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Long-term population dynamics of a persisting predator-prey system in cassava fields in Benin, West Africa

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Long-term studies of the impact of an introduced predator species on its prey populations are crucial for evaluating classical biological control. In this article, we analyse the population dynamics of the herbivorous mite *Mononychellus tanajoa* and its mite predator species *Typhlodromalus aripo* over 7 consecutive years since the introduction of the predator in a cassava field in Benin, West-Africa. After the release of *T. aripo*, *M. tanajoa* densities dropped from c. 90 to c. 7 per leaf in c. 5 months and *T. aripo* populations persisted in this field for the full 7 years. Time series analysis resulted into an annual model showing one absolute peak population size and one lower local peak for both predator and prey species. The pronounced herbivore peak coincided with a trough in rainfall intensity, whereas the lower local peak fell in a period of high rainfall. The pronounced peak in *T. aripo* densities occurred near the time when *M. tanajoa* densities reach a peak soon after the onset of the dry season (December). The lower local peak of *T. aripo* occurred during the rainy season (July), near the time when *M. tanajoa* densities reach a trough and maize pollen is available as an alternative food source.

Regression analysis of the log-transformed data-series shows that – except for the first year after predator release – *M. tanajoa* fluctuates around an almost time-invariant mean population density, but the densities of *T. aripo* show a consistent decline over the full observation period from 1995 to 2001. Nevertheless, *T. aripo* populations persist for 7 years (and beyond 2001). This is remarkable in itself but also in view of the fact that the cassava field under study was replanted on average twice a year. However, replanting is done asynchronously and this allows persistence via immigration from adjacent fields. To explain the observed trends and periodic components in the data-series of predator and prey densities, we review hypotheses that are based on (1) the annual pattern and trends in abiotic factors (rainfall, drought), (2) mechanisms endogenous to the predator-prey system (using the Rosenzweig-MacArthur predator-prey model as a starting point), and (3) a combination of exogenous and endogenous influences.
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**Key words** Biological control, *Typhlodromalus aripo*, *Mononychellus tanajoa*, predator-prey interactions, Phytoseiidae, abiotic and biotic factors, endogenous and exogenous factors, alternative food, time series

Classical biological control aims at permanent control of a pest by the introduction and establishment of natural enemies from the geographic origin of the pest. Permanent control of course requires that the introduced natural enemies would persist and respond to increasing prey densities to prevent outbreaks of the pest. Population ecologists have had a keen interest in long-term monitoring of biological control systems because such systems may help in testing hypotheses on key factors promoting predator-prey persistence (Hassell, 1978; Murdoch et al., 2003). However, long-term time series of terrestrial predator-prey systems are scarce. The best examples to date are the control of rabbits by myxoma virus in Australia (Fenner and Fantini, 1999), aphids by ladybeetles (Caltagirone and Doutt, 1989) and the California red scale by parasitoids in California (Murdoch and Briggs, 1996). The hypotheses tested against these data sets were usually derived from models that highlighted one or another or more biotic traits of predator and prey as key to understanding persistence of predator-prey systems in local populations (Hassell, 1978), in metapopulations (Murdoch, 1994) and in other types of spatially extended populations (Hassell, 2000). Although biotic factors are likely to provide the key to persistence by population regulation, abiotic factors may be important in determining absolute population levels at a local or regional scale and thereby population persistence at that scale (Andrewartha and Birch, 1954). Moreover, their influence may well be season-dependent, as it is well known that seasonality can add new properties to the dynamical repertoire emerging from predator-prey models (Rinaldi et al., 1993; Rinaldi and Muratori, 1993; Scheffer et al., 1997).

The data presented in this article consist of monthly estimates of *T. aripo* and *M. tanajoa* densities in a cassava field (Ikpinlé) in Southeast Benin, starting at first introduction of *T. aripo* in October 1993 and extending through March 2001, covering in effect a period of 90 months. We used a time series model with cross-correlation (Lingeman, 1980, 1981) fitted to the time series data of predator and prey densities to identify trends in population densities (moving averages) of both predator and prey, and evaluate periodicity in their population fluctuations. The results of the time-series analysis are interpreted in three ways. First, we compare the period of predator-prey fluctuations with the annual pattern of intense rainfall (May-October) and drought (January-March). Both factors have been shown to cause substantial mortality of *M. tanajoa* on cassava in Africa (Yannick et al., 1989a; Bonato, 1993) - intense rainfall by wash-off, and drought by reducing oviposition, egg eclosion, and increasing immature and adult mortality. Second, we use a mechanistic predator-prey model (Rosenzweig and MacArthur, 1963; May, 1976) parameterized with independent laboratory observations on predator and prey mites to assess their life
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histories and predation rates (Gnanvosso et al., 2003; Hanaa et al., IITA, unpublished data). Model predictions were then compared with observed cycle periods of M. tanajoa and T. aripo. Third, to explain observed population fluctuations and trends, we formulate hypotheses that emphasize either exogenous (abiotic) factors or (biotic) mechanisms endogenous to the predator-prey system, or a combination of exogenous and endogenous factors. In this approach, we analyze the extent to which the main features of the observed predator prey fluctuations in cassava fields can be explained from biotic traits inherent to the biology of predator and prey, and the extent of the significance of abiotic factors in determining population levels.

In short, the broad objective of this study is to test alternative hypothesis on the relative impact of biotic and abiotic factors on population dynamics of M. tanajoa in cassava fields, and to obtain insights into the persistence of a predator introduced for the biological control of a plant pest. Our bottom line interest of course is to determine to what extent the introduced predator T. aripo is contributing to cycling of M. tanajoa while limiting this pest’s populations to levels that could be considered as control.

MATERIAL AND METHODS

Observation site

The data used in this study consist of observations conducted in a cassava field (ca. 0.5 ha), located near the town of Ikpine (6°52.52’ N, 2°36.70’ E) in southern Benin, West Africa, where the predatory mite T. aripo was released on 20 October 1993 and where it has been continuously present since its introduction. The field is located in the humid Forest Savannah mosaic ecology, characterized by a bimodal rainfall pattern that begins in late March and ends in November, providing an average of 1200 mm of rainfall per year. The field was continuously planted with cassava and inter-cropped with maize between April and July. Cassava was also continuously present in the vicinity of our field. Neither fertilizers nor pesticides were used in this field site during the entire duration of our observations.

Mite census

Census of M. tanajoa and T. aripo populations was initiated respectively in October and December 1993, and continued at monthly intervals through March 2001, with a few interruptions of 1-2 month periods due to logistical difficulties. To monitor mite populations for this remarkably long period, it was necessary to shift sampling to an adjacent field when the sampling field was harvested, as cassava is generally harvested after a period of nine to twelve months from planting. Cassava fields included in our mite census were between four and ten months old and were all planted with the cultivar ‘Agric’, the most common cassava cultivar in southern Benin. From the start of the data
collection (October 1993) until 11 January 1995, densities of *M. tanajoa* were determined on 30 randomly selected plants using the rapid count method described in Yaninek *et al.* (1991). Due to lower catch efficiency of this method compared to direct counting under binocular microscope in the laboratory, mite counting was shifted to the laboratory from February 1995 to the last census in March 2001. On each census date, the first fully developed leaf and the apex were removed from each of 30 randomly selected plants. The leaves were individually placed in a paper bag and immediately chilled until processing in the laboratory, while the apices were placed individually in glass vials containing 70% ethanol. In the laboratory, eggs and mobile stages (larvae + nymphs + adults) of predator and prey mites were counted under a dissecting binocular microscope and recorded separately. Mobile stages of phytoseiid mites were mounted in Hoyer's solution for positive species identification. Monthly rainfall data (amounts and frequency) were obtained from the agro-meteorological station in Pobé, located at 10 km north of the experimental field.

### Time series analysis

**Data pre-conditioning**

All original data series are discrete time series of monthly data *X* on rainfall or on the population density of *M. tanajoa* and *T. aripo*. The general form of the series is \( \{X[t]\} \), with *X* = monthly rainfall (mm) or monthly mean number of mobile stages of *M. tanajoa* per leaf, or *T. aripo* per apex, \( t_m = \) month and \( i = \) number of months from the first sampling in October 1993. As the rapid sampling method used initially between October 1993 and January 1995 was considered inaccurate, the first sample in the time series analysis for both *T. aripo* and *M. tanajoa* is the one taken in February 1995, corresponding to month 17 \( (t_1 = 17) \), and the last sample is the one taken in March, 2001, corresponding to month 90 \( (t_2 = 90) \). To achieve reasonable variance homogeneity (see Lingeman and van de Klashorst, 1992) inherent in predator and prey populations that grow exponentially, we log-transformed predator and prey counts to generate the following series:

\[
X_1'[t] = \ln X[t] 
\]

(1)

We replaced zero values with 0.03 to allow their transformation to log values. This replacement also corrected for the high probability of missing one mite in the sample of 30 leaves or apices of cassava plants. The minimum value of \( X_1'[t] \) is, therefore, -3.40. The number of missing data was relatively low (7%). Densities of *T. aripo* and *M. tanajoa* that were missing were estimated by linear interpolation between neighbouring values after transformation.

To correct for the lack of equidistance in sampling days, all log-transformed values (including rainfall data which were not transformed for obvious reasons) were calculated
by interpolation for the 15th of each month throughout the sampling period. In effect, each of the interpolated values now represented the ‘month-value’ of the parameter considered. Furthermore, to reduce ‘short-term’ (high frequency) fluctuations, mainly caused by sampling errors, all time series were digitally filtered through smoothing by threes. The series of the following form were thus generated:

\[ Y[t] = \frac{X'[t-1] + X'[t] + X'[t+1]}{3} \]  

with \( t = 18, \ldots, 89 \) months.

**General statistics**

The first step in the analysis of each series was to estimate any temporal trends in the series, generally, by linear regression (Southwood and Henderson, 2000). Then, the ‘level’ and total ‘power’ of the series are estimated by means of the sample mean \( \bar{Y} \) and variance \( \sigma^2 \), for each series. Estimations of the mean level and/or trend are needed to adjust the series to zero mean value and no trend, \( i.e. \) stationarity at zero level, which is a prerequisite to spectral analysis (Lingeman, 1981; Lingeman and van de Klashorst, 1992; Janssen et al., 1997). The resulting stationary series \( y[t] \) can then be analysed to determine the total power of the series, which now represents the integral variance contributions of periodical components and noise, and provides a preliminary impression of the variability of the data.

**Auto-covariance and power spectrum**

The auto-covariance function (ACF) is the mean shifted product of the signal by itself and describes the dependence between values of the time series at neighbouring points in time. An unbiased estimate of the ACF (Lingeman, 1981) is provided by the sample auto-covariance function \( C_{YY}[k] \) defined as follows:

\[ C_{YY}[k] = \sum_{t=k+1}^{N} y[t] \cdot y[t-k] \]  

with \( y[t] \) being the reduced (stationary) signal, with zero mean and \( N = \) the total number of data points and lag \( k = 0, 1, \ldots \)

The autocorrelation function (R) is obtained by dividing the ACF by the total variance:

\[ R_{YY}[k] = \frac{C_{YY}[k]}{C_{YY}[0]} \]  

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where \( C_{ij} \) is the estimated variance of \( Y_i \).

The \( \hat{A} \) can be used to demonstrate the presence of periodicities in the time series and serves as a necessary intermediate step for estimating the spectral density function.

Fourier transformation of the \( \hat{A} \) provides the spectral density function or power spectrum. The (smoothed) power spectrum is estimated by the sample spectrum:

\[
\hat{S}_y = 2 \left( C_{ii}(0) + 2 \sum_{k=1}^{M} w(k)C_{ii}(k)\cos(2\pi f) \right)
\]

where \( w(k) \) is the chosen lag window and \( M \) is the chosen truncation point (= maximum lag; Lingeman, 1981). The choice of \( M \) is based on trade-off between high frequency accuracy (i.e., resolution) and high stability of the estimate. Large \( M \) gives high frequency accuracy (i.e., high resolution) but poor stability, whereas a small \( M \) gives high stability but bad resolution. We chose \( M = 36 \), which gives a satisfactory resolution. From the wide range of windows in signal analytical literature, the Tukey window was used in the present study.

Finally, the power spectrum of the series is used to localize the frequency peaks and/or bands. The procedures for estimating the covariance and spectral density functions have been extensively described by Lingeman (1981) and Lingeman and van de Klashorst (1992).

The annual models

As a consequence of the results of the auto-covariance and the spectral density functions, we fitted the reduced data to the following annual model:

\[
Y = H_{1T} \sin \frac{2\pi t}{T} + H_{2T} \cos \frac{2\pi t}{T} = A_T \cos \left( \frac{2\pi t}{T} - \varphi_T \right)
\]

with \( t \) = time in months and period \( T = 12 \) months and 6 months respectively, to account for the one cycle per year or two cycles per year, which were identified in the \( \hat{A} \)F and power spectra (as well as the original time series).

Amplitude \( A \) and phase \( \varphi \) at period \( T \) are, respectively:

\[
A_T = \sqrt{H_{1T}^2 + H_{2T}^2} \quad \text{and} \quad \tan \varphi_T = \frac{H_{1T}}{H_{2T}}.
\]

Unbiased estimates of the parameters \( H_{1T} \) and \( H_{2T} \) were calculated by means of the least squares method, as described by Lingeman (1980).

Consequently, the complete models for \( M. \) lamina and rainfall are:
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\[ Y = H_0 + A_1 \cos \left( \frac{2\pi t}{12} - \varphi_1 \right) + A_2 \cos \left( \frac{2\pi t}{6} - \varphi_2 \right) \]

where \( H_0 \) is the mean level of the series, and the complete model for \( T. aripo \) is:

\[ Y = a + bt + A_{12} \cos \left( \frac{2\pi t}{12} - \varphi_{12} \right) + A_6 \cos \left( \frac{2\pi t}{6} - \varphi_6 \right) \]

where \( a + bt \) is the estimated regression equation.

For each time series, the model gives the amplitude and the phase of the periodical components observed in the signal for a one-year period, starting from January and ending in December. The significance of the fitted model is expressed as the ratio between explained and total sum of squares of the data (Lingeman, 1980).

**RESULTS**

**Trends in \( M. tanajoa \) and \( T. aripo \) densities**

Figure 1 shows the dynamics of mobile stages of \( M. tanajoa \) and \( T. aripo \) in the cassava field over the seven-year sampling period. Monthly densities of \( M. tanajoa \) per leaf decrease rapidly during the first few months following introduction of the predatory mite \( T. aripo \) from 90 mobiles per leaf to a mean of 7 mobiles per leaf and later cycling with peaks never exceeding 40 mobiles of \( M. tanajoa \) per leaf. \( Typhlodromalus aripo \) increased to 17 mobiles per apex during the first 3 months, a period equivalent to 3-4 predator generations (Gnanvosso et al., 2003). In subsequent years, the mean density of \( T. aripo \) was 4 mobiles per apex. Thus, there is convincing evidence that (1) \( T. aripo \) persisted over 7 years since its introduction in 1993, and that (2) \( M. tanajoa \) density dropped to lower levels after predator introduction. Scrutiny of population peaks and the rainfall data in Figure 1 also reveals that the December peaks of \( M. tanajoa \) and \( T. aripo \) coincided with the onset of the dry season.

The overall mean and variance of the log-transformed and smoothed data of the time series are shown in Table 1. To achieve an impression of the long-term behavior of the annual means (= levels) of the series, the moving annual means are presented in Figure 2. Here the moving annual mean is defined by the mean \( \ln(N) \) averaged over the interval \( t_i - 6 \) till \( t_i + 6 \) for every \( t_i \). By doing so, seasonal variations are filtered out. The regression lines also presented in Figure 2 are estimated by least square fitting of these annual means.

Excluding the first year data to eliminate the large amplitude cycle following predator introduction, the remainder of the data reveal trends in the moving annual means. The regression line of moving annual means of \( T. aripo \) against time has a highly significant negative slope (with coefficient of determination \( R^2 = 0.877 \)), whereas the regression for \( M. tanajoa \) has only a weak and non-significant negative slope (\( R^2 = 0.117 \)). Rainfall
intensity does not show a trend through time ($R^2 = 0.011$). Including moving annual means of the first 16 months of observations (after correction for the lower efficiency of the rapid field counting method using the coefficient of $1.3021$ obtained from an independent data set comparing laboratory and field counting, R. Hanna and D. Ojo, IITA, unpublished data) provides a slightly different view of the trends in the moving annual means of $M. tanajoa$. With the initial 16 months of observations included in the regressions, $M. tanajoa$ densities show a significant decline through time (slope $=-0.0209$, $R^2 = 0.3145$, $P < 0.001$, $n = 79$), principally due to the steep initial decline during the first 16 months (slope $=-0.3329$, $R^2 = 0.8492$, $P < 0.001$, $n = 11$), while the decline in $T. aripo$ moving annual means remains nearly unchanged (slope $=-0.0335$, $R^2 = 0.9075$, $P < 0.001$, $n = 79$). The results of the regression analysis on the smoothed monthly data $Y(t)$ are presented in Table 1. The means and slopes presented in Table 1 were used to achieve stationarity around a zero level in the data series.

Due to the absence of seasonal variation in the series of the moving annual means, the negative trend in $T. aripo$ densities is much more pronounced than it is from analysing the monthly data, yet also here the trend is significant.

![Image of rainfall pattern and population trends](image)

**Figure 1** Rainfall pattern and population trends of mobile stages of $M. tanajoa$ and $T. aripo$ in the cassava field site at Ikpriâlè
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Table 1 General statistics for the time series of *M. tanajoa*, *T. aripo* and rainfall. Computations were performed on the log transformed numbers for *M. tanajoa* and *T. aripo*, ns: non significant. For non-significant slopes, intercepts are ignored, as they are not different from the means.

<table>
<thead>
<tr>
<th>Statistics</th>
<th><em>M. tanajoa</em></th>
<th><em>T. aripo</em></th>
<th>Rainfall</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean</td>
<td>1.602</td>
<td>0.401</td>
<td>101.1</td>
</tr>
<tr>
<td>Variance</td>
<td>0.852</td>
<td>1.596</td>
<td>4593</td>
</tr>
<tr>
<td>Slope</td>
<td>-0.0038 (ns)</td>
<td>-0.0293</td>
<td>0.3564 (ns)</td>
</tr>
<tr>
<td>Intercept</td>
<td>-</td>
<td>1.939</td>
<td>-</td>
</tr>
<tr>
<td>$R^2$</td>
<td>0.008</td>
<td>0.250</td>
<td>0.012</td>
</tr>
</tbody>
</table>

Figure 2 Moving annual means of Log-transformed data series for *M. tanajoa* and *T. aripo*. Straight lines indicate the estimated regression lines. Regression equations are given for each series.

Scrutiny of the data on a per-season basis shows that the decline in the annual mean *T. aripo* densities over the 7 year period is paralleled by a decline of the minima reached in March (dry season), the maxima reached in July (early wet season), but not in the minima reached in September (middle of wet season) and in the maxima reached in December (onset of dry season), as these show a rather erratic pattern. This might indicate some drought-season-related factor that happens to become gradually more intense in the period from 1995 to 2001 or a gradual change in parameters driving predator-prey interactions or the food web interactions in which the predator-prey system is embedded (see section on mechanistic predator-prey model).
Chapter 3

Figure 3 Auto-correlation functions of *T. aripo*, *M. tanajoa* and rainfall

Figure 4 Power spectra of *T. aripo* and *M. tanajoa*
Annual fluctuations

A plot of mean prey and predator densities per month (calculated over the last 6 years of the time series, not shown here) gives evidence for the existence of at least one cycle and perhaps even two cycles per year (see Figures 3-5 below). Densities of *M. tanajoa* show a very weak trough in early March, a weak peak in May, a deep trough in August during the rainy season and a pronounced peak in December, early in the dry season. Densities of *T. aripo* show a deep trough in March-April, a distinct peak during the rainy season in July, a weak trough in September, and a steep rise to a pronounced peak in December, early in the dry season. The predator peak in December tends to coincide with that of *M. tanajoa*, whereas the predator peak in July follows 2 months after the prey reach a peak. These analyses point to the existence of one or two predator-prey cycles. The latter case is not consistent with rainfall data as it shows a single cycle per year. To resolve this issue, we first apply time series analysis to test for the annual cycle frequency in prey, predator and rainfall data and then use a mechanistic predator-prey model to infer how many cycles are expected from processes intrinsic to the biology of the interacting organisms.

Time series analysis

The time series analysis presented here provides strong evidence for at least one cycle and perhaps 2 cycles per year (cpy). The autocorrelation function (Figure 3) for *T. aripo* shows a strong maximum at intervals of 12 months plus a lower, yet pronounced maximum at lags of 6 months. The corresponding power spectrum shows pronounced peaks at both 1 cpy and 2 cpy (Figure 4). For *M. tanajoa*, both autocorrelation function and power spectrum show an evident 1 cpy component but only a much less pronounced 2 cpy period. Thus, the evidence for a component of 2 cycles per year is stronger for the predator than for its prey. Because rainfall intensity has precisely 1 cycle per year (Figure 3), this abiotic factor alone cannot explain the existence of a second cycle, especially that of the predator.

To estimate the periodical components of the annual behaviour of predator and prey in both amplitudes and phases, we fitted equation (6) to the stationary data series. The resulting estimates of the model-parameters are presented in Table 2. To quantify the significance of the estimates, the percentages of the explained sums of squares are given for both periodical components found in the time series analysis. For both predator and prey this simple two-component harmonic annual model explains ca. 45% of the total variation in the data series.

Graphs of the annual models of both species and rainfall are presented in Figure 5. It should be emphasized that these models represent averaged annual behaviour over a period of 7 years. Based on these model fits, the estimated phase shifts between *M. tanajoa* and *T. aripo* are 2.7 months, assuming one cycle per year, and 0.9 month, assuming two cycles per
Figure 5  Annual models of the periodical components of rainfall and of Log-population densities of $M.\ tanajoa$ and $T.\ aripo$.

Table 2  Parameters of the models and proportions of sum of squares explained

<table>
<thead>
<tr>
<th>Variables</th>
<th>$H_1$</th>
<th>$H_2$</th>
<th>$A$</th>
<th>$\phi$ in radians (months)*</th>
<th>SS explained</th>
<th>Total explained</th>
</tr>
</thead>
<tbody>
<tr>
<td>$M.\ tanajoa$</td>
<td>0.1406</td>
<td>0.7141</td>
<td>0.7278</td>
<td>0.1945 (0.4)</td>
<td>32%</td>
<td></td>
</tr>
<tr>
<td>$T.\ aripo$</td>
<td>-0.6946</td>
<td>0.2675</td>
<td>0.7443</td>
<td>-1.2032 (-2.3)</td>
<td>25%</td>
<td></td>
</tr>
<tr>
<td>Rainfall</td>
<td>0.0251</td>
<td>-0.7413</td>
<td>0.7418</td>
<td>-0.0339 (0.1)</td>
<td>61%</td>
<td></td>
</tr>
<tr>
<td>2 Cycles per year</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$M.\ tanajoa$</td>
<td>-0.4044</td>
<td>0.1814</td>
<td>0.4432</td>
<td>-1.1491 (-1.1)</td>
<td>12%</td>
<td>43%</td>
</tr>
<tr>
<td>$T.\ aripo$</td>
<td>-0.1659</td>
<td>0.6902</td>
<td>0.7098</td>
<td>-0.2359 (-0.2)</td>
<td>23%</td>
<td>47%</td>
</tr>
<tr>
<td>Rainfall</td>
<td>-0.0828</td>
<td>-0.1229</td>
<td>0.1482</td>
<td>0.5931 (0.6)</td>
<td>2%</td>
<td>63%</td>
</tr>
</tbody>
</table>

* The number in brackets is the phase ($\phi$) expressed in months.

year. This indicates a delay in the response of $T.\ aripo$ densities to changes in $M.\ tanajoa$ densities. On close examination, Figure 5 shows that the delay in the increase of predator populations is easily recognized when comparing prey peak in April-May and predator peak in July; however, the delay is virtually absent when comparing prey and predator peak.
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peaks in December. Cross-correlation analysis (e.g., Lingeman and van de Klashorst, 1992) does little more than confirming the results discussed above, and is therefore not presented here.

To estimate the phase differences of predator and prey relative to rainfall intensity, it should be kept in mind that the latter had only one cycle per year. Under this regime, the phase shift of *M. tanajoa* varies between 0 and 1 month, whereas that of *T. aripo* is 2 months.

**A mechanistic model of the acarine predator-prey interaction**

To obtain an independent estimate of the phase difference and to guide our discussion on hypotheses explaining the dynamical phenomena observed in the field, we now consider the classical Rosenzweig-MacArthur model (Rosenzweig and MacArthur, 1963; May, 1976) for the interaction between prey (*N*) and predators (*P*):

\[
\frac{dN}{dt} = NH(N) - PF(N)
\]

\[
\frac{dP}{dt} = PGM
\]

Here, \(H(N)\) represents a density dependent per capita growth rate and is given by the logistic function with \(r\) = the intrinsic rate of prey population growth and \(K\) = the carrying capacity:

\[
H(N) = r(1 - N/K)
\]

Here, \(r = 0.21\) day\(^{-1}\), being the average value taken for the range from 22°C to 31°C (Yaninek *et al.*, 1989b) and \(K \approx 3400\) prey mites/plant (expressed in “adult female” equivalents) estimated from Yaninek *et al.* (1991).

A Holling type II functional response gives the form of \(I(N)\) with \(k\) = the maximum predation rate and \(D\) = the prey density at which the per capita predation rate is half its maximum:

\[
I(N) = \frac{kN}{(N + D)}
\]

The maximum predation rate of adult females of the predatory mite, *T. aripo*, equals 15.3 *M. tanajoa* (all prey stages) per day. Adult females of the predatory mite contribute by far the most to the overall predation rate (Sabelis, 1985) and, to a good approximation, they make up c. 10\% of the predator population. This yields \(k = 15.3 \times 0.1 = 1.53\). The value of \(D\) is estimated to be 22 adult equivalents per plant. It is obtained by extrapolating its
value from predation experiments on mixed stage prey, carried out at the scale of a leaf disc: first (1) to the scale of a leaf (255 cm²), then (2) to the scale of the relevant part of the plant (top 10 leaves, representing the home range of *T. uripa* on a cassava plant) and finally (3) by expressing the prey mixture offered in the predation experiments in terms of adult equivalents, assuming a stable age distribution (80% adults, 20% immatures and 69% eggs; Bonato, 1993) and using stage-specific weight data (Yaninek and Gnanvosso, 1993). Note, that this extrapolation assumes a random distribution of the prey population within a plant. This assumption, however, does not hold because *M. tanajoa* exhibits a highly aggregated within plant distribution (Yaninek et al., 1989a; Onzio et al., submitted). For such aggregated distribution of *M. tanajoa*, *D* values will be lower than the estimate given above.

Conversion of prey biomass eaten into new predator offspring is assumed to be linear with coefficient *β* and the per capita death rate of the predator is taken to be a constant *(b)*. This yields:

\[
G_i(N) = -b + \beta H_i(N)
\]

The per capita death rate of the predator is estimated as the inverse of its mean longevity (in the range from 22°C to 31°C). This yields \(b = 0.043\) (Hanna et al., IITA, unpublished data). Finally, \(b\) is set to 0.114 to make \(-b + \beta H_i(N)\) for \(N\) goes to infinity equal to 0.132, which is the intrinsic rate of population growth of *T. uripa*, averaged over a temperature range of 22°C to 31°C (Hanna et al., IITA, unpublished data).

For this set of parameters, the Rosenzweig-MacArthur model shows stable limit cycles. Unfortunately, there are no exact analytical expressions for the cycle period (but see Murdoch et al. (2002) for a lower bound derived for infinitely large prey growth rates and a discrete generation predator-prey model). Based on simulations with the parameterised Rosenzweig-MacArthur model, we obtain a period equal to c. 6 months and a phase difference between predator and prey density equal to c. 1 month. This estimate of the period and the phase difference of the predator-prey cycle is close to that estimated from the time series analysis. However, it should be noted that the estimate of the phase difference matches especially the observed value in the period May-July, but not the one observed in December (Table 2, Figure 5).

Taken together, simulations with the parameterised Rosenzweig-MacArthur model gives room for the hypothesis that there is an endogenous mechanism (i.e. intrinsic to the predator-prey interaction) explaining the existence of a predator-prey cycle in the time series of *T. uripa* and *M. tanajoa* on cassava. If so, this mechanism should be consistent with other characteristic features of the time series. For example, to explain the observed constant prey densities and the decline in predator densities during the year period, consider the following equilibrium expressions (equilibria denoted by an asterisk):
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\[ N^* = D/(k\beta/b - 1) \]

\[ P^* = r N^*(1 - N^*/K)\beta/b \]

These show that this phenomenon can only be brought about by a decline in the per capita growth rate \( (r) \) and/or a decline in the carrying capacity \( (K) \) of the prey population per plant. Such a decline should then also become apparent as an increase in the period and a decline in the amplitude of the predator-prey cycle. The first effect is unlikely due to the phase-resetting impact of abiotic factors such as drought, whereas the second effect is open to test. Figure 6 shows the amplitude estimated from the cycle observed in the second half of each year and this reveals a clear decline in the amplitude of the prey cycle, but not in that of the predator cycle nor in that of the single annual cycle in rainfall intensity. This suggests a declining trend in the per capita growth rate of the prey over the 7-year period, but if so, then one would also expect to see a decline in the amplitude of the predator cycle, which is not the case.

**Figure 6** Annual amplitudes of densities of *M. tanajoa* and *T. aripo*, and of rainfall intensity, starting one year after introduction of *T. aripo* in the cassava field at Ikpînle. For *M. tanajoa* and *T. aripo*, amplitudes are calculated using densities observed in the second half of the year, whereas it was calculated over the whole year for rainfall intensity. Regression equations are: \( y = -4.54x + 43.71, R^2 = 0.878 \) for *M. tanajoa, y = 0.23x + 11.22, R^2 = 0.002* for *T. aripo; y = 0.05x + 2.15; R^2 = 0.009* for rainfall intensity.
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DISCUSSION

In this article we show that – since its release in a cassava field in Benin, West Africa – the exotic predatory mite, *T. aripo*, has overall reduced densities of *M. tanajoa*, and that this predator has persisted for a period of at least 7 years. In addition, we show that annual mean density of predator and prey declined over time. Furthermore, we provide strong evidence with the time series analysis for the presence of two predator cycles per year and at least one prey cycle, and weak evidence for two prey cycles.

To explain these results we consider first the role of abiotic factors. Most likely the troughs in predator population cycles observed generally in March of each year are due to a combination of high temperature, reduced access to water, and hence dehydration, which were shown to cause substantial decline in egg eclosion and overall population growth of *T. aripo* (Bakker, 1993; Hanna et al., HTA, unpublished data). The same explanation applies to troughs of prey population in March (Yaninck et al., 1989a,b; Bonato, 1993), but the prey are probably less affected than the predators because they can still acquire moisture from the plant. Although *T. aripo* seemingly acquires moisture from the plant (Magalhães and Bakker, 2003; Gnanvossoou et al., submitted), the extent to which this plant water use by *T. aripo* can alleviate the effects of low humidity on its biology remains to be shown. In addition to drought effects, prey population densities also decline during periods of heavy rainfall, largely due to wash-off mortality caused by rainfall as well as the impact of higher predator populations occurring during the period of high rainfall intensity (May-July; Figure 1). This increase in predator population density may result from increased access to water, pollen and prey, and from protection against wash-off since the predators hide in the apex during the day and are thus not exposed to rainfall that normally occur in late afternoon. As far as we know, the decline in predator populations after the July peak is not associated with a change in abiotic factors that could cause predator mortality, but it likely occurs as a result of both low prey densities, lower temperatures, and disappearance of maize pollen which is used as alternative food (maize is generally present with cassava between April and July). The subsequent increase in both prey and predator populations (November through February) coincide with a period of increasing temperature (data not shown) and declining rainfall intensity (Figure 1). Apart from *M. tanajoa* wash-off during intense rainfall for which there is compelling evidence (Yaninck et al., 1989a), the effects of other abiotic factors (temperature and humidity) and alternative food (maize pollen) on predator (and prey) populations in the field are largely an extension of life history data from laboratory studies. Rigorous experimental evidence from the field is needed to test the validity of the effects of these abiotic factors (temperature, humidity and alternative food).

The question now arises whether this association between population fluctuations and abiotic factors excludes the possibility that the cycles result from mechanisms intrinsic to the predator-prey system. Our analysis based on the parameterised Rosenzweig-MacArthur model suggests that the predator-prey cycles observed in the cassava field may well be
Internally driven, i.e. they are generated by mechanisms intrinsic to the predator-prey system. This is because the period of the cycles observed in the field (i.e. 6 months) is close to the period predicted from the Rosenzweig-MacArthur predator-prey model provided with precise estimates for the growth and maximum predation rates. Moreover, the phase difference between predator and prey cycles observed in the period from May to July (i.e. approximately 2 months; Figure 5) is also close to that predicted from the predator-prey model. Note that such a phase difference is absent from the field data in the period preceding the dry season, but this may well be due to the onset of drought itself. Thus, apart from this synchronizing effect of drought, the cycles observed may well be genuine (Lotka-Volterra) predator-prey cycles. However, a more quantitative test of our explicit predator-prey model against the data is still to be desired (e.g. Ellner et al., 1997, 1998, 2001; Kendall et al., 1999). Moreover, temperature dependencies of parameters and the consequent seasonal trends may add to the dynamical repertoire of the Rosenzweig-MacArthur predator-prey model (Wollkind et al., 1988a,b; Collings and Wollkind, 1990a,b; Collings et al., 1990).

One of the questions requiring such a quantitative test emerges from the fact that – after the first year of predator introduction – annual mean prey densities stay constant, yet the predator densities decline. This is not expected from the Rosenzweig-MacArthur model. Since the equilibria are unique (assuming constant parameters), changes in one variable (e.g. predator) should be accompanied by changes in the other (e.g. prey) (assuming strong coupling between predator and prey) and the period of the cycles is much less than a year (and thus do not correspond to the time scale at which the trend in predator densities is expressed, i.e. >1 year). The only way to reconcile the difference between the observed trend and this predator-prey model is to assume that there is a trend in either the growth rate or the carrying capacity of the prey population. A decline in either of the two or both causes the equilibrium values of predator density to go down while leaving the density of the prey population unaffected. We cannot exclude a decline in either of the two prey-related parameters. For example, a decline in $K$ may result from a decline in soil fertility and the absence of external fertilizer inputs, and a gradual decline in $r$ may result from a gradually increasing tendency among the prey to feed on older (photosynthetically less active) leaves at night, thereby avoiding encounters with T. aripo predators foraging on the young leaves at night (Magalhães et al., 2002; Onzo et al., 2003). Given that the prey adapted to African conditions without this predator for more than 20 years before the predator entered Africa from South America, it is conceivable that such avoidance behaviour of the prey is favoured by selection starting at predator release. We can think of only one alternative to explanations that take the Rosenzweig-MacArthur predator-prey model as a starting point, and this relates to selection for increased competitive ability of African vs. South-American predatory mites. In fact, there is evidence from field experiments carried out in 1999-2000 that the indigenous predatory mites play a more important role than formerly thought (Onzo et al., 2003).
explanations discussed above seem quite speculative, it should be stressed that they are selected based on their compatibility with the mechanistic predator-prey model used for our analysis, and therefore represent a small subset of the possibilities one would consider without such a model (e.g. predator emigration seems a possibility at first sight, but in the model it would alter only the equilibrium prey density, not the equilibrium predator density). It is expected that testing the model-compatible hypotheses would provide new insight into the mechanisms underlying cycles and trends in observed fluctuations of *M. tanajoa* and *T. aripo* in Africa.

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