

Analysis of *Prinobius myardi* Mulsant population dynamics in a Mediterranean cork oak stand

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Abstract. The dehesa is a silvopastoral system of a high economic and ecological significance in the Iberian Peninsula that is protected under the EEC/92/43 Habitat Directive. One of the most serious problems the dehesa system is currently facing is oak decline. This tree decay process is largely caused by three xylophagous cerambycids of which *Prinobius myardi* is the least known. In this study, we used a capture–mark–recapture method to identify the models best fitting the behaviour of this species with a view to estimating basic population parameters such as survival rate (ϕ), recapture rate (p) and transiency index (T). *Prinobius myardi* adults were captured by hand following visual detection in the trees of a cork oak (*Quercus suber*) plot located in the close vicinity of the Doñana National Park (SW Spain). Males exhibited a constant survival rate exceeding 85.4% throughout their flight period, a maximum transiency index of 1.82% and a recapture rate ranging from 42.50% to 76.90%. These results are suggestive of a sedentary behaviour in *P. myardi* males. By contrast, the small number of females captured precluded calculation of the previous parameters for this gender; in any case, field observations revealed a fleeing, less sedentary behaviour with respect to the males.

Résumé. Analyse de la dynamique de population de *Prinobius myardi* Mulsant dans un peuplement de chêne-liège. La dehesa est un système sylvopastoral de grande importance économique et écologique pour la Péninsule Ibérique. Elle est protégée par la directive «Habitat» EEC/9243. Un des problèmes les plus sérieux qui menace le système de la dehesa est le déclin du chêne-liège (*Quercus suber*). Ce processus de dégradation de cet arbre est largement dû à trois cérambycides parmi lesquels *Prinobius myardi* est le moins connu. Dans cette étude, nous avons utilisé une méthode de capture-marquage-recapture pour identifier le modèle qui s'adapte le mieux au mode de vie de cette espèce. Dans ce but, on a estimé les paramètres de base comme le taux de survie (ϕ), le taux de recapture (p) et l'index de transition (T). Les *Prinobius myardi* adultes ont été capturés à la main, après une détection à vue, dans des placeaux de chêne-liège au voisinage du Parc National de la Doñana (SW Espagne). Les mâles ont présenté un taux de survie constant qui dépasse 85,4% tout au long de leur période de vol, un index de transition maximal de 1,82% et un taux de recapture de 42,5 à 76,90%. Ces résultats suggèrent un mode de vie sédentaire chez les mâles de *P. myardi*. Par contraste, le faible nombre de femelles capturées empêche de calcul de ces paramètres pour ce sexe. De toute façon, les observations montrent qu'elles sont moins sédentaires que les mâles au cours de leur période de vol.

Keywords: Cerambycids, Mark-recapture, *Quercus suber*, dehesa, CJS model.

The dehesa in the southwest of the Iberian Peninsula (Huelva) is a traditional silvopastoral system associated to production and conservation practices. By virtue of its efficient integral, extensive management, the SW Spanish dehesa possesses a high environmental value (Olea & San Miguel-Ayán 2006) and is protected under the EEC/92/43 Habitat Directive. Also, its high biological diversity and careful preservation of its natural and cultural heritage (Marañón 1988) endow it with a high ecological significance. Most trees in the SW Spanish dehesa belong to the genus *Quercus* and are largely evergreen Mediterranean species such as holm oaks (*Quercus ilex* L.) or cork oaks (*Quercus suber* L.).

These agroforestry systems are currently facing three problems that may threaten their permanence, namely: substantial migration from rural places to cities by effect of social and economic changes; little or no tree regeneration; and tree decay processes (Olea & San Miguel-Ayán 2006). The latter two factors are closely related inasmuch as the disappearance of adult trees by effect of the pathologies associated to decay processes is worsened by the absence of renovation or regeneration actions.

Tree decay involves a number of factors ranging from environmental conditions to the presence of biotic agents such as fungi or insects. The triggers and/or aggravators of tree decay processes in the SW Spanish dehesa include drilling insects and, especially, the cerambycid species *Cerambyx welensii* (Küster 1846), *Cerambyx cerdo* L. 1758 and *Prinobius myardi*

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Mulsant 1892 (Montoya 1992; Muñoz *et al.* 1996; Sánchez *et al.* 2000). *C. welensii* and *P. myardi* are the predominant cerambycids in the province of Huelva (Sánchez-Osorio 2005). Both have additionally been reported among holm oak drillers in the province of Córdoba (Soria *et al.* 1996), and encountered in a number of holm oak and cork oak formations in Andalusia and Extremadura (Barreda 2001, 2002; González *et al.* 2007; López Pantoja *et al.* 2004; López Pantoja *et al.* 2008; Llinares 2002; Naveiro & Morcuende 1994; Sánchez-Osorio *et al.* 2007; Verdugo 2006; Vives 2000).

Proliferation of these insects is favoured by deficient implementation of the cultivation practices systematically applied to dehesa land (Martín *et al.* 2005). Thus, harrowing usually causes wounds in tree feet that are used by females to lay their eggs; also, inappropriate stripping can leave wounds in the generating cork layer and facilitate access to females for laying. This can accelerate tree decay even in the absence of pathogens (fungi, bacteria); in fact, poorly planned and/or executed silvicultural practices can easily turn xylophagous cerambycids into the main culprits for adult tree decay. Thus, the damage caused by cerambycid larvae makes tree aerial organs more prone to breaking by effect of the wind, heavy rain or their own weight (Sánchez-Osorio 2005). Also, like other phytophages, adult cerambycids can play a prominent role as vectors for fungi and various other pathogens (Ragazzi & Tiberi 1998). Specifically, the coexistence of xylophagous cerambycids such as *C. cerdo* and fungal pathogens such as *Biscogniauxia mediterranea* or *Botryosphaeria* spp., or rots of the genus *Stereum*, on the same host can facilitate their propagation (Sánchez-Osorio 2005; Martín *et al.* 2005).

Because *P. myardi* adults are found in both weakened and seemingly healthy trees, this species can be deemed a primary xylophage (Hanks 1999). Most often, however, adults are found in strongly weakened trees or dead, thick fallen branches (Vives 2001), so this species also behaves as a secondary xylophage. Its individuals can thus use trees spanning a wide range of vigour. The extent of tree damage caused by *P. myardi* depends not only on the previous vigour status of the trees, but also on the pest status of the particular insect population a factor which has scarcely been studied in xylophages in general and this species in particular.

Careful study of the cerambycid populations present in dehesa systems is crucial with a view to understanding their specific role in tree decay. The information obtained from capture–mark–recapture samplings can be used to develop models based on basic population parameters such as the survival and

recapture rates in order to identify differences in life strategy in each species and derive useful information about its biology, all of which is indispensable with a view to accurately interpreting behavioural patterns in the field. In this work, we used the software MARK (White & Burham 1999) to construct Cormack–Jolly–Seber (CJS) models in order to examine the behaviour of the studied population. Similar models were previously used to interpret some population parameters for *C. welensii* (López-Pantoja *et al.* 2008), a species with which *P. myardi* often shares habitat.

The primary aims of this work were as follows: (a) to identify the emergence period and flight period of *P. myardi* adults; and (b) to obtain a better knowledge of the basic behavioural patterns of this species by interpreting the CJS models established and the ensuing population parameters.

Materials and methods

Target species

Prinobius myardi is a holo-Mediterranean species the distribution of which in the Iberian Peninsula overlaps with that of its main host: cork oak (*Q. suber*). Adults are 30–50 mm in size and have markedly nocturnal habits. They tend to hide in holes and cracks of trunks and branches and they do not seem to feed. Larvae, which take several years to develop completely, feed on xylem from the trunk and main branches; also, they pupate on the spring of the year where adults emerge, inside the galleries they carve as they develop (Vives 2000, 2001). Their flight period falls in the summer.

Study area

The present study was conducted in a *Q. suber* plot located in Almonte (Huelva, SW Spain) and spanning an area of 2.8 ha (120 long × 250 m wide). The plot contained 211 trees, so the average density was 75 tree/ha. The proportion of trees with a normal diameter (20–70 cm) amounted to 91%. The physical or natural boundaries of the plot include the A-484 regional road –beyond which the cork oak mass extends in the north; a sunflower (*Helianthus annuus* L.) plantation in the west; a fig tree (*Ficus carica* L.) plantation in the east; and the rest of the oak mass in the south.

The mean annual temperature of the area is 17.2 °C and its precipitation 627 mm. Based on Allué's classification, the climate is of the IV2 genuine Mediterranean type. The average temperature during the active period for the adult insects (June to August) is 23.9 °C and precipitation virtually zero (23 mm) (Ministerio de Medio Ambiente y Medio Rural Y Marino 2008). The plot trees are strongly affected; nearly one-third of all have exit holes typical of the action of these insects. Most have been stripped at least once –the last stripping work was done in 2003– and many several times and somewhat carelessly. This has left trunk wounds many of which have evolved into cracks. A few trees have never been stripped, however. One other feature of the trees directly reflecting the potential presence of xylophagous cerambycids is that the larger ones have been pruned but left untreated. The plot provides pasture for wool

Table 1. Numbers of captured and recaptured *Prinobius myardi* specimens.

Year	Captures			Recaptures				Female/male ratio
	Females	Males	Total	Females	Max nb. recaptures	Males	Max nb. recaptures	
2002	32	105	137	2	2	59	8	0.305
2003	37	59	96	4	1	38	8	0.627
2004	9	40	49	0		26	15	0.225
2005	4	21	25	0		14	11	0.190
2006	6	33	39	0		21	7	0.182
2007	14	59	73	0		31	12	0.237
2008	15	69	84	4	2	56	12	0.217

sheep in addition to cork. At present, the land soil is sown with grasses and tilled by complete surface harrowing. As a result, bushes are virtually completely absent.

Capture–mark–recapture study

Field work spanned the period from 2002 to 2008. The sampling frequency, which was established under the assumption that the studied population was of the open type (Southwood & Henderson 2000), was a visit on each second day during June and July, and one on each third day during August, from 2002 to 2006; and a visit on each second day during the adult activity period in 2007 and 2008. Insects were captured and recaptured by hand following visual detection in the trees. Sampling was started at 9:30 pm owing to the crepuscular habits of the insects and finished once all trees had been inspected (around 1:00 am). Insects were marked on an individual basis on their thorax and elytra, using a permanent marker (Pilot Paintmarker). On each visit, the presence or absence of marked insects was recorded and those captured for the first time were marked.

Identification of the emergence period

The emergence period of insects is usually established by using light or bait traps (Robredo 1975; Southwood & Henderson 2000) or some plant residue capable of attracting adults (Coulson & Witter 1991; Sierra & Martín 2004); very often, however, these methods destroy the captured insects. The method used in this work (capture–mark–recapture) involves releasing the insects following recording. Only the capture data

for new individuals found on each visit were considered—with provision for the potential error made in assuming that the insects captured for the first time were newly emerged individuals—in order to obtain a rough estimate of the emergence period. The flight period was estimated from the capture and recapture data recorded on each sampling visit.

Estimation of population parameters

The field data for *P. myardi* were fitted with the method previously used by López-Pantoja *et al.* (2008) to calculate population parameters for a similar species (*C. welensii*). The method involves applying a general model of the Cormack–Jolly–Seber (CJS) type [$\Phi(t^*g)P(t^*g)$], where Φ (survival) and P (recapture) are both time and sex dependent. The model should fit field data closely and fulfill the five basic hypotheses for the capture–recapture method used, namely: (a) all insects have the same recapture likelihood (π); (b) all marked individuals present in the population immediately after time i have the same likelihood of surviving until time $(i + 1)$; (c) marks are neither lost nor erased; (d) all samplings are instantaneous relative to the interval between time i and time $(i + 1)$; and (e) insects are released immediately after sampling and marked individuals intersperse randomly with unmarked individuals.

Violation of any of the previous hypotheses was detected from the results of the comparison tests used (Test2.SM, Test3.SM and Test3.SR) as calculated with the software U-care (Choquet *et al.* 2003). Specially important in this respect was the significance of Test3.SR, provides a measure of the presence

Table 2. Selected dates for the flight and emergence periods of *Prinobius myardi*

Year	Males					Females				
	Date			Duration (days)		Date			Duration (days)	
	First capture	Last capture	Last recapture	Emergence period	Flight period	First capture	Last capture	Last recapture	Emergence period	Flight period
2002	Jun 22	Aug 23	Aug 23	62	62	Jun 28	Aug 18	Jul 16	51	18
2003	Jun 13	Jul 29	Aug 06	46	54	Jun 19	Jul 31	Jul 7	42	18
2004	Jul 11	Aug 10	Aug 22	30	42	Jul 07	Jul 21	–	14	–
2005	Jun 30	Aug 03	Aug 01	34	32	Jun 26	Jul 22	–	26	–
2006	June 18	Jul 25	Aug 02	37	45	Jun 24	Jul 15	–	21	–
2007	Jun 18	Aug 12	Aug 15	55	58	Jul 08	Jul 31	–	23	–
2008	Jun 28	Aug 11	Aug 13	44	46	Jul 04	Jul 31	Aug 03	27	30

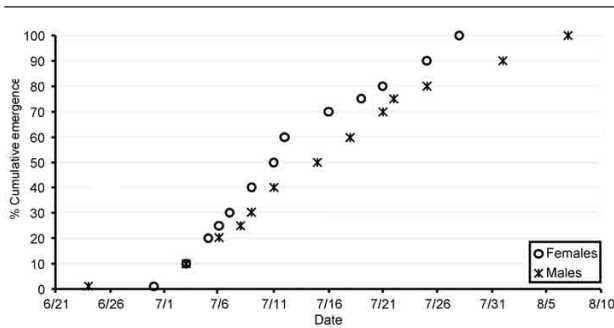


Figure 1
Percent cumulative emergence of *Prinobius myardi* females and males.

Results

Emergence period and flight period

The capture–mark–recapture method used allowed a total of 503 specimens (386 males and 117 females) to be sampled in seven years (see tab. 1). The emergence period for *P. myardi* males lasted an average 44.0 (SE 11.5) days and their flight period 48.8 (SE 10.3) days. Therefore, the flight period was slightly longer than the emergence period, the difference amounting to 4.4 (SE 5.0) days (tab.1–2).

The emergence period for the females lasted an average 29.0 (SE 12.8) days. Also, it started later and finished earlier than that for the males (fig. 1). However, the differences in this respect between the two groups were not significant (Student’s $t = 1.9$, $p = 0.1$, $\alpha = 0.05$). It therefore seems unlikely for this species to exhibit a protandric behaviour (fig. 1).

Fitting of field data

Careful analysis of the different elements of the comparison tests via the results of the programme U-care revealed that the basic hypotheses for the capture–recapture method used, were violated to some extent (tab. 3). The only Test3.SR results reported here correspond to the females in 2002 and 2008, which were the only years where at least one female was recaptured. This precluded accurate analysis of behavioural models and calculation of population parameters for the female group.

Test3.SR was significant in 2002, 2004, 2007 and 2008 (all with $p < 0.007$) (tab.3).

Selection of the most suitable model

Table 4 shows the models that have lower QAICc values each year and differing by at least 2.5 units in this index — none of the models used included any

of transient individuals (*viz.* individuals that are seen only once) in a population. This required using models considering the effect of age on survival such as those of the Time Since Marked (TSM) type, which are more generally designated by $[m(m_2-t/t) f(m_2-t/t)] P(g)$ [survival rate as function of the male (m) and female (f) group, each considered over two sampling intervals (m_2) and variable in time recapture group-dependent] (Pradel 1997; Prévot-Juliard *et al.* 1998). The potential lack of fit of the model was corrected by using the variance inflation factor (C-hat).

The next step involved choosing the most parsimonious model in terms of Akaike’s Information Criterion (AIC) or the quasi-likelihood adjusted (QAICc) if there is a lack of fit between the general and saturated models (noted that if $c-hat=1$ QAICc reduces back to AICc).

The survival and recapture rates for *P. myardi* were also calculated as previously done by López-Pantoja *et al.* (2008) for *C. welensii*. The procedure involved obtaining the maximum likelihood estimators for the statistically equivalent models and correcting each estimate as a function of its weight in the model (Seber & Schwarz 2002).

TSM models facilitate calculation of the survival rate for transient individuals (first sampling interval, Φ_{i1}), which in turn affords calculation of the proportion of such individuals present in the sample (τ) and in the whole population (T) (Cooch & White 2006; Perret *et al.* 2003).

Table 3. Results of the U-care test for *Prinobius myardi*

<i>Prinobius myardi</i>		2002		2003		2004		2005		2006		2007		2008	
		♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
TEST3.SR	$N(0,1)$ statistic for transient > 0	0.87	1.66	0.67	–	2.12	–	0.00	–	0.32	–	1.15	–	0.45	0.00
	P-level two-sided test	0.39	0.09	0.50	–	0.03*	–	1.00	–	0.75	–	0.25	–	0.65	1.00
TEST3.SM	Quadratic chi2	10.42	–	3.73	–	3.63	–	1.64	–	3.39	–	10.29	–	5.16	–
	P-level	0.88	–	0.98	–	0.60	–	0.90	–	0.85	–	0.33	–	0.98	–
TEST2.CT	$N(0,1)$ signed statistic for trap dependence	–2.77	–	0.02	–	–3.40	–	–1.00	–	–1.07	–	–3.91	–	–5.81	–
	P-level two-sided test	0.006**	–	0.98	–	0.0006**	–	0.32	–	0.28	–	0.0009**	–	0.0006**	–
TEST2.CL	Quadratic chi2	3.80	–	6.84	–	1.42	–	–	–	0.94	–	2.81	–	1.95	–
	P-level	1.00	–	0.74	–	0.70	–	–	–	0.92	–	0.97	–	1.00	–

Table 4. Selection of CJS and TSM models in terms of QAICc for *Prinobius myardi*.

2002		c-hat = 1.19		
Model	QAICc	Delta QAICc	QAICc weights	Num. par
{Phi(.) p(.)}	492.29	0.000	0.69	2
{Phi(m(m2 ./)) p(.)}	493.94	1.65	0.30	3
2003		c-hat= 1.00		
Model	QAICc	Delta QAICc	QAICc weights	Num. par
{Phi(.) p(.)}	465.19	0.00	0.71	2
{Phi(m(m2 ./)) p(.)}	467.07	1.88	0.28	3
2004		c-hat=1.22		
Model	QAICc	Delta QAICc	QAICc weights	Num. par
{Phi(m(m2 ./)) p(.)}	283.00	0.00	0.59	3
{Phi(.) p(.)}	283.75	0.75	0.40	2
2005		c-hat=1.35		
Model	QAICc	Delta QAICc	QAICc weights	Num. par
{Phi(.) p(.)}	113.44	0.000	0.74	2
{Phi(m(m2 ./)) p(.)}	115.58	2.14	0.25	3
2006		c-hat=1.00		
Model	QAICc	Delta QAICc	QAICc weights	Num. par
{Phi(.) p(.)}	284.38	0.00	0.66	2
{Phi(m(m2 ./)) p(.)}	286.31	1.93	0.25	3
2007		c-hat=1.22		
Model	QAICc	Delta QAICc	QAICc weights	Num. par
{Phi(.) p(.)}	298.20	0.00	0.51	2
{Phi(m(m2 ./)) p(.)}	298.30	0.10	0.49	3
2008		c-hat=1.28		
Model	QAICc	Delta QAICc	QAICc weights	Num. par
{Phi(.) p(.)}	524.42	0.00	0.73	2
{Phi(m(m2 ./)) p(.)}	526.38	1.96	0.27	3

females. Although there was no unambiguous sign of the presence of transient males in the population, we started with a classical general model of the CJS type and then used one incorporating the variable age (TSM) in its definition. Clearly, none of the models exhibiting the best QAICc values included time as a limiting factor for the population parameters (tab.4).

A global analysis of the sampling years revealed that the best model for all – 2004 excepted – as regards the proportion of population accounted for was that considering males with a time-independent survival rate and recapture rate (Phi(.) P(.)).

Survival rate and transiency index

The survival rate (apparent survival where death is a combination of actual mortality and emigration) for resident males was constant over time. In fact, their survival likelihood throughout a given emergence period remained constant between sampling times irrespective of their dates. Also, differences between years were small (see Hilton & Miller 2003 for a statistical interpretation) (fig. 2).

The results provided by the TSM models were used to calculate the proportion of transient individuals present in the sample (τ) and in the population (T) (tab. 5). The highest transiency rate (T) was 0.018 (0.015–0.021, 95% CI) in 2007 and the lowest 0.0004

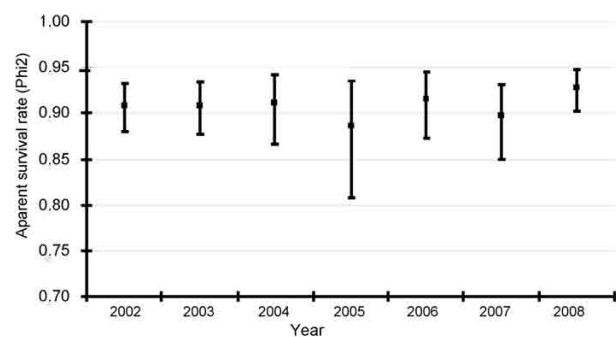


Figure 2 Apparent survival rate (Phi2) and 95% confidence interval for resident individuals of *Prinobius myardi* as calculated with respect to the yearly flight period.

Table 5. Population parameters calculated with the TSM model.

Phi₁, apparent survival between the first two sampling times; **Phi₂**, apparent survival for all other sampling times; **τ** proportion of transient individuals in the sample; **T** proportion of transient individuals in the whole population.

Year	Phi ₁	95% CI	Phi ₂	95% CI	τ	95% CI	T	95% CI
2002	0.89	0.87–0.93	0.91	0.89–0.92	0.011	0.00–0.043	0.004	0.003–0.005
2003	0.90	0.88–0.93	0.91	0.89–0.92	0.006	0.00–0.063	0.002	0.001–0.003
2004	0.86	0.80–0.91	0.91	0.89–0.93	0.057	0.00–0.121	0.016	0.013–0.018
2005	0.87	0.85–0.89	0.88	0.87–0.89	0.008	0.00–0.039	0.003	0.000–0.005
2006	0.91	0.88–0.95	0.91	0.89–0.93	0.001	0.00–0.044	0.0004	0.000–0.003
2007	0.85	0.72–0.93	0.89	0.85–0.93	0.048	0.00–0.110	0.018	0.015–0.021
2008	0.93	0.88–0.96	0.93	0.90–0.95	0.003	0.00–0.028	0.0007	0.000–0.001

(0.000–0.003, 95% CI) in 2006. Differences between years were generally very small except for 2004 and 2007, with 1.5 and 1.8%, respectively. These values, while low, were significantly different from those for the other seasons (tab. 5).

The results were consistent with those discussed under “Fitting of field data”. As can be seen from Table 3, Test3.SR was only significant for males in 2004.

Recapture rate

The recapture rate, *P*, ranged from 0.4 (0.3–0.5, 95% CI) in 2002 to 0.7 (0.6–0.8, 95% CI) in 2004. As can be seen from the differences in *P* between years in figure 3, the 2004, 2005, 2008 results differed markedly from all others in this respect (see Hilton & Miller for a statistical interpretation) (tab.6).

One parameter of interest in addition to the recapture rate (tab. 6) is the largest number of recaptures for each year (tab. 1). In 2004, some specimens were recaptured up to 15 times; also, more important, most such specimens were recaptured in the same hole they had been marked the first time. This was not the case with the females, which were recaptured a maximum of two times and in a different tree each (2002 and 2008).

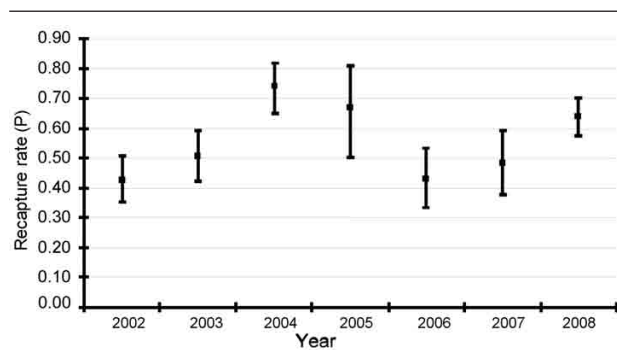


Figure 3 Recapture rate (*P*) and 95% confidence interval of *Prinobius myardi* as calculated with respect to the yearly flight period.

Discussion

The models best describing the behaviour of *P. myardi* were of the Cormack–Jolly–Seber (CJS) type. In fact, such models accounted for the behaviour of a proportion of males ranging from 74.4% in 2006 to 40.5% in 2004. Based on the results, the studied population exhibits a homogeneous behaviour (Phi(.) p(.)). Another fraction of the population fitted TSM models more closely; such a fraction consisted of a group of mobile males (transient individuals) which exhibited a constant recapture rate throughout the emergence period and another group consisting of sedentary males (*i.e.* individuals never leaving the sampled zone) (Phi (m(m2_./.) p(.)).

These results suggest the presence of transient males throughout the studied period. However, the results of a careful analysis of the models and their weight for the studied population, and the transience index (T) obtained, somehow depart from this conclusion.

The weight of the TSM models ranged from 58.9% in 2004 (the only year where Test3.SR was significant) to 25.2% in 2006. Therefore, 58.9% of the males sampled in 2004 exhibited the typical behaviour of transient individuals. However, the transience index for 2004 was 0.015 (0.013–0.018, 95% CI), so only 1.5% of all potential transient individuals actually were.

Table 6. Recapture rate for *Prinobius myardi*.

Year	<i>P</i>	95% CI
2002	0.42	0.35–0.50
2003	0.51	0.42–0.59
2004	0.74	0.65–0.81
2005	0.67	0.50–0.80
2006	0.43	0.33–0.53
2007	0.48	0.38–0.59
2008	0.64	0.57–0.70

The transience index for the overall population was greater in 2004 and 2007 than in the other years. This may have been a result of worsened habitat conditions leading males to move to more favourable zones or of the population dynamics being dictated by the low density of individuals (both females and males) present in the zone. Under these conditions, males can be expected to search for zones with a higher mating likelihood (Lawrence 1988). Neither hypothesis, however, can seemingly justify the slight increase in transient individuals detected by the models. In any case, it affected the behaviour of males, which appeared to be dictated by that of resident individuals. Thus, some males were recaptured up to 12 times in the same hole as in the initial capture, which reveals site-fidelity in *P. myardi* — so much so that it dictated the results of Test2.CT and confused sedentary and territorial character with trap dependence. Although, in fact, the results of the previous tests suggested the need to use models including the effect of marking on the adult recapture likelihood (*i.e.* trap dependence) (Cooch & White 2006), the field observations seem to reveal that unmarked, but readily identified individuals, behaved identically with marked individuals; therefore, it was not marking that governed the behaviour of this species and no need therefore existed to use specific models providing for its effect.

However presence of both groups (transients and residents) may lead to heterogeneity among insects (Schwartz 2010 *in it*), therefore it would be interesting the use of the models proposed in Pledger *et al.* (2009) and Pledger *et al.* (2010) for future studies.

The survival rate (per day) for *P. myardi* resident individuals was time-independent, and close to or even greater than 90%, throughout each sampling season. Such high rates are similar to those previously found for *C. welensii* (with a maximum rate of 91.9% and a minimum value of 81.4%) (López *et al.* 2008), largely as a result of the absence of exogenous and endogenous limiting factors capable of controlling the population behaviour via an increased mortality rate. The behavioural habits of *P. myardi* males are typical of saproxylic insects (Dajoz 2001). This, together with the sedentary and fleeing nature of this species, suggest that the studied population was under the effect of no limiting factors since its environmental conditions and habitat were identical with those for *C. welensii* (López *et al.* 2008).

Differences in survival rate between years were very small. This suggests that changes in biotic and abiotic factors in the study area have little effect on the mortality rate of the target population (Covas *et al.* 2004; Oro *et al.* 2004). In addition, the marked

sedentary habits of *P. myardi* males reduce the risk of death by considerably diminishing those of being confronted with a serious hazard such as the presence of a predator, crashing into a tree trunk or the need to overcome a spatial barrier (*e.g.* a road).

The extremely high recapture rates for males in 2004, 2005 and 2008, which exceeded 63.8%, may be indicative of a confined population (Prieto *et al.* 2005) with a negligible number of individuals joining or leaving it. However, the study area is part of a continuous plant formation of identical characteristics, so the target population cannot be deemed an isolated population. One can therefore reasonably think that the high recapture rates obtained are a result of low mobility in the males. The recapture rates for the other years were significantly lower, but still much higher than those for *C. welensii* reported by López-Pantoja *et al.* (2008), *viz.* $P_{\max} = 0.190 \pm 0.0065$; therefore, even in the years with the lower recapture rates, *P. myardi* males flew very rarely.

As recommended by some authors (Bart *et al.* 1998), the mobility of insects in the population can be established by interpreting their survival rate in terms of site loyalty. Using the factor “residency” instead of “survival” (Lawrence 1988; Prieto *et al.* 2005) and calculating it from the expression $\ln(\Phi) - 1$ proposed by Fisher & Ford (1947) (in Cook *et al.*, 1967) and Cook *et al.* (1967), led to an average insect permanence value of 10 and never exceeding 12. Since sampling visits were done every 2 or 3 days, the resulting permanence time ranged from 30 to 36 days. If we use the estimated lifetime calculated from the overall capture – recapture data (38 days or more), then these results, consistent with previous conclusions, can be ascribed to a population — the male group — of little mobility.

Based on the foregoing, *P. myardi* males are highly site loyal. This contradicts the observations for females. Although the number of recaptured females was very small — so much so that it precluded calculation of the basic population parameters for their group —, one can easily infer that females and males exhibit a radically different behaviour. Thus, while males are sedentary — which facilitates their capture and subsequent recapture —, females are quite mobile and seemingly stay very little time in the same place, which hinders their location. The presence of pseudo-forensic scorpions (*Mesochelifer fradei* Vachon), especially on females (Domínguez *et al.* 2008 and results pending publication) may provide additional support for this hypothesis (Ranius 2002).

The markedly sedentary behaviour of one sex may be associated to its releasing short- or long-

rage sex pheromones. Thus, the morphological and behavioural characteristics of some species of the subfamily prioninae (*Prionus californicus* Motschulsky and *Prionus laticollis* Drury) (Cervantes *et al.* 2006) are in some way associated to the production of sex pheromones by females, which are more sedentary than males — which possess a more complex antenna system (Barbour *et al.* 2006). In *P. myardi*, it is males that exhibit a sedentary behaviour and females those apparently moving in their pursuit. This suggests that it may be males that release some sex pheromone. The presence of pores in their prothorax may be associated with that of pheromone releasing structures. This is quite common among some species in the subfamily cerambycinae (Ray *et al.* 2006), but has not been confirmed in prioninae, a more primitive subfamily to which *P. myardi* belongs. However, sharing taxonomic affiliation does not necessarily mean sharing evolutionary characters; in fact, each species can have its own life strategy (Ray *et al.* 2006). This makes it advisable to examine the prothorax of *P. myardi* males with a view to confirming whether it actually contains any pheromone releasing structures.

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