used to analyse the occurrence of species in the sand-shingle gradient. For some comparisons, the sand-shingle gradient was subdivided into the following three classes: shingle: >70% shingle and <30% sand; medium: 10–60% shingle and 40–90% sand; sand: >90% sand and <10% shingle. To analyse the abundance in these gradients, Kruskal-Wallis ANOVA was used with subsequent U test and Bonferroni correction using the program STATISTICA. The status of endangered species refers to the red list of Schleswig-Holstein [18].

3. Results

3.1. Environmental Parameters. The highest soil moisture contents were found at the lagoons and wooded cliffs, while all beach habitats have very low soil moistures without significant differences (Table 2). Sand content was high at the sandy beaches and the primary dunes and lowest at the wooded cliffs and the shingle beaches. The shingle content differs between shingle beach with 77% on average and all other habitats. Soil pH was on a high level in a narrow range. Nevertheless, significant differences were also found for this parameter. The highest soil pH was found at the woodless cliffs and at the shingle beaches, and the lowest pH at the primary dunes. Thus, sandy beaches and primary dunes that show no differences in all other parameters vary significantly in their soil pH. Organic material was low in all habitats, but highest in wooded cliffs and lagoons. Overall, each habitat type reflected a specific combination of soil parameters. They could be significantly separated by at least one of the measured parameters.

3.2. Species Composition. From a total of 4324 specimens collected, 165 species have been identified. The highest number of species was found at lagoons, and the lowest number of species on shingle beaches (Table 3). Jackknife species richness was also highest at lagoons and lowest at shingle beaches. The highest number of endangered species was found on sandy beaches. Only primary dunes have no endangered species.

In correspondence to the environmental differences between the habitats, the detrended correspondence analysis revealed assemblages of rove beetle that are clearly separated by their habitat characterisation (Figure 2). Only the shingle beach at Weissenhaus was attributed to the sandy beaches and not to the other three shingle beaches. According to the canonical correspondence analysis, 3 of the 6 factors have a significant effect on the species composition of the assemblages and account for 76% of the total variance. The most important factor was soil moisture ($F = 3.6$) which accounted for 34% of the total variance. Wooded or non-wooded situation accounted for 23% ($F = 2.8$), and soil pH accounted for 21% ($F = 2.7$). Neither sand content nor shingle content nor content of organic matter were significant for the separation of the assemblages.

The composition of dominant species in the 6 habitat types shows that several species are widely distributed along the different habitat types (Table 4). The widely distributed *Aleochara sparsa* was found highly dominant in the cliff habitats. While several species frequently found in Schleswig-Holstein revealed highest dominance in the wooded cliffs,

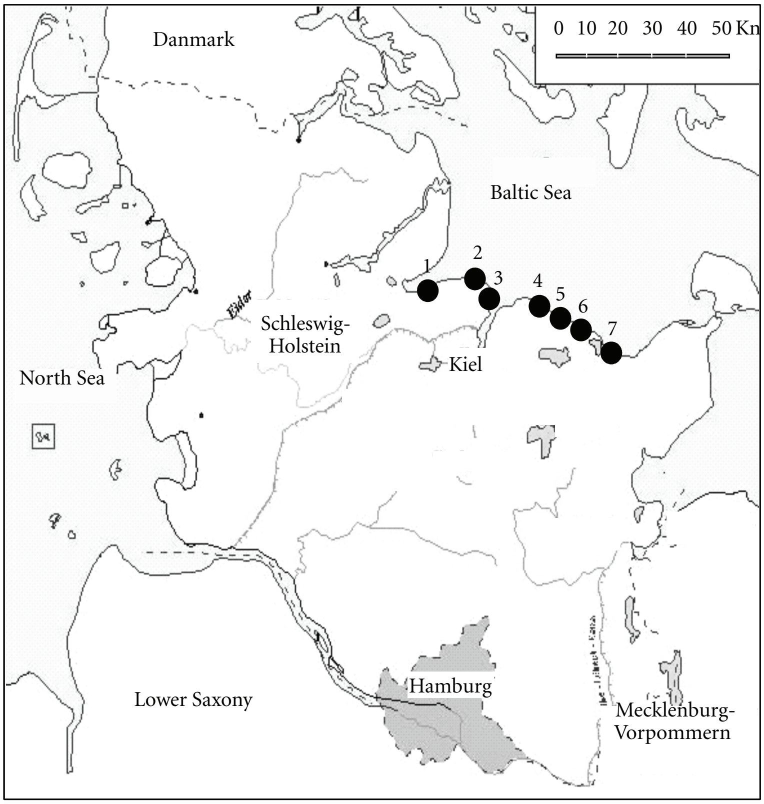


Figure 1: Investigated locations at the Baltic Sea coast: Lindhöft (1), Dänisch-Nienhof (2), Stohl (3), Stakendorf and Hohenfelde (4), Hubertsberg (5), Behrensdorf and Lippe (6), and Weißenhaus (7).

Table 1: Habitats at the investigated locations and abbreviations of locations and habitats; x indicates a number of 4 replicate pitfall traps.

Location/Habitat (abbreviation)	Tourism on sandy beach	Lagoon (L)	Sandy beach (SB)	Shingle beach (GB)	Primary dune (PD)	Woodless cliff (Wl)	Wooded cliff (Wc)
Behrensdorf (BD)	Closed	x	x	—	—	—	—
Dänisch-Nienhof (DN)	—	—	—	x	—	x	x
Hubertsberg (HB)	—	—	—	x	—	x	—
Hohenfelde (HF)	Open	x	x	—	x	—	—
Lippe (KB)	Closed	—	x	—	x	—	—
Lindhöft (LH)	Open	—	x	—	—	—	x
Stakendorf (SD)	Closed	x	x	—	x	—	—
Stohl (ST)	—	—	—	x	—	x	—
Weißenhaus (WH)	Closed	—	x	x	x	x	x

Table 2: Mean values of environmental parameters for the differentiated staphylinid assemblages; different exponents indicate significant differences by ANOVA and consecutive LSD test.

Parameter	Wooded cliffs	Woodless cliffs	Lagoon	Sandy beach	Primary dune	Shingle beach
Soil moisture (%)	$^{a}18 \pm 3.0$	$^{b}8 \pm 1.1$	$^{a}31 \pm 5.9$	$^{c}1 \pm 0.5$	$^{c}1 \pm 0.5$	$^{c}1 \pm 0.6$
Wood	yes	no	no	no	no	no
Sand content (%)	$^{b}36 \pm 6$	$^{c}46 \pm 3$	$^{c}51 \pm 16$	$^{a}89 \pm 9$	$^{a}92 \pm 9$	$^{b}22 \pm 21$
Shingle content (%)	$^{b}5 \pm 2$	$^{b}8 \pm 2$	$^{b}21 \pm 20$	$^{b}8 \pm 10$	$^{b}6 \pm 8$	$^{a}77 \pm 20$
Soil pH	$^{b}7.4 \pm 0.1$	$^{a}7.9 \pm 0.2$	$^{b}7.5 \pm 0.2$	$^{b}7.3 \pm 0.2$	$^{c}7.2 \pm 0.1$	$^{a}7.9 \pm 0.3$
Organic content of soil (%)	$^{a}6.6 \pm 2.6$	$^{b}1.1 \pm 0.1$	$^{a}5.6 \pm 0.9$	$^{b}0.2 \pm 0.2$	$^{b}1.4 \pm 2.2$	$^{b}0.3 \pm 0.1$

TABLE 3: Species richness in the investigated habitats and Jackknife II species richness; RL species richness of endangered species (only status 1 and 2).

Habitat type	Localities									Species richness			
	BD	DN	HF	HB	KB	LH	SD	ST	WH	Total	Per trap	Jackknife II	RL
Lagoon	37	—	47	—	—	—	51	—	—	85	13.9 ± 2.5	154 ± 6.5	2
Sandy beach	36	—	10	—	27	18	21	—	22	70	10.0 ± 4.2	116 ± 6.6	5
Shingle beach	—	9	—	21	—	—	—	13	5	33	4.4 ± 3.3	61 ± 5.5	2
Primary dune	—	—	21	—	17	—	28	—	28	75	9.4 ± 4.0	88 ± 5.3	0
Woodless cliff	—	18	—	38	—	—	—	27	20	58	10.7 ± 3.5	99 ± 7.1	1
Wooded cliff	—	22	—	—	—	26	—	—	19	43	8.7 ± 3.4	72 ± 4.8	1

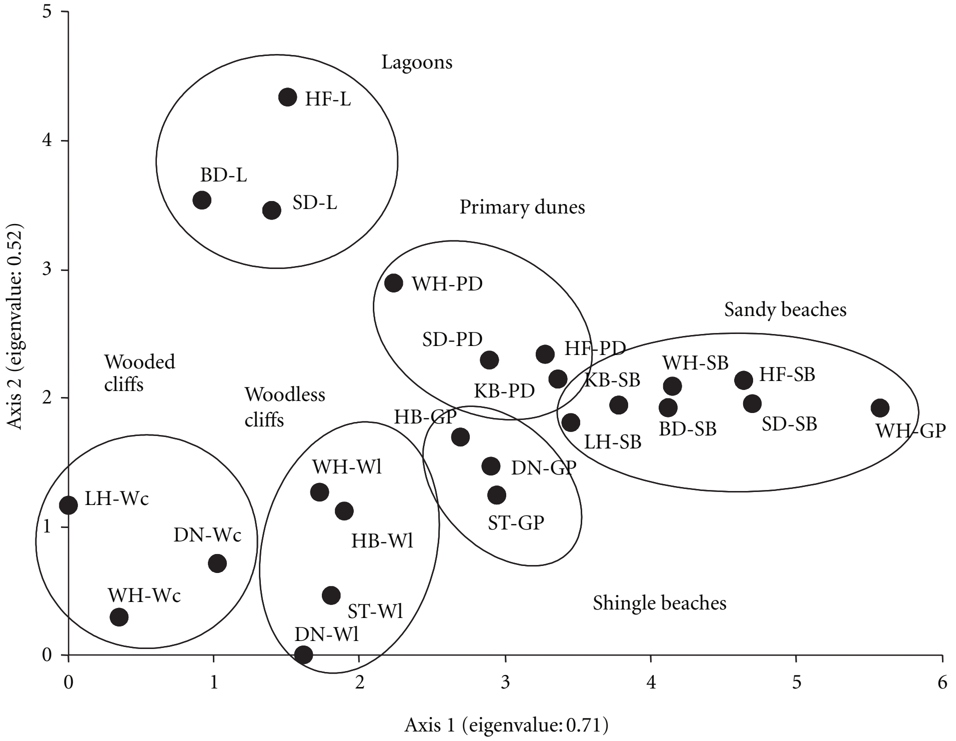
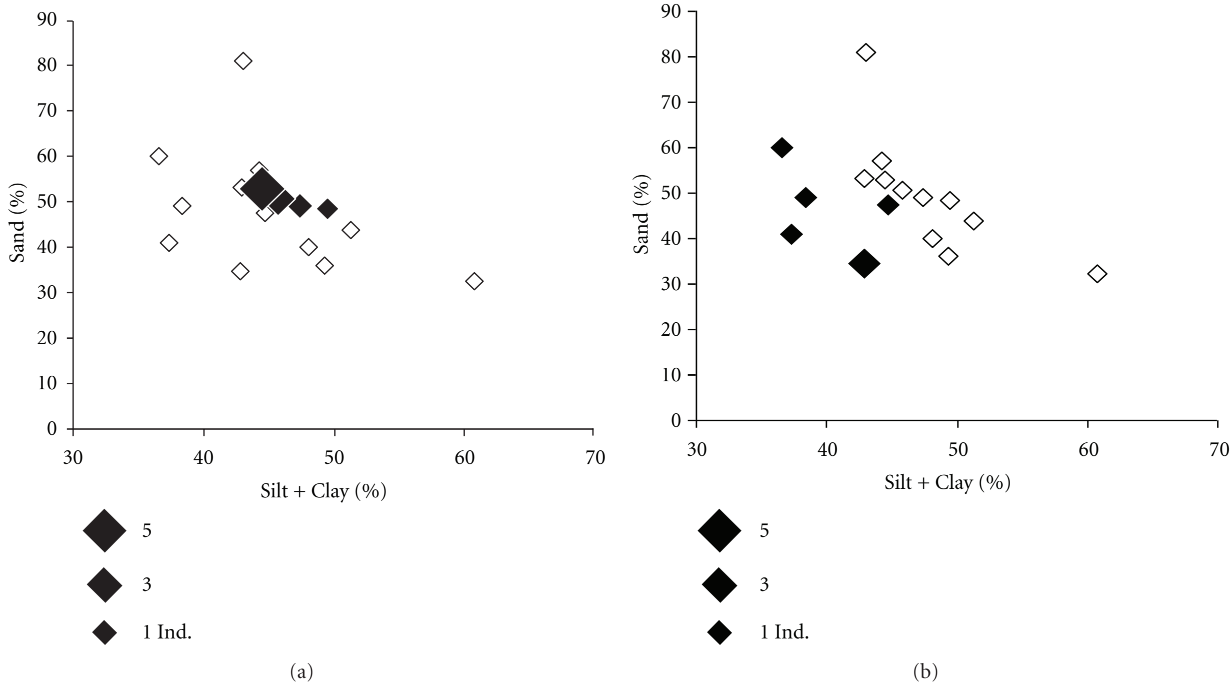


FIGURE 2: Results of the detrended correspondence analysis showing the separation of the 6 habitat types along the first two axes.

a higher number of specialised species were found in the woodless cliffs. In particular, rare species of bare soils, for example, *Stenus fossulatus*, *Bledius erraticus*, *Bledius defensus*, and *Anotylus insecatus*, were almost exclusively recorded there. Lagoons as wooded cliffs have no remarkable species that are restricted to the specific lagoon situation. All dominant species are frequently found also on mainland lake shores. Primary dunes showed only one specific species, that is *Ocypus brunnipes*, in contrast to the two beach habitats, where a number of 8 species can be regarded as typically independent from the soil situation. Shingle beaches thus seem to have no specific species in comparison to sandy beaches. In contrast, 3 species, that is, *Phytosus balticus*, *Bledius subniger*, and *Atheta vestita*, seem to prefer the sandy beaches.

3.3. Relationships between Individual Species and Environmental Parameters. Although the differences between shingle beaches, sandy beaches, and primary dunes are minor in rove beetle assemblages, individual species show significant differences concerning their occurrence. *Cafius xantholoma* only inhabits the beach habitats and was never found on the adjacent primary dunes (ANOVA: beach versus primary dune: $F = 6.7$, $P < 0.01$). Along sand gradient of beaches, the species significantly prefers the shingle beaches; a significant linear increase along the sand-shingle gradient was found (abundance = $0.02 \cdot$ shingle content + 0.36, $r = 0.66$, $P = 0.04$). A similar restriction to the beach habitats was found for *Polystomota grisea* (ANOVA: beach versus primary dune: $F = 17.2$, $P < 0.001$) and *Polystomota punctatella* (ANOVA: beach versus primary dune: $F = 10.9$, $P < 0.002$). In contrast



(a)

(b)

Figure 3: Occurrence of *Bledius defensus* (a) and *Anotylus insecatus* (b) in the sand-silt/clay relationship of woodless cliffs.

to *C. xantholoma*, both species significantly preferred the sandy beaches: *P. grisea* abundance = 0.03 · sand content − 0.27, $r = 0.73$, $P = 0.02$; *P. Punctatella* abundance = 0.02 · sand content + 0.19, $r = 0.67$, $P = 0.03$. Furthermore, *Phytosus spinifer* also occurred only in the beach habitats and preferred significantly the beaches of the sand class (Kruskal-Wallis ANOVA using the three classes: $\text{Chi}^2 = 7.8$, $P = 0.02$). The species was absent on beaches with a shingle content greater than 10% and on beaches with a sand content lower than 80%. In contrast to the four species restricted to beaches, *Aleochara bipustulata* was found on sandy beaches and primary dunes in similar abundance (ANOVA: $F = 2.1$, $P = 0.1$, not significant). However, the species significantly preferred the sandy habitats. Using all sites of beaches and primary dunes for the correlation between abundance and sand content, abundance increases with an increase in sand content of the habitat (abundance = 0.53 · sand content − 6.18, $r = 0.67$, $P = 0.006$).

For three species of the woodless cliffs, preference for specific mixtures of silt/clay and sand is assumed in regard to their occurrence in the silt/clay-sand relationship (Figure 3). *Anotylus insecatus* was mainly found on woodless cliffs between 30% and 40% silt/clay content, while it was absent from cliffs with silt/clay contents higher than 50% (Kurskal-Wallis ANOVA: $\text{Chi}^2 = 8.8$, $P = 0.01$). *Bledius defensus* was found in a silt/clay range between 40% and 50% (Kurskal-Wallis ANOVA: $\text{Chi}^2 = 5.8$, $P = 0.04$). The species was not found at cliffs with silt/clay contents lower than 40%. Only 1 specimen was found at cliffs with silt/clay contents higher than 50%. The species seems to occur in a very restricted range having a sand content between 45% and 50% and silt/clay content between 35% and 52%. Another typical species of woodless cliffs, that is *Stenus fossulatus*, showed no significant preference of specific sand-silt/clay mixtures. It occurred in woodless cliffs with a range of sand content between 42% and 50% and a wide range of silt/clay content between 36% and 81%. However, soil moisture on woodless cliffs was important. Abundance increased with increasing soil moisture (abundance = 0.39 · soil moisture − 2.21, $r = 0.96$, $P = 0.03$).

3.4. Effect of Tourism. Sandy beaches closed to tourists have significant higher species richness than beaches open to tourism (Table 5). The closed beaches revealed nearly twice as many species as the beaches open to tourists. No species was found exclusively on beaches open to tourists. Thus, half of the species of closed beaches are absent from open beaches. The difference between the two beach types is still more obvious if Jackknife II species richness is considered. Three species of the aleocharinae subfamily were abundant enough to analyse their occurrence in the two beach types. Both *Aleochara bipustulata* and *Polystomota grisea* showed significantly higher abundance on the beaches closed to tourists. A significant difference between both beach types concerning their sand content was not found (U test: $Z = 8.8$, $P = 0.06$). Thus, the differences found can be referred to the tourist impact. Only in *Polystomota punctatella* was the difference not significant.

4. Discussion

Unfortunately, no other studies concerning staphylinids from beach habitats considering environmental parameters are available for comparison. Rose [3] investigated

Table 4: Dominance of species that contribute to the species characterisation of the habitats.

Species	Wooded cliff	Woodless cliff	Lagoon	Primary dune	Shingle beach	Sandy beach
Tasgius morsitans	**5.0**	0.4	0.1	0.2	—	—
Omalium rivulare	**4.3**	—	0.6	—	0.8	0.1
Atheta crassicornis	**3.2**	0.1	0.8	0.2	0.8	—
Lathrimaeum unicolor	**2.8**	0.4	0.2	0.2	—	0.1
Quedius fuliginosus	**2.8**	0.3	1.0	—	—	—
Atheta atramentaria	**2.1**	0.4	0.1	0.4	—	2.2
Aleochara sparsa	**50.2**	**13.5**	0.8	1.8	2.3	1.7
Stenus fossulatus	0.7	**2.2**	—	—	—	—
Tachyporus dispar	1.1	**5.4**	—	0.3	—	0.1
Bledius erraticus	—	**1.6**	—	—	—	0.1
Bledius defensus	—	**1.3**	—	—	—	0.1
Tasgius winkleri	—	**0.9**	0.1	—	—	—
Anotylus insecatus	—	**0.9**	—	—	—	—
Tachyporus nitidulus	1.8	**27.1**	0.4	0.1	12.5	0.1
Drusilla canaliculata	1.1	**24.6**	**18.3**	**13.2**	**16.4**	1.1
Stenus pallipes	—	—	**3.3**	—	—	—
Stenus juno	0.4	—	**4.1**	0.2	—	—
Atheta graminicola	—	0.3	**8.9**	—	—	0.1
Stenus canaliculatus	—	0.4	**3.3**	—	—	—
Pachnida nigella	—	—	**2.6**	—	—	0.1
Ocypus brunnipes	—	—	0.2	**1.6**		0.4
Aleochara bipustulata	0.7	2.8	2.9	**72.5**	**19.5**	**56.7**
Polystomota grisea	—	—	0.1	—	**7.0**	**5.4**
Polystomota punctatella	—	—	—	—	**1.6**	**5.1**
Cafius xantholoma	—	—	—	—	**7.8**	**4.7**
Omalium riparium	—	—	—	0.1	**0.8**	**0.8**
Phytosus spinifer	—	—	—	—	**0.2**	**0.8**
Phytosus balticus	—	—	—	—	—	**0.3**
Bledius subniger	—	—	—	0.2	—	**0.8**
Atheta vestita	—	—	0.1	0.3	—	**2.2**

Table 5: Species richness and median abundance of three species in four sandy beaches closed to tourists and two beaches open to tourists with results of *t*-test or *U* test; significant differences are underlined.

Situation of beach	*n* traps	Species richness				*Aleochara bipustulata*	*Polystomota grisea*	*Polystomota punctatella*
		Species per trap	S.D	Jackknife II	S.D.	Median	Median	Median
Closed	16	11.6	4.2	109	6.3	28.0	2.0	1.0
Open	8	6.8	1.8	56	3.4	2.5	0.0	0.0
t/Z		3.1				3.7	2.5	0.6
P		0.005		<0.001		<0.001	0.01	0.5

the staphylinid fauna of three North Sea islands of Lower Saxony, but beaches were not included. In his study of dunes, salt marshes, and bushy vegetations, the eigenvalues of the first axes ranged between 0.26 and 0.41. This is remarkably lower than the value of 0.71 in the present study, which indicates a greater dissimilarity between the habitats of the Baltic Sea coast. The higher similarity of the species compositions on the North Sea islands might be referred to the island situation, where a lower diversity might have developed than in mainland habitats. However, the high species richness on the three North Sea islands, ranging between 227 and 269 species, does not support this hypothesis; the number of species was higher than the 165 species found in the present study. It is more likely that the similar sandy soil conditions of the three North Sea islands are responsible for the higher similarity of the rove beetle assemblages. In the present study, clay, sand, and shingle soils were included. Similar results concerning environmental parameters were found

Table 6: List of staphylinid species (total number of individuals) at the investigated sites.

Species	Lindhof	Dänisch-Nienhof	Stohl	Stakendorf	Hohenfelde	Hubertsberg	Behrensdorf	Weißenhaus
Acidota crenata	—	—	—	—	—	—	1	—
Aleochara bilineata	—	—	1	—	—	3	5	—
Aleochara binotata	—	—	—	—	1	—	4	—
Aleochara bipustulata	—	12	5	141	363	29	878	221
Aleochara brevipennis	—	—	—	—	—	—	1	—
Aleochara sparsa	26	104	28	14	1	22	25	65
Aleochara verna	—	—	—	—	1	—	3	4
Aloconota gregaria	1	2	1	8	7	3	11	13
Amischa analis	—	—	—	4	2	2	10	9
Amischa decipiens	—	—	—	—	—	—	2	—
Amischa soror	—	—	1	1	1	3	2	—
Anotylus insecatus	—	2	—	—	—	3	—	1
Anotylus rugosus	2	1	1	28	23	2	15	3
Anotylus sculpturatus	1	1	1	1	—	3	—	3
Anotylus tetracarinatus	—	3	—	2	11	—	2	—
Atheta amicula	—	—	1	1	—	1	1	—
Atheta atramentaria	4	4	—	5	8	1	18	3
Atheta cauta	—	—	—	1	—	—	1	—
Atheta celata	—	—	—	1	—	1	1	—
Atheta crassicornis	7	2	—	5	2	2	—	2
Atheta elongatula	—	—	—	—	1	—	—	—
Atheta fungi	1	8	—	9	136	1	12	19
Atheta gagatina	—	—	—	—	—	—	—	1
Atheta graminicola	—	—	—	11	52	2	19	—
Atheta ischnocera	—	—	—	—	—	—	1	—
Atheta laticollis	—	—	—	5	—	—	—	—
Atheta liliputana	—	—	—	—	—	—	1	1
Atheta luteipes	—	—	—	—	4	—	1	—
Atheta marcida	—	—	—	—	—	—	2	—
Atheta melanaria	—	—	—	—	—	—	1	—
Atheta nigricornis	1	2	2	—	—	—	—	1
Atheta oblita	—	—	—	1	—	—	1	1
Atheta palustris	—	—	1	—	—	8	—	1
Atheta sodalis	2	—	—	—	—	1	—	—
Atheta sp.	3	—	—	—	—	—	—	—
Atheta triangulum	1	1	—	—	2	6	2	2
Atheta vestita	3	—	—	13	1	—	4	1
Atheta volans	1	—	1	1	1	1	1	—
Bledius defensus	1	—	1	—	—	—	—	8
Bledius erraticus	1	11	—	1	1	—	—	1
Bledius opacus	—	—	—	1	—	—	—	—
Bledius pallipes	—	1	—	—	—	—	—	—
Bledius subniger	—	—	—	7	—	—	1	—
Brundinia marina	—	—	—	—	—	1	1	2
Brundinia meridionalis	—	—	—	—	—	—	1	—
Cafius xantholoma	—	4	3	7	—	3	15	14
Callicerus obscurus	—	1	—	—	—	—	—	—
Calodera aethiops	—	—	—	2	2	—	3	—
Carpelimus corticinus	—	—	1	5	13	3	7	—
Carpelimus elongatus	1	—	—	—	—	—	—	

Table 6: Continued.

Species	Lindhof	Dänisch-Nienhof	Stohl	Stakendorf	Hohenfelde	Hubertsberg	Behrensdorf	Weißenhaus
Carpelimus foveolatus	—	—	—	1	—	—	—	—
Carpelimus gracilis	—	—	—	—	—	—	1	—
Carpelimus rivularis	—	—	—	—	—	—	—	1
Cordalia obscura	—	—	—	—	—	—	—	1
Cryptobium collare	—	—	—	—	1	—	—	—
Cypha discoideus	—	—	—	—	1	—	—	—
Dacrila fallax	—	—	—	1	—	—	7	—
Dinaraea angustula	—	5	3	5	6	13	5	4
Drusilla canaliculata	1	4	6	59	9	115	123	218
Euaesthetus bipunctatus	—	—	—	—	1	—	—	—
Euaesthetus laeviusculus	—	—	—	—	—	—	1	—
Falagria thoracica	—	—	1	5	—	1	—	—
Gabrius breviventer	—	1	—	2	8	—	7	—
Gabrius vernalis	—	—	—	—	—	—	2	—
Geostiba circellaris	—	—	—	1	—	—	—	—
Gnypeta carbonaria	—	—	—	—	—	—	1	—
Gyrohypnus angustatus	—	—	—	—	—	1	—	5
Habrocerus capilaricornis	—	1	—	—	—	—	—	—
Halobrecta puncticeps	2	—	—	6	5	—	2	1
Haploglossa nidicola	—	—	—	—	—	—	—	1
Heterothops dissimilis	—	—	—	2	—	—	—	—
Hydrosmecta longula	3	—	—	1	—	2	1	1
Ilyobates bennetti	—	—	—	—	1	—	—	—
Ischnosoma splendidus	—	—	1	1	3	—	1	—
Lathrimaeum unicolor	6	—	—	1	—	2	1	6
Lathrobium brunnipes	1	—	—	1	—	—	—	—
Lathrobium fulvipenne	—	—	1	1	—	—	—	—
Lathrobium longulum	—	—	—	—	1	—	—	—
Lathrobium rufonitidum	—	—	—	2	—	—	—	—
Lesteva longoelytrata	—	3	10	3	—	3	1	4
Lesteva sicula	—	—	—	—	1	—	—	—
Liogluta alpestris	—	—	—	1	—	—	—	1
Lordithon thoracicus	—	—	—	—	—	—	1	—
Myllaena intermedia	—	—	—	—	1	—	1	—
Myllaena minuta	—	—	—	—	2	—	3	—
Myrmeocephalus concinnus	—	—	—	—	—	1	—	—
Nehemitropia lividipennis	—	—	—	—	—	—	2	—
Neobisnius procerulus	—	—	—	1	—	—	—	—
Ocalea picata	4	—	—	—	—	—	—	—
Ocypus brunnipes	—	—	—	2	19	—	1	4
Ocypus similis	—	—	—	2	1	—	—	—
Omalium littorale	—	—	—	1	—	—	3	2
Omalium riparium	5	—	1	1	—	—	1	1
Omalium rivulare	5	1	1	6	—	—	—	6
Omalium rugatum	—	—	—	—	—	—	—	3
Othius punctulatus	2	—	—	—	—	—	—	—
Oxypoda acuminata	—	1	—	1	—	—	—	2
Oxypoda brachyptera	—	1	2	—	—	2	—	—
Oxypoda brevicornis	—	—	—	—	—	—	2	—
Oxypoda elongatula	—	—	—	4	3	—	8	—
Oxypoda haemorrhoa	—	—	—	—	—	—	—	1

Table 6: Continued.

Species	Lindhof	Dänisch-Nienhof	Stohl	Stakendorf	Hohenfelde	Hubertsberg	Behrensdorf	Weißenhaus
Oxypoda procerula	—	—	—	2	8	—	5	—
Oxytelus fulvipes	—	1	—	—	—	—	—	—
Oxytelus sculptus	—	—	—	—	1	—	—	—
Pachnida nigella	—	—	—	18	6	—	1	—
Paederus riparius	—	—	—	8	—	—	—	—
Philonthus cognatus	—	—	—	—	—	1	—	—
Philonthus decorus	1	—	—	—	—	—	—	—
Philonthus fumarius	—	—	—	6	—	—	—	—
Philonthus fuscipennis	—	—	—	—	—	—	—	1
Philonthus micans	—	—	—	2	—	—	—	—
Philonthus quisquiliarius	—	—	—	—	—	—	1	—
Phytosus balticus	—	—	—	2	—	—	—	—
Phytosus spinifer	—	1	—	1	—	—	6	—
Placusa depressa	—	—	—	—	—	—	1	—
Placusa pumilio	—	1	—	—	—	—	—	—
Plataraea brunnea	2	—	—	—	—	—	—	—
Platydracus stercorarius	—	—	—	1	—	—	—	1
Polystomota grisea	2	—	9	21	1	—	17	3
Polystomota punctatella	10	1	1	5	—	—	26	—
Quedius fuliginosus	5	—	2	4	3	—	2	3
Quedius fumatus	1	—	—	—	—	—	—	—
Quedius molochinus	—	—	2	—	—	—	—	—
Quedius picipes	1	—	—	—	—	—	—	—
Quedius xanthopus	1	—	—	—	—	—	—	—
Rugilus rufipes	1	—	—	—	—	1	—	2
Scopaeus minutus	—	—	—	—	—	1	—	—
Sepedophilus marshami	—	—	—	1	—	—	—	—
Stenus atratulus	—	—	—	—	1	—	—	—
Stenus bimaculatus	—	1	—	12	9	—	13	—
Stenus boops	—	—	—	—	—	—	1	—
Stenus brevipennis	—	—	—	—	—	—	1	—
Stenus brunnipes	—	—	—	—	—	—	1	—
Stenus canaliculatus	—	—	—	3	—	3	28	—
Stenus clavicornis	1	—	—	6	6	2	6	2
Stenus formicetorum	—	—	—	3	21	—	—	—
Stenus fossulatus	—	2	4	—	—	3	—	8
Stenus juno	—	—	—	1	30	—	6	3
Stenus nigritulus	—	—	—	—	—	—	3	—
Stenus nitens	—	—	—	—	3	—	—	—
Stenus pallipes	—	—	—	5	3	—	22	—
Stenus palustris	—	—	—	—	—	—	1	—
Stenus pusillus	—	—	2	—	2	—	—	—
Stenus solutus	—	—	—	1	—	—	—	—
Tachinus corticinus	—	—	1	—	1	—	—	—
Tachinus signatus	1	—	—	3	7	2	—	1
Tachyporus atriceps	—	2	—	1	—	—	—	—
Tachyporus chrysomelinus	—	—	—	1	—	—	—	—
Tachyporus dispar	1	4	1	1	—	34	2	2
Tachyporus hypnorum	—	4	—	2	—	1	2	6
Tachyporus nitidulus	3	44	12	2	4	110	—	36
Tachyporus obtusus	—	—	—	—	—	1	—	1

Table 6: Continued.

Species	Lindhof	Dänisch-Nienhof	Stohl	Stakendorf	Hohenfelde	Hubertsberg	Behrensdorf	Weißenhaus
Tachyporus pusillus	—	—	—	—	1	1	—	—
Tachyporus quadriscopulatus	—	—	1	—	—	—	—	—
Tachyporus solutus	—	—	—	2	—	—	—	—
Tasgius ater	—	—	—	—	—	1	—	—
Tasgius compressus	—	2	—	—	—	—	—	—
Tasgius melanarius	1	5	1	3	—	—	1	1
Tasgius morsitans	10	4	1	2	1	1	—	1
Tasgius winkleri	—	5	—	1	—	1	—	—
Thinonoma atra	—	—	—	1	1	—	—	3
Tinotus morio	—	—	—	—	—	—	1	—
Xantholinus linearis	1	—	1	—	2	3	—	5
Xantholinus longiventris	3	1	—	3	7	3	1	—
Zyras limbatus	—	—	—	—	—	—	—	2

in both investigations. Factors connected with wooded or nonwooded situations and moisture conditions were mainly responsible for the different species compositions of the habitats in both studies. Moreover, in a similar analysis of the spider fauna from the same sites analysed in the present investigation, the wood situation and moisture content were the main environmental parameters responsible for the separation of spider assemblages [19].

In specific investigations of North Sea salt marshes, Schaefer [20] found two habitat types: one from 80 cm to 130 cm above NN and one from 20 cm to 60 cm above NN. Consequently, elevation and frequency of inundation were the most important environmental factors. This was also true for a comprehensive study of staphylind assemblages in Baltic Sea salt marshes that included sites from the states of Schleswig-Holstein (north-western Germany) and Vorpommern (north-eastern Germany) [9]. In the salt marshes, soil conditions were less important than in the investigations on the sandy islands of Lower Saxony and in the present study of the Baltic Sea coast habitats.

The vertical gradient from sea level to higher elevations certainly affects the staphylinid assemblages of beaches and primary dunes. There has been no increase in species richness of Staphylinidae found between sandy beaches and primary dunes. However, specific species occurred on beaches that were not found in primary dunes, for example, *Polystomota grisea* and *Phytosus spinifer*. In contrast to Staphylinidae, a significant increase of species richness from beaches to primary dunes was found for spiders [7, 19]. Schaefer [7] also found an increase in species richness in the adjacent habitats of dunes and dry grassland, representing a gradient of increasing elevation. The decrease of species richness from higher elevated sites to lower elevated sites in coastal habitats was referred to the higher instability of habitats exposed to the sea [20]. This effect of instability was also supposedly responsible for the decrease of species richness of other organisms such as meiofauna and macrofauna [21, 22] and might also account for the elevation gradient of species richness in salt marshes [23]. Since the high-energy input by wind and waves combined with high erosion is greater on shingle beaches than on sandy beaches, the low species richness of shingle beaches might be referred to the effect of instability. Nevertheless, several species are adapted to such unstable habitats as could be shown for the aleocharine species, for example, *Aleochara bipustulata*, *Polystomota grisea*, and *P. punctatella* that all live as parasitoids in flies without host specificity except host size [24]. The first species occurs in many sandy habitats of the mainland, but the abundance decreases from high elevated dune sites to low elevated beach sites at coasts. On the other hand, the two other species are restricted to beach habitats only although host species are the same as in *A. bipustulata*. It can be assumed that the flies live off the rich wrack debris on beaches which exhibit rich food resources for parasitoid staphylinids and can compensate for the loss in species richness found in other animal groups.

When considering all investigated parameters, lagoons are certainly the most species-rich habitats for staphylinids in this study. However, sandy beaches also reveal high numbers of species, particularly the endangered species. 5 species on the red list of endangered species status 1 and 2 have been found on sandy beaches, whereas only 2 were found at lagoons. Moreover, total species richness on sandy beaches as estimated by the Jackknife II method is only slightly lower than at lagoons, but distinctly higher than in all other habitat types. The eminent status of sandy beaches becomes still more relevant concerning exclusive species for the habitat. According to this investigation, only one exclusive species has been found at lagoons, *Stenus pallipes*. However, this species is abundant at most lake margins in northern Germany. In comparison, 5 exclusive species have been found at beaches. Overall, beaches support a higher number of endangered species and a much higher number of exclusive species compared to lagoons. Therefore, from a regional point of view, sandy beaches are the hot spots of species richness.

Another habitat also seems to be of great value for the coastal species richness at the Baltic Sea: the woodless cliffs. Species richness is distinctly lower than on beaches, but many exclusive and rare species live there. In particular, *Stenus fossulatus*, *Bledius defensus* (RL, 2), and *Anotylus insecatus* seem to be adapted to open, bare soil habitats on clay or silt soils. The distribution of the two species *A. insecatus* and *B. defensus* also indicates that the specific mixtures of sand and silt material are responsible for the occurrence of these species. Regarding their occurrence in the sand-silt gradient, they prefer completely different mixtures of sand and silt/clay. *B. defensus* seems to be restricted to a very narrow range of the mixture gradient. Thus, not only the conservation of the cliff situation is needed but also the whole range of sand and silt mixtures is necessary to preserve habitats for the different demands of species.

The present results show that tourism significantly decreases species richness on sandy beaches. According to both species per trap and Jackknife II species richness, beaches open to tourists reveal approximately half of their potential species richness. The loss of species on beaches has been attributed to tourist activities for several species and animal groups. Unfortunately, this ecological problem has not been investigated at the species level in Germany. In South Africa, Moffett et al. [25] quantified the damage by tourist trampling for intertidal macrofauna and found a loss of 5% to 70% depending on the species. The negative effect of trampling on *Talitrus saltator* (Crustacea) has been determined in different studies [26–28]. According to their results, it is not possible to compensate for the losses during short periods of tourist activity during summer. The loss of the ground beetle *Cicindela maritima* to near extinction on Baltic Sea beaches has also been referred to tourist activity [29]. Discussions about this species considered not only the sensibility of larvae against trampling but also the large home range to be the cause for the high losses. The high sensibility of beach species to trampling can certainly be referred to the porous sandy soils. The existing instability of the sandy soils caused naturally by wind and waves increases dramatically if tourist trampling is added. It can be assumed that the increase of instability triggering the species loss from sandy to shingle beaches also causes the species loss from closed to open beaches. At present, no studies investigating the degree of loss under different intensities of tourist activity are available. According to Kammer and Schernewski [30], tourist activity fluctuates in relation to weather, season, and week day. In their study, they found tourist densities between $7\,\mathrm{m}^2\ \mathrm{person}^{-1}$ and $84\,\mathrm{m}^2\ \mathrm{person}^{-1}$. However, no studies are available that provide information about the level of tourist density which can be tolerated while preserving the species richness of beaches. Nevertheless, the present study documents that beach conservation is needed in order to preserve the species richness of coasts, not only for birds.

Appendix

For more details, see Table 6.

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