

Population dynamics of the bark beetle *Phloeotribus scarabaeoides* Bernard (Coleoptera: Scolytidae), a pest of African olive orchards in Morocco

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Studies on mortality in the four annual generations of the bark beetle *Phloeotribus scarabaeoides* Bernard were conducted in a Moroccan olive orchard by placing cut logs for oviposition. Neither the density of eggs and larvae per maternal gallery nor the density of maternal galleries per dm² of cut log affected the mortality of the eggs, larvae or pupae. The density of reproducing females on cut logs reduced the number of adult females that successfully established maternal galleries. A model, based on the information presented, showed that beetle populations were regulated by density-dependence in the level of female attack, that stabilized the population at 2–3 females/dm² of cut log.

Key words: *Phloeotribus scarabaeoides*, Coleoptera, Scolytidae, population dynamics, models, olives, Morocco.

INTRODUCTION

The bark beetle *Phloeotribus scarabaeoides* Bernard (Coleoptera: Scolytidae) is a pest of olive trees throughout northern Africa, the Near and Middle East and Mediterranean Europe (Arambourg 1986). In the Taroudant region of Morocco, *P. scarabaeoides* is one of the principal pests and is capable of reducing olive fruit production by 60%, and occasionally also kills the trees (Benazoun 1992).

In the Taroudant region, olive trees are constantly exposed to attack by *P. scarabaeoides* because of the semiarid climate and insufficient cultural control. The beetles reproduce in the trunks and branches of drought-stressed olive trees and in cut logs left in the orchards. The adults reproduce in subcortical galleries excavated in these tissues, but also feed on living trees. The galleries in which reproduction takes place are the double transverse type, with eggs laid by the female on both sides of the two arms of the gallery. Upon hatching, the larvae excavate individual secondary galleries that radiate at right angles to the maternal galleries. Once mature, the larvae construct pupal cells in the sapwood. Adults emerge from the reproduction galleries and disperse to other olive twigs, where they excavate feeding galleries (Benazoun 1992).

In Morocco, there are four generations of *P. scarabaeoides* per year, in spring (February to June), summer (April to October), the summer-autumn

generation (June to December) and winter (August to May) (Benazoun & Oubrou 1995).

In this paper available information is integrated into a model, together with new data on the fecundity and mortality of the different life stages of the beetle during the four annual generations. The model is used to determine the relative importance of the different factors that affect beetle populations and to determine their abundance in Moroccan olive orchards.

MATERIAL AND METHODS

Beetle populations were monitored in an olive orchard in the Taroudant region (30.21N 08.56W), 80 km west of Agadir. The orchard harbours some 5000 olive trees, that are seldom subjected to cultural control.

Six logs, measuring 30–50 × 4–8 cm, were obtained from the pruning of healthy olive trees and placed in the orchard at different time intervals. Log placement was carried out in February, April, June and August of 1990, 1992 and 1994, to coincide with colonization by adult bark beetles and parasitoids from each of the four annual generations. The logs remained in the field from the time of attack until the emergence of the next generation of beetles and parasitoids. The logs were then transferred to the laboratory where the numbers of emerged adult beetles and parasitoids were

Table 1. Mean mortality of eggs, larvae and pupae, fecundity of adult females and emergence of adults and parasitoids in each generation of *Phloeotribus scarabaeoides* during 1990 (A), 1992 (B) and 1994 (C).

	Generations							
	Spring		Summer		Summer–Autumn		Winter	
A (1990)	% Mortality	C.V.	% Mortality	C.V.	% Mortality	C.V.	% Mortality	C.V.
Eggs	26.0	97.7	28.8	98.1	24.4	59.0	27.1	50.4
Larvae	26.4	65.9	86.9	25.0	20.9	43.8	23.2	51.8
Pupae	37.4	90.2	52.7	7.4	14.8	83.2	19.8	103.5
Adult females	Fecundity	S.D.	Fecundity	S.D.	Fecundity	S.D.	Fecundity	S.D.
	48.3	23.1	28.6	12.1	60.6	14.9	57.5	10.4
Adults/dm ²	Emergence	S.D.	Emergence	S.D.	Emergence	S.D.	Emergence	S.D.
	19.6	22.7	4.5	1.8	186.5	114.0	86.2	65.6
Adults/gallery	17.9	17.8	3.7	0.3	32.7	13.9	27.0	12.8
Parasitoids/dm ²	2.2	3.9	1.0	0.8	33.2	28.0	22.8	17.6
B (1992)	% Mortality	C.V.	% Mortality	C.V.	% Mortality	C.V.	% Mortality	C.V.
Eggs	32.4	79.4	27.5	40.6	30.6	22.7	18.3	57.8
Larvae	40.2	40.8	30.8	52.5	27.3	15.3	19.9	63.0
Pupae	8.0	17.3	19.5	18.1	32.5	30.2	23.8	103.4
Adult females	Fecundity	S.D.	Fecundity	S.D.	Fecundity	S.D.	Fecundity	S.D.
	45.9	13.6	54.3	20.5	57.5	16.4	63.8	17.3
Adults/dm ²	Emergence	S.D.	Emergence	S.D.	Emergence	S.D.	Emergence	S.D.
	63.7	28.1	71.4	72.0	116.8	48.4	71.6	43.8
Adults/gallery	16.5	4.7	24.6	18.6	19.8	7.3	32.0	15.7
Parasitoids/dm ²	21.2	22.1	23.9	25.5	36.6	16.2	31.8	29.2
C (1994)	% Mortality	C.V.	% Mortality	C.V.	% Mortality	C.V.	% Mortality	C.V.
Eggs	24.7	14.7	28.9	54.8	17.9	48.6	35.6	40.8
Larvae	27.6	61.3	50.2	91.0	50.7	39.4	25.3	51.8
Pupae	25.8	40.6	28.0	90.6	15.9	46.2	20.5	106.8
Adult females	Fecundity	S.D.	Fecundity	S.D.	Fecundity	S.D.	Fecundity	S.D.
	54.1	9.9	37.7	20.9	46.3	8.3	49.2	20.0
Adults/dm ²	Emergence	S.D.	Emergence	S.D.	Emergence	S.D.	Emergence	S.D.
	89.2	50.7	8.6	6.7	36.5	32.6	46.4	29.7
Adults/gallery	23.3	11.3	13.9	21.7	15.0	4.8	19.3	13.5
Parasitoids/dm ²	30.5	9.2	6.5	12.9	8.2	10.1	13.9	10.4

determined by the number of exit holes. Parasitoid emergence was indicated by exit holes that were smaller than those of the beetles. The logs were then dissected to determine the number and density (per dm²) of reproduction galleries, eggs (number of egg chambers), larvae (number of larval galleries) and pupae (number of pupal chambers), to calculate the mortality at each developmental stage.

RESULTS

The mean fecundity of adult females, mean mortality of eggs, larvae and pupae and mean emergence of adults were determined for each generation (Table 1). These ranged from 46.4–86.2 adults/dm² in the fourth generation (winter) during the years studied. Between 13.9–31.8 parasitoids/dm² also emerged from the logs of this

Table 2. Analysis of the correlations between egg, larval and pupal mortalities and the density of eggs and larvae per maternal gallery and maternal galleries per dm². For every r^2 value, $P > 0.05$.

Generations	Eggs/gallery			Larvae/gallery			Gallery/dm ²		
	1990	1992	1994	1990	1992	1994	1990	1992	1994
% egg mortality in:									
spring	0.052	0.479	0.073	—	—	—	0.150	0.373	0.081
summer	0.034	0.487	0.073	—	—	—	0.158	0.48	0.247
summer-autumn	0.158	0.003	0.212	—	—	—	0.069	0.203	0.106
winter	0.131	0.172	0.090	—	—	—	0.314	0.459	0.010
% larval mortality in:									
spring	0.121	0.487	0.469	0.004	0.461	0.429	0.015	0.112	0.469
summer	0.033	0.496	0.306	0.119	0.500	0.218	0.099	0.509	0.090
summer-autumn	0.092	0.292	0.480	0.231	0.195	0.457	0.105	0.498	0.009
winter	0.019	0.027	0.010	0.006	0.038	0.014	0.422	0.130	0.376
% pupal mortality in:									
spring	0.079	0.437	0.429	0.319	0.565	0.454	0.038	0.497	0.468
summer	0.403	0.326	0.213	0.438	0.369	0.200	0.402	0.472	0.497
summer-autumn	0.443	0.376	0.063	0.463	0.490	0.016	0.491	0.175	0.503
winter	0.068	0.064	0.143	0.491	0.169	0.137	0.461	0.113	0.055

generation.

The influence of the densities of eggs, larvae and maternal galleries on the mortality of the eggs, larvae and pupae during the four annual generations was analysed (Table 2). Neither the density of eggs or larvae per maternal galleries nor the density of maternal galleries/dm² of cut log were significantly correlated ($P > 0.05$) with any of these mortalities during the different generations.

Lozano *et al.* (1996a) suggested that the proportion of adult female *P. scarabaeoides* that successfully established maternal galleries declined at higher adult densities because of interference or intraspecific competition. This density-dependent relationship was defined by the equation: $\mu = \beta \log(n) + 48.06$, where μ = proportional female loss, β = the coefficient of density-dependence acting on females (calculated as 27.75) and n = the number of females/dm².

The effect of mortality of the different life-stages on the population dynamics of *P. scarabaeoides* was analysed using the population model of Lozano *et al.* (1993). The model defined the following functions for each generation of beetles: $E_{t+1} = f(n_t)$; $L_{t+1} = f(E_{t+1})$; $C_{t+1} = f(L_{t+1})$; $A_{t+1} = f(C_{t+1})$; where E_t = number of egg/dm² at time t , n_t = number of females/dm² (= number of galleries/dm²), L_t = number of larvae, C_t = number of pupae and A_t = number of adults per dm². The equations defined the following: $E_{t+1} = p(n_t)$; $L_{t+1} = s_e(E_{t+1})$; $C_{t+1} = s_l$

(L_{t+1}); $A_{t+1} = s_c(C_{t+1})$; where p = fecundity of females, s_e = egg survival, s_l = larval survival and s_c = pupal survival. The values of these variables are indicated in Table 1.

Taking into account the observed sex ratio of 1:1, the number of females/dm² (n_{t+1}) = $0.5 A_{t+1}$. Considering the establishment of adult females on the cut logs, before reproduction, the number of females/dm² (n_{t+1}) = $(1-\mu) n_{t+1}$, where, according to Lozano *et al.* (1996a), $\mu = \beta \log n_{t+1} + 48.06$ with $\beta = 27.75$.

Starting with n_t females, we then calculated the number of females for the next generation (n_{t+1}) using the model as follows: n_{t+1} (spring generation) = $f(n_t)$, n_{t+2} (summer generation) = $f(n_{t+1})$. By replacing the value of n_t with n_{t+1} , the numerical changes in the second and subsequent years could be calculated by iteration.

Simulations estimated over a 20-year period revealed that the beetle population was stable at an equilibrium of between 2.2–3.3 reproducing females/dm² (Fig. 1). Analysis of the sensitivity of the model to changes in parameter values suggested that variations in the mortality of the developmental stages have a mild effect on the amplitude of the oscillations and the equilibrium level, with no influence on stability (Fig. 2). Although changes in the density-dependence of adult female mortality did not influence stability, they had a marked effect on equilibrium levels.

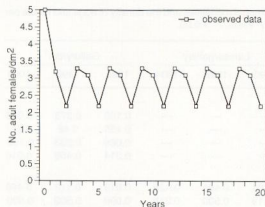


Fig. 1. The number of reproducing adult females/dm² of *Phloeotribus scarabaeoides* estimated by the model over 20 years.

Decreases in the density-dependence coefficient (β), raised the equilibrium level (Fig. 3).

DISCUSSION

Previous studies on the population dynamics of *P. scarabaeoides* on the Iberian Peninsula (Lozano *et al.* 1996a,b, 1997) indicated one annual generation, with the population stabilizing without oscillations at an equilibrium density of 3.1 reproducing females/dm². Density-dependence in the rates at which breeding females established in the logs was the main factor regulating the population.

Using the data from Morocco, where *P. scarabaeoides* has four annual generations, the model predicted that populations should stabilize annually at an oscillating equilibrium density of 2.2–3.3 reproducing females/dm², that represents an adult emergence density of 46.1–104.0/dm² and 15.9–35.9/gallery. These predicted densities were a fairly accurate reflection of the observed emergence densities of 46.4–86.2/dm² and 19.3–32.0/gallery. Direct density-dependence in the rates at which breeding females establish in the logs also appeared to regulate Moroccan populations. These laboratory data must be confirmed by field experiments.

The larvae of *P. scarabaeoides* are attacked by several species of Hymenoptera parasitoids during their development in the cut logs (Benazoun & Oubrou 1995). During this study, between 1.0 and 36.6 parasitoid emerged per dm² of cut log, during each generation of *P. scarabaeoides* (Table 1). The effect of parasitism on population densities

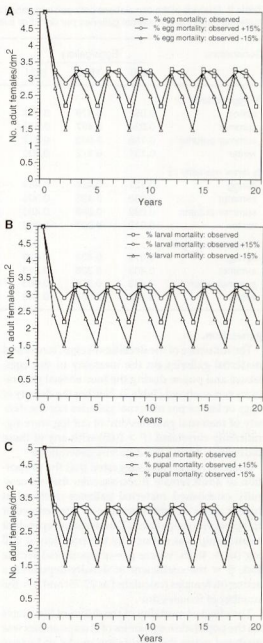


Fig. 2. The number of reproducing adult females/dm² of *Phloeotribus scarabaeoides* estimated by the model over 20 years, following changes of $\pm 15\%$ in the observed percentage mortality of eggs (A), larvae (B) and pupae (C) in the four annual generations.

could not be determined as it could not be distinguished from other factors causing larval mortality. Future studies on the role of parasitism are

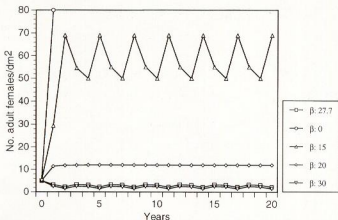


Fig. 3. The number of reproducing adult females/dm² of *Phloeotribus scarabaeoides* estimated by the model over 20 years, following changes in the coefficient of density-dependence acting on females (where $\beta = 0, 15, 20, 27.75$ and 30).

planned to clarify the effect on mortality.

This predictive model constitutes a framework to determine new factors that could influence the abundance of beetle populations, and those which could be used to control them (e.g. parasitism). It would be theoretically possible to define an appropriate Integrated Pest Management system because the beetle population densities in the field,

after the application of different methods of control, could be predicted.

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