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# Second-order density-dependence in a Drosophilid community in La Florida, Santiago, Chile

## Denso-dependencia de segundo orden en una comunidad de Drosofílidos en La Florida, Santiago, Chile.

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## ABSTRACT

Six Drosophilid species were collected monthly from 1984 to 1991 in La Florida, Santiago, Chile. The resulting time-series were tested for delayed (lag 2) density-dependence by traditional autocorrelation analyses and by fitting the data to Turchin's equation. Both methods detected delayed density-dependence for *Drosophila simulans*, *D. subobscura* and *Scaptomyza denticauda*. No delayed density-dependence was shown for *D. melanogaster*, *D. immigrans* and *D. pavani*. Competitive interactions that occur between the species may explain the presence of delayed density dependence in the community.

**Key words:** Drosophilids, Chile, delayed density-dependence, Turchin.

## RESUMEN

Se colectaron mensualmente 6 especies de Drosofílidos en La Florida, Santiago, Chile, entre 1984 y 1991. Se generó así 6 series de tiempo en las que se trató de detectar denso-dependencia de segundo orden, a través de análisis de autocorrelación tradicionales y por ajuste a la ecuación de Turchin. Ambos métodos detectaron denso-dependencia de segundo orden en *Drosophila simulans*, *D. subobscura* y *Scaptomyza denticauda*. Por el contrario, *D. melanogaster*, *D. immigrans* y *D. pavani* no mostraron este tipo de denso-dependencia. Se discuten estos resultados en términos de interacciones competitivas que ocurren entre las especies.

**Palabras clave:** Drosofílidos, Chile, denso-dependencia de segundo orden, Turchin.

## INTRODUCTION

The Drosophilid community of La Florida, in the outskirts of Santiago, has been studied since 1953. However, it came under close attention in 1979, when *Drosophila subobscura* Collin was first detected there (Brncic & Budnik 1987), coinciding with changes in the relative abundances of other Drosophilids in the locality (Brncic & Budnik 1987; Benado & Brncic 1994; Benado et al. 1995; see Ayala et al. 1989 for a summary on the *D. subobscura* colonization of the Americas). This observation led to a systematic sampling of the community, that generated monthly abundance series for 1984-1991 (Benado & Brncic 1994). It turned out that 6 species, viz., *D. melanogaster* Meigen 1830, *D. pavani* Brncic 1957, *D. immigrans* Stutervant 1921, *D. simulans* Stutervant 1919, *D. subobscura* Collin 1936 and *Scaptomyza denticauda* Malloch 1934, made up for more than 95% of the abundances, and that their series displayed significant autocorrelations at several lags (Benado & Brncic 1994).

An immediate, albeit difficult, question is what processes may be regulating the abundances in La Florida. A hypothesis to test is that the population numbers are regulated by density dependent processes. Density-dependence can be defined as a depen-

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dence of per capita growth rate on present and/or past population densities (Reddingius & den Boer 1989). In particular, a single lag dependence between abundance and the per capita growth rate is defined as non-delayed (first order) density-dependence, whereas a dependence for a lag 2 is called delayed (second order) density-dependence (Holyoak 1994). The general issue of detecting delayed versus non-delayed density-dependence in time-series has recently been reviewed by Holyak (1994).

In this paper, I attempt to detect second-order density-dependence in the time-series of the 6 Drosophilids referred to above. A search for delayed density-dependence was suggested by the formal structure of the data, i.e., the autocorrelations at lags >1 (Benado & Brncic 1994; see Results), which are indicative of delayed or lagged statistical density-dependence (Berryman 1992, Royama 1992, Turchin 1990), and by the biology of the species, that, in general, were known to compete pairwise within rotting fruits (Brncic 1987): interspecific competitive interactions are one of the mechanisms that may cause second-order density-dependence (Royama 1992).

## METHODS

The flies were sampled monthly from August 1984 to December 1991 over fermented banana baits in an old orchard in La Florida, in S. Santiago. In each occasion, 6 to 8 baits were placed directly on the ground early in the morning. Collections were made by sweeping a net over the baits around sunset (Benado & Brncic 1994). I emphasize that all the collections were made by the same individual under identical sampling conditions.

First, I estimated the autocorrelation function (ACF) and the partial autocorrelation function (PACF), as well as their standard errors (Box & Jenkins 1976; Diggle 1990; Royama 1992), to diagnose the broad lag structure of the abundance series. The ACF identifies whether the series is stationary or not (Box & Jenkins 1976), and if particular periods are present (Berryman 1992, Royama 1992), whereas the PACF gives an estimate of the lag of the density-dependence (Berryman 1992, Royama 1992). Second, I tested for delayed density-dependence by assuming a modified Ricker equation of the form:

$$N_t = N_{t-1} \exp(r_o + a_1N_{t-1} + a_2N_{t-2} + e_t),$$

where $N_t$ is the population abundance in month t, $e_t$ is an exogenous random component, and $r_o$, $a_1$, and $a_2$ are parameters (Turchin 1990). I estimated the parameters by regressing $\ln(N_t / N_{t-1})$ on $N_{t-1}$ and on $N_{t-2}$ in a stepwise manner. In terms of the model, $a_1 = 0$ tests the null hypothesis that there is no direct density-dependence, and $a_2 = 0$ tests the null hypothesis that there is no lagged density-dependence. As indicated by Royama (1992), I did not search for density-dependence at lags>2.

It was shown in a previous paper that the series for all the species had no trends, except for *D. immigrans*, that had a linear positive one (Benado et al. 1995). I notice that differencing, the standard and elegant way of detrending time series is not compatible with Turchin's equation (Saucy 1994). Thus, for *D. immigrans*, I detrended the data by substracting the linear trend from the original series and afterwards I carried out the regressions both for the original and for the detrended data. The results were the same and I report the analysis for the former.

I used the Trend module and the regression procedure of SPSS to perform all the analyses.

## RESULTS

The 89 monthly abundances for all the species are graphed in Figs. 1 and 2, and their ACFs and PACFs are set out in Figs. 3 and 4, respectively. All the species displayed significant autocorrelations at several lags. In particular, the ACFs indicate strong periodicities for all the species, except for *D. melanogaster*; this is also apparent in their abundances. *S. denticauda*, *D. subobscura*, and *D. simulans*, displayed a significant partial correlation at lag 2, making them likely candidates to show delayed density-dependence by Turchin's test.

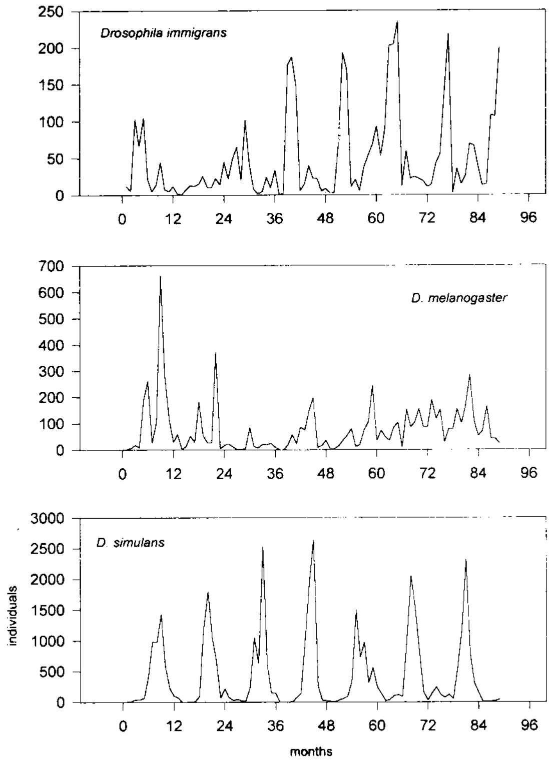

*Fig. 1:* Monthly abundances. Notice the vertical axis.

Abundancias mensuales. Nótese la escala vertical.

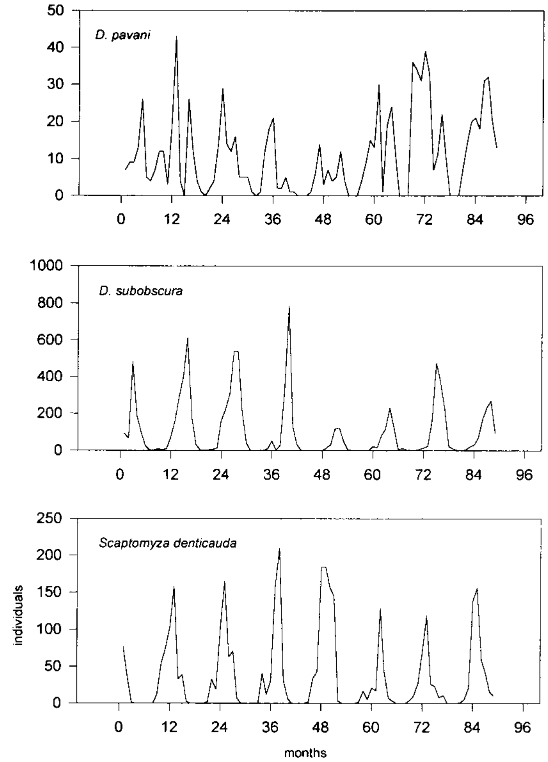

*Fig. 2:* Monthly abundances. Notice the vertical axis.

Abundancias mensuales. Nótese la escala vertical.

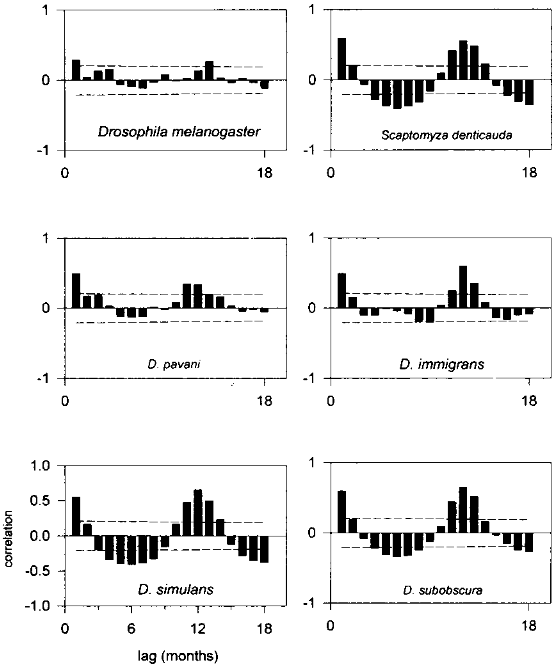

*Fig. 3:* Autocorrelations. Dashed lines: 95% confidence limits.

Autocorrelaciones. Líneas quebradas: límites de confianza al 95%.

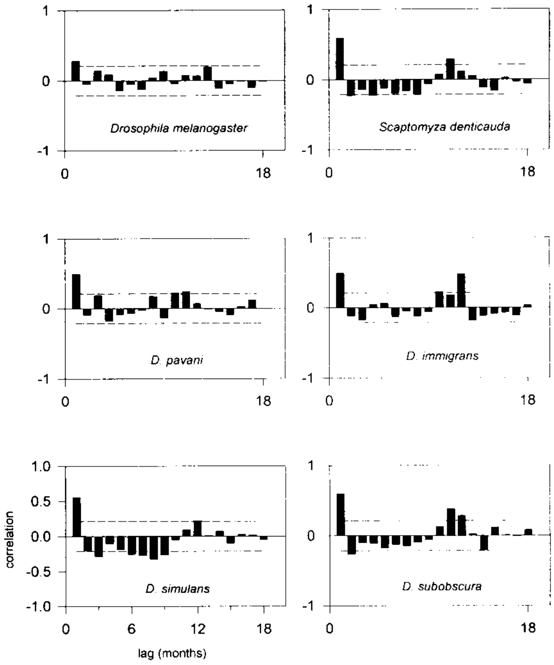

*Fig 4:* Partial autocorrelations. Dashed lines: 95% confidence limits.

Autocorrelaciones parciales. Líneas quebradas: límites de confianza al 95%.

The results of fitting Turchin's equation are shown in Table 1. The regression on $N_{t-1}$ was significant in all the cases, indicating direct density-dependence. Adding the extra term $N_{t-2}$ improved the fit significantly just for *S. denticauda*, *D. subobscura*, and *D. simulans*. Thus, these 3 species showed statistical lagged density-dependence.

## DISCUSSION

It has been pointed out that statistical tests of density-dependence test for a "return tendency" in population size and that they do not test for specific density-dependence mechanisms (Hanski et al. 1993, Lima 1995, Solow & Steele 1990). Clearly, information on what is regulating the population is a distinct issue from the detection of return tendencies.

In principle, if density dependent mechanisms are operating, generation times will per se generate numerical responses at specific lags. Lab estimates for generation times that roughly apply to the field conditions in La Florida (Benado & Budnik 1995) are 2 weeks for *D. melanogaster* and *D. simulans* (Par-

TABLE 1

Parameters of Turchin's equation for six Drosophilids.

Parámetros de la ecuación de Turchin para seis especies de Drosofílidos.

Equation I: regression on $N_{t-1}$ only. Equation II: regression on $N_{t-1}$ and on $N_{t-2}$ in a stepwise fashion. $N_t$, $r_0$, $a_1$, and $a_2$ are defined in the text. se: standard error for the parameter in the corresponding equation. *: 10% significance level; **: 5% significance level; ***: 1% significance level.

Equation I: regresión únicamente contra $N_{t-1}$. Equation II: regresión por pasos, sucesivamente contra $N_{t-1}$ y $N_{t-2}$. $N_t$, $r_0$, $a_1$ y $a_2$ se definen en el texto. se: error estándar del parámetro en la ecuación respectiva. *: significación estadística al 10%; **: significación estadística al 5%; ***: significación estadística al 1%.

| SPECIES | EQUATION | $r_0$ | $a_1$ | $a_2$ | $R^2$ |
|---|---|---|---|---|---|
| *D. melanogaster* | I | 0.5329*** | -0.0064*** | | 0.220 |
| | se | 0.1667 | 0.0013 | | |
| | II | 0.5024*** | -0.0066*** | 0.0005 | 0.222 |
| | se | 0.1850 | 0.0014 | 0.0014 | |
| *S. denticauda* | I | 0.2687* | -0.0075*** | | 0.105 |
| | se | 0.1570 | 0.0024 | | |
| | II | 0.4118*** | -0.0021 | -0.0090*** | 0.203 |
| | se | 0.1555 | 0.0028 | 0.0028 | |
| *D. pavani* | I | 0.5102*** | -0.0426*** | | 0.177 |
| | se | 0.1607 | 0.0100 | | |
| | II | 0.6230*** | -0.0332*** | -0.0191* | 0.204 |
| | se | 0.1726 | 0.0113 | 0.0114 | |
| *D. immigrans* | I | 0.5432*** | -0.0102*** | | 0.210 |
| | se | 0.1628 | 0.0021 | | |
| | II | 0.5379*** | -0.0103*** | 0.0002 | 0.210 |
| | se | 0.1741 | 0.0025 | 0.0025 | |
| *D. simulans* | I | 0.2824* | -0.0006*** | | 0.083 |
| | se | 0.1666 | 0.0002 | | |
| | II | 0.4329** | -0.0002 | -0.0007*** | 0.174 |
| | se | 0.1666 | 0.0002 | 0.0002 | |
| *D. subobscura* | I | 0.2221 | -0.0021** | | 0.065 |
| | se | 0.1637 | 0.0008 | | |
| | II | 0.3844** | 0.0003 | -0.0040*** | 0.219 |
| | se | 0.1557 | 0.0010 | 0.0010 | |

sons & Stanley 1981), 2.5 weeks for *D. immigrans* (op. cit.), 3-5 weeks for *D. subobscura* (Benado & Budnik 1995), and 3-7 weeks for *D. pavani* (op. cit.). The figures in general are compatible with the observed lags.

Other processes that take place in the field may modify the basic pattern set by the generation times. A clue is the paper by Brncic (1987), who worked exactly in the same spot where the present data were gathered. He found that *D. immigrans*, *D. melanogaster*, *D. simulans*, and *D. subobscura* competed in pairs at larval stages within the rotting pulps of several fruits, when he compared the number of flies reared under mono- and bi-specific conditions (see also Budnik & Brncic 1983, Budnik & Cifuentes 1989, Benado & Budnik 1995, for experimental competition studies).

Competitive interactions between species can be represented as equations with a lag 2-response that can generate complex cyclic trajectories (Royama 1992), and my analysis bears out this prediction for *D. simulans* and *D. subobscura*. It is worth noticing that periodicity of other insects has been explained by interactions between species rather than by seasonality of density independent factors (e.g., Berryman 1996), so the results for the two species above are consistent with that fact. Leaving aside both *D. pavani* and *S. denticauda*, whose natural substrates and life cycles are poorly known, the question remains open for *D. immigrans* and *D. melanogaster*, that show competitive interactions in the field and no responses at lag 2 (Figs. 3 and 4). I notice that in studies of this kind, the choice of a specific model to test for density-dependence is not easy, since it should ideally be derived from first principles, or realistic assumptions about the underlying ecological processes (Berryman 1992). I picked up Turchin's equation simply because it dealt both with direct and delayed density-dependence and because I knew that the species interacted, thus making it a reasonable choice; as a matter of fact, it has been used extensively to detect delayed density-dependence in insects (Turchin 1990, Woiwod & Hanski 1992) and in voles (Saucy 1994). Yet, for *D. immigrans* and *D. melanogaster*, delayed density-dependence was detected neither by Turchin's equation nor by the autocorrelation analysis, making it unlikely that the negative result was due to the model's idiosyncrasy. Given the rather scarce knowledge about the natural history of the species involved in this study, I feel that speculating on how the competitive interactions detected in the field translate into specific numerical responses is unwarranted, but it seems safe to say that these interactions are not regulating *D. immigrans* and *D. melanogaster*.

I further notice that the issue in La Florida about density regulating mechanisms around the year is unsettled, since little is known about the life cycle of the species out of the fruiting season; several of the species reported here are known to overwinter as adults with retarded reproductive development (Begon 1976, Begon & Shorrocks 1978, Hoffman & Watson 1993, Izquierdo 1991, Kimura & Beppu 1993); this pattern of protracted overwintering generations with no new recruits will limit the population numbers, because the individuals will be coming from a closed Winter pool and this may translate into statistical density-dependence, not necessarily implying that density dependent mechanisms are operating. Clearly, this suggests an alternative hypothesis that the periodicity observed for 5 of the 6 species is generated in a density independent way by seasonal variability in climatic factors. Given the present knowledge of the biology of the species at the local level, this remains an open and interesting question.

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