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Correlations between the abundances of fruits and frugivorous birds: the effect of temporal autocorrelation

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INTRODUCTION

Many studies have documented seasonal significant correlations between fruit availability and avian frugivore abundance within years (Levey, 1988; Jordano, 1992 and references therein). However, the time-autocorrelated nature of these types of data has not been explicitly accounted for, and therefore the relationship may be spurious. Temporal autocorrelation may happen, for instance, because the number of both birds and fruits cannot increase significantly after a certain date in winter (Debussche & Isenmann, 1992). Temporal autocorrelation is a form of pseudoreplication (*sensu* Hulbert, 1984) because the observations are not independent and therefore a new observation contributes but a fraction of a degree of freedom (Legendre & Fortin, 1989).

Several techniques allow to introduce time in the model. Many of these techniques rely on corrections in the standard error of the parameter estimates of the simple linear regression, multiple regression, t-test and one-way analysis of variance in presence of autocorrelation. The parameter estimations are performed by maximum likelihood or by permutational methods (see Legendre & Fortin, 1989; Legendre, 1993 for a review). The significance test used in the canonical ordination, as well as the Mantel test are two permutational methods which allow to model the effect of the data's temporal structure. Mantel test is used to distinguish among the following seasonal relationships between the abundances of fruits and frugivorous birds:

Model 1: Fluctuations in the abundance of frugivores are a result of temporal fluctuations in fruit abundance.

TIME ⟶ FRUITS ⟶ FRUGIVORES

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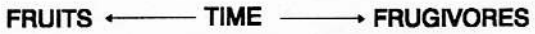
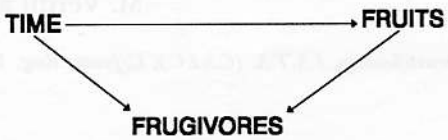
Model 2: Fluctuations in the abundance of frugivores have a temporal component which is independent from the temporal fluctuations in fruit abundance.



Model 3: Fluctuations in the abundance of frugivores are partly determined by the fluctuations in fruit abundance and partly by other temporal factors not explicitly identified in the model.



Mantel test allows to determine which model is best fitted by the data. Mantel statistic is the sum of the cross-products of the corresponding distances in two matrices which is tested against a distribution of values obtained by repeated random permutations of the rows and columns of one of the distance matrices and recomputation of the coefficient (LEGENDRE, 1993). SMOUSE *et al.* (1986) developed an extension of the Mantel statistic to test causal models by means of the correlation between two matrices controlling for the effect of a third matrix.

The aim of this study is to test the kind of relationship between the changes in the abundance of frugivorous birds and the fluctuations in fruit abundance taking into account the possible temporal autocorrelation within the wintering season.

MATERIAL AND METHODS

This study was carried out in a mediterranean sclerophyllous scrubland located in the Natural Park of L'Albufera, Valencia, Spain (39°20′N, 00°02′E; 0 m a.s.l.) during the wintering season (October-March) of 1989-1990 and 1990-1991.

Bird abundance was estimated using transect counts (EMLEN, 1971). Every two weeks approximately, an observer recorded the birds sighted within a 500 m transect with three parallel census bands of 15 m to each side. Every census was always performed by the same observer, two hours after sunrise and avoiding adverse climatological conditions. The species considered in this study were all seed-disperser passerines, the trophic category which shows the greatest dependence on fruit resources (HERRERA, 1984). These species were *Erithacus rubecula, Sylvia atricapilla, S. melanocephala, Turdus merula, T. philomelos* and *Phoenicurus ochruros. T. philomelos* and *P. ochruros* were present in such a low density that it was not possible to compute their detectability coefficients (EMLEN, 1971) and were excluded in subsequent analysis.

Fruit abundance was estimated at the same dates that bird counts, in six 28×1.25 m plots. The species considered were *Myrtus communis, Smilax aspera* and *Pistacia lentiscus*, the three plant species that provide most of the fruits consumed by the birds during autumn-winter in the study site (VERDU, pers. obs.). All the ripen fruits of these species were counted in each plot.

The three models were tested, taking into account the possible time autocorrelation, by means of approximate Mantel t-tests and partial Mantel tests (LEGENDRE & FORTIN, 1989). In these tests, the

variable time was the number of days since the censuses began. Approximate Mantel t-tests were used to test for temporal autocorrelation in frugivorous bird abundance and in fruit abundance and to test the correlation between the abundances of fruits and frugivorous birds. Temporal autocorrelation in fruit abundance was tested performing the approximate Mantel t-test between the distance matrices of fruit abundance and time. Temporal autocorrelation in bird abundance was tested performing the approximate Mantel t-test between the distance matrices of bird abundance and time. Correlation between the abundances of fruits and frugivorous birds was tested performing the approximate Mantel t-test between the distance matrices of bird abundance and fruit abundance.

Partial Mantel statistics were used to test causality relations between two variables controlling for the effect of the third variable. Computations to test the partial Mantel statistic between two matrices (A and B) controlling for the effect of the third matric (C) were made following LEGENDRE & FORTIN (1989): (1) A new matrix A′ is computed with the residuals of the linear regression between A and C; (2) Likewise, B′ is computed with the residuals of the linear regression between B and C; (3) An approximate Mantel t-test is run between A′ and B′.

The abundances of fruits and birds were log-transformed to fulfill the linearity assumption of the model (LEGENDRE & FORTIN, 1989).

Bonferroni procedure has been used to prevent the accumulation of statistical errors (KRAUTH, 1988).

The first of the three models would be supported if the partial Mantel statistic between time and frugivorous bird abundance, controlling for the effect of fruit abundance, does not differ significantly from zero. The second model would be supported if the partial Mantel statistic between the abundances of fruits and frugivorous birds, controlling for the effect of time, does not differ significantly from zero. The third model would be supported if all three approximate Mantel t-tests (fruit abundance autocorrelation, bird abundance autocorrelation and fruit-frugivorous bird abundances correlation) and all three partial Mantel tests are significantly different from zero.

RESULTS

The abundances of both ripen fruits and frugivorous birds showed a decreasing trend over the two periods of study (fig. 1).

During the first wintering season (1989-1990), approximate Mantel t-tests showed that fruit abundance was highly time-autocorrelated ($t=4.89$; $p<0.01$), and so was frugivorous bird abundance ($t=3.63$; $p<0.01$). There was also a highly significant correlation between fruit and frugivorous bird abundances ($t=4.46$; $p<0.01$).

Among the three partial Mantel tests only the statistic describing the relation between time and frugivorous bird abundance, controlling for the effect of fruits, is not significantly different from zero (table I). Thus, the first model that states that fluctuations in the abundance of frugivores are caused by temporal fluctuations in fruit abundance is supported by the observed data.

During the 1990-1991 wintering season, the sample size was too small to calculate Mantel tests due to the early depletion of fruits (fig. 1).

DISCUSSION

The results of this study support the hypothesis that it is necessary to account for temporal autocorrelation. Although there was a parallel decreasing trend of

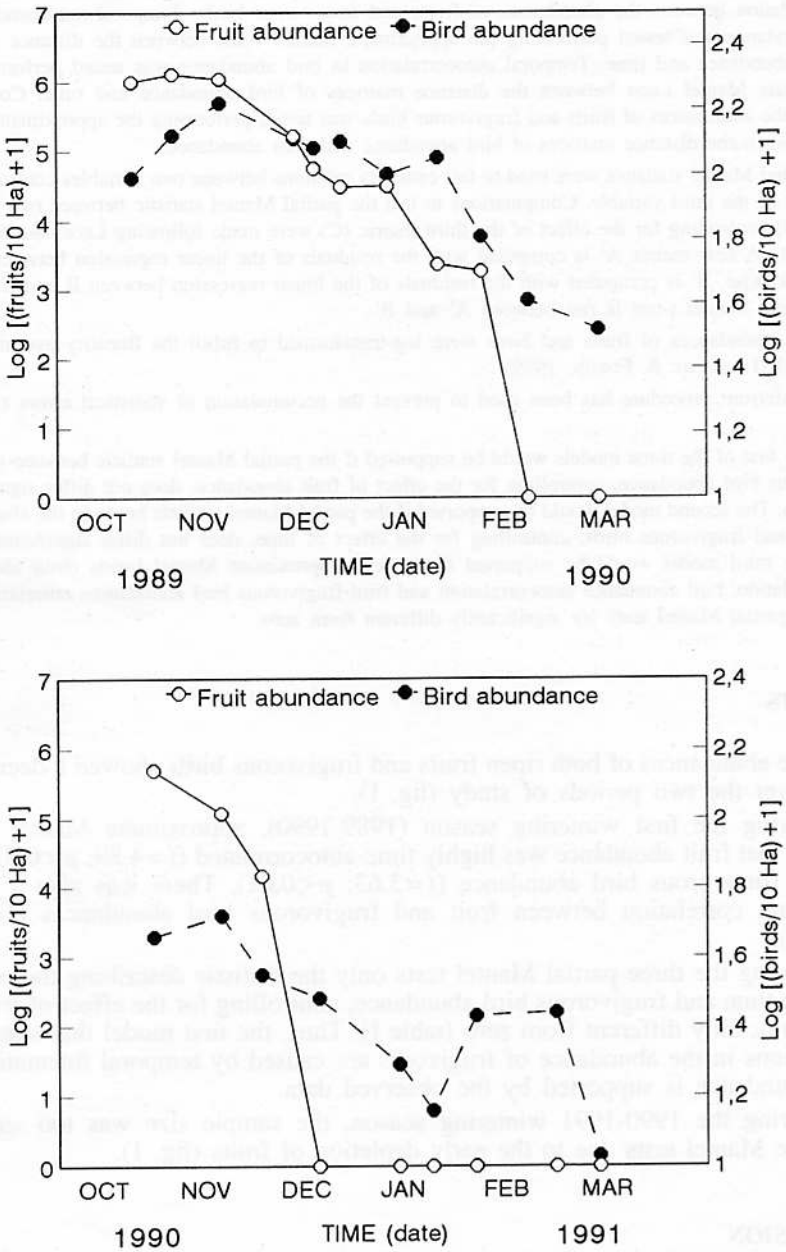


FIG. 1. – Abundance of fruits and frugivorous birds during the 1989-1990 and 1990-1991 wintering seasons.

TABLE I. – *Partial Mantel tests, controlling for the effect of the third matrix, and the associated probabilities corrected by Bonferroni procedure.*

	Frugivorous bird abundance	Fruit abundance
Fruit abundance	$t = 3.64$*	–
Time	$t = 1.14$	$t = 3.15$*

* $p < 0.01$

both fruit and frugivorous bird abundances during the wintering season, both variables were highly time-autocorrelated. Therefore, the observations are not independent and the relationship may be spurious. However, after controlling statistically for the effect of time, the relation between the abundances of fruits and frugivores remained significant, indicating that fluctuations in the abundance of frugivorous birds are non-spuriously correlated with temporal fluctuations in fruit abundance. The interpretation of these parallel fluctuations in fruit and frugivorous bird abundances can be that frugivores are able to adapt to changing resource levels, as shown in tropical sites (LOISELLE & BLAKE, 1991). Foraging efficiency is enhanced by local movements tracking resource levels and selecting the best patches (CHARNOV, 1976; MARTIN, 1985).

Following the model found above, if fruit abundance is around zero (as it was during a long period in 1990-1991), the abundance of frugivorous birds should also be zero if frugivorous birds were feeding on fruits exclusively. However, data showed that bird abundance never decreased to zero, suggesting that there is a lower threshold in the model. When fruit abundance is lower than the threshold, birds could either leave the patch or diversify their diet. In the first case, erratic movements of birds tracking fruits should be observed. In the second case, the fluctuations in frugivorous bird abundance should be explained with other variables (i.e. insect abundance, snail abundance). Without these new data and their temporal variation it is not possible to infer if the response of frugivorous birds to the scarcity of fruits is a shift in the diet or erratic movements among patches. Complex models taking into account not only fruit abundance but other resources and their temporal variability are needed to explain the fluctuations in frugivorous bird abundance in periods of fruit scarcity.

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