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Monitoring the performance of wild-born and introduced lizards in a fragmented landscape: Implications for *ex situ* conservation programmes

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ABSTRACT

Ex situ conservation of animal populations may benefit from captive-breeding programmes, but these are criticised because they are assumed to be difficult, time-consuming and expensive, while they do not guarantee success. However, such assumptions remain untested in most organisms; for example, introductions could be very useful for recovering populations of small-sized species with short generation time, no learned behaviours, and ease to rear in captivity. Here, we document an easy, cheap and successful reintroduction programme of the lacertid lizard *Psammodromus algirus*. Two captive-bred cohorts (178 juveniles in 2001 and 187 in 2002) were released in four woodland fragments (0.9–5.2 ha) at two localities (B and V); B housed a stable lizard population whereas V apparently lacked a viable population of lizards. We monitored introduced and native lizards during 2002 and 2003, and carried out a corroborative searching in 2006 which confirmed the existence of a lizard population at site V. Introduced lizards had higher activity and dispersed more frequently among woodland fragments than native ones. Survivorship and growth rates were similar for both groups, but introduced juveniles were about 25% larger than native ones, due to both early hatching and better rearing conditions. The whole procedure was easily implemented in our Faculty facilities (mean hatching and hatchling survival rates of 0.90 and 0.87), and cost less than 20,000 € (excluding salaries). Therefore, similar programmes may be of wide application in small animals and of practical importance for species with a meta-population structure living in fragmented landscapes.

1. Introduction

Animal reintroductions and population reinforcements are customary procedures in conservation practice (IUCN, 1998; Fischer and Lindenmayer, 2000; Seddon et al., 2007). It is common wisdom that these procedures 'are always very lengthy, complex and expensive' (IUCN, 1998), in particular if populations are started with captive-bred founders (Snyder et al., 1996; Mathews et al., 2005). However, captive animals are much more frequent as a population source than wild stocks, a tendency that has increased in recent years (Fischer and Lindenmayer, 2000; Seddon et al., 2007). In spite of this, the success of reintroductions with wild animals is twice that of captive stocks (Rahbek, 1993; Fischer and Lindenmayer, 2000), most likely due to the various problems associated with captive breeding, such as domestication, behavioural or other phenotypical changes, or increased mortality after release in the wild (Snyder et al., 1996; Banks et al., 2002; Kelley et al., 2006; Seddon et al., 2007; Connolly and Cree, 2008). However, these drawbacks may be less important in species of small-sized animals with low space requirements and short generation times, without parental care or learned behaviours, and which are easy to reproduce in the laboratory (Snyder et al., 1996; Seddon et al., 2007). In such species, the use of captive-bred animals might have several advantages over wild stocks: (1) low cost of captive breeding compared to capturing a similar number of wild individuals to be translocated; (2) easy maintenance of adequate populations of genetically varied breeders captured in the wild; (3) high reproductive success (e.g., high laying and hatching rates and low hatchling mortality in oviparous species); (4) low cost of maintenance until juveniles reach a size or age which decreases their mortality in the wild; and (5) reduced impact on native stocks if adult survival during the breeding season is higher in captivity than in the wild.

Species fulfilling the above conditions may be suited to management with an alternative approach in which the best of both captive breeding and translocation of wild animals is combined. In many species, it is possible to capture breeders in the wild and bring them in captivity to complete their reproductive cycle. In these cases, breeders can be released at the site of capture as soon as reproduction is over, and captive-born individuals can be

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reared in advantageous conditions before being released. Such approaches may help to increase the success prospects of *ex situ* conservation programmes while reducing their costs.

Conservation benefits attained with species fulfilling the above conditions should be sound. Firstly, reintroductions or reinforcements could be carried out with relatively large populations (some hundreds of individuals), to a low cost, and after short periods of captive breeding (some months). This is specially relevant because high costs prevent the development of many captive-breeding programmes, and the size of relocated populations has important effects on relocation success (Fischer and Lindenmayer, 2000; Earnhardt et al., 2001; Tenhumberg et al., 2004; Germano and Bishop, 2008). Secondly, undesirable behavioural changes of the breeding stock or the cohorts of captive-bred individuals should be absent or very small, given the lack of consequences of experimental manipulation in these species and the short stay in captivity (Snyder et al., 1996; Kraaijeveld-Smit et al., 2006). This would facilitate a rapid acclimatization to natural conditions when released into the wild. Finally, the procedure minimizes the effects on wild populations, because the breeding stock is released back into the wild.

In this paper we analyse the utility of captive-bred cohorts of the lacertid lizard *Psammodromus algirus* for founding or reinforcing local sub-populations in a fragmented landscape in which this species faces conservation problems (Díaz et al., 2005; Santos et al., 2008). We use the terms reintroduction and reinforcement following IUCN (1998) and Fischer and Lindenmayer (2000). Our main purpose is to show, using *P. algirus* as a model species, that captive breeding can be a valuable option for the successful reintroduction of species with similar husbandry requirements. In addition, we try to demonstrate that such reintroductions can be effective in fragmented landscapes in which meta-population dynamics produce local extinctions in patches of suitable habitat. We had the following goals: (1) to obtain a diverse stock of breeding adults from nearby fragments just before the beginning of reproduction; (2) to obtain a large stock of captive-bred hatchlings; (3) to rear the juveniles in the lab under conditions allowing them to grow up to a size that should increase survival and favour their emergence from first hibernation with an advantageous size (Díaz et al., 2005; Iraeta et al., 2008); (4) to monitor the activity, dispersal, and survival of released individuals and to compare them with those of native individuals (which should provide a control of the assumption that captive breeding has no undesirable collateral effects); (5) to check the success of reintroductions; and (6) to evaluate the costs of our breeding programme.

2. Methods

2.1. Origin of captive populations

The large *Psammodromus* (*P. algirus*) is a medium-sized (adult snout-vent length 65–90 mm; mass 6–15 g) lacertid lizard inhabiting shrubby and cleared forested habitats of the western Mediterranean region (Iberian Peninsula, south-eastern France and northwest Africa; Salvador, 2006). It has a reproductive cycle typical of temperate species (Díaz et al., 1994; Carretero and Llorente, 1997): females lay one or two clutches between April and July (spring–summer), and hatchlings appear between August and October (summer–autumn).

The study area (Lerma, central-northern Spain; 42°5′N, 3°45′W; 850 m above sea level) is a farming landscape where agricultural practices have produced an archipelago of oak forest remnants intermingled among cereal fields. Our captive population originated from a sector of ca. 100 km^2 where we have previously studied the distribution and habitat selection of large *Psammodromus* in 50 small fragments and three extensive forests (Santos et al., 2008). The area is near the northern edge of the species' range; lizards reach very low densities in the large forests (Díaz et al., 2000), and they are absent from many fragments (Santos et al., 2008). The breeding stock originated from 15 different sub-populations (the three forests over 200 ha, and 12 fragments sized between 0.6 and 6.8 ha). A preliminary analysis of six microsatellite loci suggests that our breeding stock included a genetically varied sample of the wild meta-population (authors, in preparation). The captive stock has already been used to document the negative effects of habitat fragmentation on the reproductive investment of the species (Díaz et al., 2005).

2.2. Captive breeding and hatchling husbandry

Ex situ conservation methods can embrace a wide array of strategies, ranging from short-term head-starting of eggs or juveniles collected in the wild to long-term captive-breeding programmes. For our model species, probably the best way of producing viable captive-born juveniles is bringing gravid females in the laboratory for egg-laying, because finding eggs in the wild is impracticable. Such an approach is cheap because it does not require a permanent infrastructure to keep a captive population, and also avoids potentially reduced breeding success due to interference with natural processes of mate choice or egg formation. In addition, the procedure also maximizes hatching success by reducing egg predation or the probability of clutch failure associated to the selection of inadequate laying sites.

Adult lizards were captured in the breeding seasons of 2001 (25 females and 24 males) and 2002 (29 females and 15 males) and transported to the lab (Universidad Complutense, Madrid) between 21 May and 8 June. Two females and one male died in the laboratory, which means a mortality rate in captivity below 5%, and 85% of females laid viable eggs. After the study, adult lizards were released at their site of capture.

The laboratory had natural light–dark conditions and ventilation. We housed lizards in terraria (40 × 60 × 30 cm) with white, opaque walls and with their tops covered with a green net (0.5-cm mesh) that prevented escape, let daylight enter the cages, and created a shrubby-like shelter. We filled the terraria with moistened soil about 10 cm deep and covered the soil with leaf litter. A lamp created a photothermal gradient (approximately 25–50 °C) that allowed thermoregulation within the preferred temperature range (Díaz et al., 2006). Shade and shelter were provided by an earthenware tile (approximately 10 × 15 cm) and thin sticks. We fed lizards with crickets (*Acheta domestica*), mealworms (*Tenebrio mollitor*), and waxworms (*Galleria mellonella*) that had been dusted with a commercial diet supplement. All terraria contained water at all times.

We detected egg-laying by palpation or daily weighing of gravid females. Immediately after laying, we removed the female and carefully searched for the eggs. Upon finding the clutch, eggs were wiped clean of sand, weighed, and individually placed in 150-ml closed plastic cups filled with 35 g of moistened vermiculite (10 g vermiculite: 8 g water, equivalent to −200 kPa; Tracy et al., 1978). Eggs were completely surrounded by the vermiculite, and we closed the containers hermetically to minimize evaporation. Eggs were incubated at a constant temperature of 30 ± 0.5 °C.

When incubation was about to end (45.2 ± 0.2 days, mean ± SE), we searched daily for newly hatched lizards. Hatchlings were weighed and given unique toe-clip marks before being transported to nursery terraria. These terraria were similar to those used for housing adults, except for the fact that they received direct ultraviolet light 4 h/day (F30 W/6500 K Reptistar terrarium lamp, SLI Sylvania, Madrid). Small crickets, dusted with commercial vitamins and calcium supplements, and water were provided *ad libitum*.

We sorted juveniles from the same clutch among different terraria to separate environmental and familial effects.

2.3. Release of captive-bred juveniles

Juveniles were released into the wild on 18 September 2001 ($n = 178$) and 26 September 2002 ($n = 187$). Mean hatching dates were 31 July ±0.8 days (mean ± SE) in 2001 and 22 July ±0.7 days in 2002, and mean SVL at release was 36.2 ± 0.3 mm in 2001 and 36.3 ± 0.2 mm in 2002. Mean age at release was 48.5 ± 0.8 days in 2001, and 65.6 ± 0.7 days in 2002.

For the liberation of the captive-bred stock, groups of five to seven unrelated juveniles of different terraria were released in both years at 30 spots distributed among four woodland fragments in two pairs of sites (B and V) located 8 km apart (Fig. 1): two fragments of 1.0 and 5.2 ha separated by a distance of 150 m (B-30 and B-32, respectively), and two fragments of 0.9 and 4.1 ha separated by a distance of 40 m (V-2 and V-1, respectively). B-30 and B-32 were remnants of deciduous Pyrenean Oak (*Quercus pyrenaica*) forests whereas V-1 and V-2 were remnants of evergreen Holm Oak (*Quercus ilex*) forests. Details about thermal quality and food availability in these four forests have been published elsewhere (Santos et al., 2008). Here, it suffices to say that operative temperatures were closer to the lizards' preferred thermal range (i.e. overall thermal quality was higher) in deciduous than in evergreen fragments and that arthropods (i.e. food) were nearly five times more abundant in deciduous than in evergreen fragments (Santos et al., 2008), confirming the overall higher quality of deciduous oak forests relative to evergreen ones (Díaz, 1997; Iraeta et al., 2006; Santos et al., 2008). In fact, in B-32 there was a stable lizard population that allowed us to compare the traits of introduced and native lizards (see below), whereas V-1, where no stable lizard population could be found, allowed us to test the success of our reintroductions. Release points were distributed among fragments according to their size (10 release points in each of B-32 and V-1, and five release points in each of B-30 and V-2). Overall, in B-32 we released 59 and 60 juveniles in 2001 and 2002, respectively; in B-30, 30 and 35; in V-1, 59 and 59; and in V-2, 30 and 33.

2.4. Field monitoring of captive-bred and native populations

During the activity seasons of 2002 and 2003 we searched for juveniles at B and V sites. Searching effort was similarly distributed among sites and fragments, and all fragments were visited at least 15 different days per season. We also searched for marked lizards in nearby fragments: additional searching times of 27 h 39′ and 3 h 17′ were devoted to B-31 and V-3, respectively. B-31 is a 0.6 ha fragment located between B-32 and B-30 (Fig. 1) where several lizards were captured (seven native lizards in 2002, seven native lizards in 2003, and one lab-bred lizard in 2003). V-3 is a 0.4 ha fragment close to V-2 (Fig. 1) where no lizards were ever encountered.

We walked slowly across the study fragments, and captured by hand or noose all lizards detected. Each captured lizard was examined to determine whether it was a lab-born individual (hereafter 'introduced') or not (hereafter 'native'). Native individuals were toe-clipped, and all captured lizards were measured (snout-vent length, SVL), weighed and assigned a unique paint-mark before being released at their site of capture. In order to confirm the implantation of a viable population of lizards at site V, we searched for lizards there in the spring–summer of 2006 (two visits amounting nine searching hours), 5 years after the reintroductions.

Introduced lizards were aged as juveniles (captured in their second calendar-year) or adults (captured in their third calendar-year). Native lizards were classified according to their SVL as <62 mm or ⩾62 mm (Fig. 2), which is consistent with the average SVL at maturity previously reported for this species (Bauwens and Díaz-Uriarte, 1997; Civantos and Forsman, 2000). Our data supported this criterion, because during the first part of the activity season (i.e. until 30 June) the native population was clearly divided into two size classes, with large individuals (adults in their third calendar-year or older) and small individuals (juveniles in their second calendar-year; Fig. 2). From July to September, native lizards formed a single size class in which subadults (i.e. adult-sized yet immature lizards) and adults were mixed. In contrast with this complex pattern, the population of introduced juveniles formed a single group in which SVL increased steadily throughout the activity season (Fig. 2).

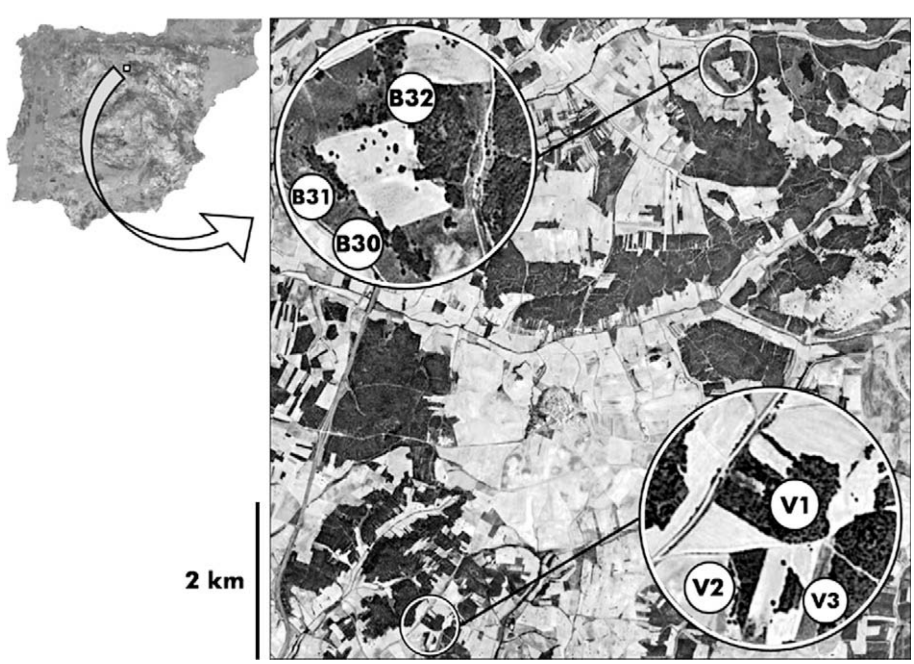

Fig. 1. Location of the forest fragments where we carried out reinforcements (B fragments) or apparent reintroductions (V fragments) with captive-bred large *Psammodromus*.

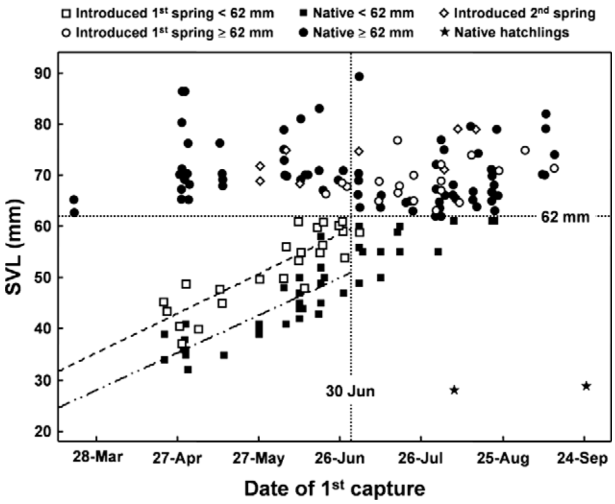

Fig. 2. Body size at first capture of introduced and native lizards. Before July, native lizards can be classified as juveniles (<62 mm) or adults (⩾62 mm). After that date, they form a single size class in which subadults (i.e. adult-sized but still immature lizards) and adults are mixed.

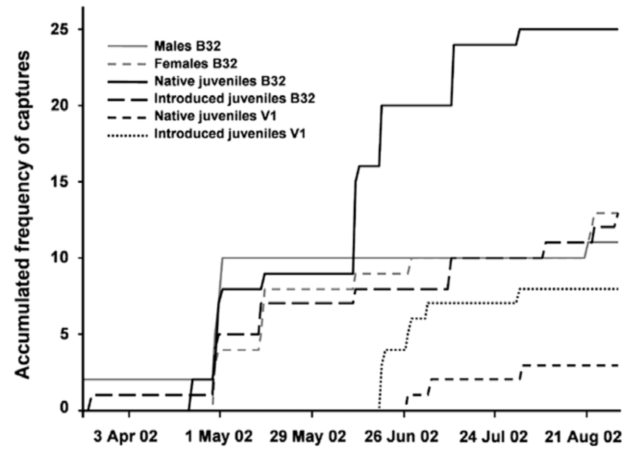

Fig. 3. Accumulated number of captures during 2001 in B-32 (adult males and females, and native and introduced juveniles) and V-1 (native and introduced juveniles).

Field data of marked individuals were recorded on 1:2000 scale maps in which the location and SVL at consecutive captures were recorded. We recorded the number of days elapsed between the first and last capture as an indicator of intra-season survival, and the date of last capture as an alternative index of survivorship, which is independent of the date of first capture. The sum of the distances moved between consecutive observations was used as an estimator of dispersal propensity, and the number of different days a lizard was seen as an indicator of activity levels. For the number of days between first and last capture and for the sum of distances moved, the comparison between introduced and native lizards was restricted to individuals with two or more captures.

We used the SVL data to assess the relative growth rates of 32 juvenile lizards with at least two captures (16 introduced and 16 native). The average number of days between measurements (±SE) was 62.9 ± 8.44 days for introduced lizards (range: 20–116) and 47.6 ± 5.87 days for native ones (range: 13–92). Growth rates were expressed on a size-specific basis (ln(SVL last capture date/SVL first capture date)/(last capture date − first capture date)). This estimate reflects the proportionate increase in size on a per-day basis (Sinervo, 1990).

For data analyses, we employed general linear models with native lizards as a control of the performance of our captive-breeding programme (for a similar procedure, see Mathews et al., 2005; Hardman and Moro, 2006; Ausband and Foresman, 2007; Cheyne et al., 2008). When necessary, variables were log-transformed to meet the requirements of parametric tests. For the sake of simplicity, 2002 and 2003 data were pooled in all analyses after having checked that year effects were never significant. Data are given as mean ± 1SE.

3. Results

3.1. Status of lizard populations before and after the release of captive-bred juveniles

In the searching season of 2002, we found a well structured native population at site B, particularly in the large forest (B-32), where we captured 24 adults and 25 juveniles (Fig. 3) in ca. 122 h (23.5 h/ha). In contrast, only three native lizards were recorded at site V (Fig. 3), all of them juveniles captured in the large forest (V-1) in ca. 95 h (23.1 h/ha). Very similar results were obtained in the searching season of 2003 (Table 1). Even clearer results emerged when we compared the searching time needed to capture the first native lizard. No native lizard was ever found in V-2 after 36 h 40 min of searching, whereas the time required to capture the first native lizard in V-1 multiplied that of B-32 by 53.2 times in 2002 and by 59.5 times in 2003 (Table 1). Thus, native lizards were much more frequent than introduced ones at site B (92 native vs. 28 introduced) whereas the opposite was true at site V (six native vs. 19 introduced; Fisher exact $P < 0.0001$).

The presence of increased numbers of lizards was easily detected at site V in the activity season of 2006, 4 years after our last reintroduction. Thus, the time elapsed until the first capture was only 17 min, 138 times shorter than in 2002 and 70 times shorter than in 2003. Lizard abundance was much higher in 2006 (six individuals in 8 h 35 min) than in 2002 (Table 1: three native individuals in 94 h 50 min) and 2003 (three native individuals in 109 h 32 min). Furthermore, two out of six individuals captured in 2006 were unequivocally aged as adults, a reasonable evidence of the presence of an established and well structured population in V-1.

3.2. Annual survivorship of introduced and native juveniles

We recorded data from 160 individual lizards throughout 2002 and 2003 activity seasons, of which 112 were native and the remaining 48 were introduced in 2001 or 2002 (Table 1). Field survivorship between consecutive years did not differ between the two cohorts of captive-bred lizards (Fisher exact $P = 0.207$), nor did it differ between the 2002 captive-bred and native cohorts (Fisher exact $P = 0.534$; Table 2). Eight lizards introduced in 2001 were re-sighted alive in 2003.

3.3. Intra-season field survival and activity and dispersal patterns

Introduced lizards had a tendency to show higher indices of intra-season field survival, activity, and dispersal than native ones, although high variance and/or small sample size precluded statistical significance in many of the comparisons (Table 3). Thus, last capture date was on average 18 days later for introduced than for native lizards, which were observed 27% less days than captive-bred ones. The difference in dispersal propensity was especially clear, because the distance moved among fragments by introduced juveniles doubled that of native ones and, more importantly, because the frequency of movement between different fragments

Table 1
Results of the monitoring of native and introduced lizards in the four fragments in which captive-bred cohorts of *Psammodromus algirus* were released at the end of the activity seasons of 2001 and 2002.

Forest	Area (ha)	Year 2002 (captive-bred lizards released in 2001)					Year 2003 (captive-bred lizards released in 2001 and 2002)				
		Searching season (day/month)	Searching time (no. of days)	Time to capture the 1st native	Native lizards captured	Introduced lizards captured	Searching season (day/month)	Searching time (no. of days)	Time to capture the 1st native	Native lizards captured	Introduced lizards captured
Site B											
B-32	5.2	19/03–13/09	122 h 21′ (20)	44′	49	13	27/05–25/09	134 h 44′ (23)	20′	34	6
B-30	1.0	22/04–13/09	33 h 28′ (17)	8 h 25′	5	5	27/05–25/09	29 h 30′ (20)	1 h 50′	4	4
Site V											
V-1	4.1	29/04–13/09	94 h 50′ (19)	39 h 02′	3	8	27/05–25/09	109 h 32′ (19)	19 h 49′	3	9
V-2	0.9	14/05–13/09	19 h 24′ (17)	–	0	0	5/06–25/09	17 h 16′ (15)	–	0	2

Table 2
Annual field survivorship of introduced and native lizards. Note that searching effort was rather similar in the activity seasons of 2002 and 2003 (Table 1).

	No. of lizards	No. captured the next year (2002 or 2003)	First year survival (%)
Captive-bred released in 2001	178	26[a]	14.6
Captive-bred released in 2002	187	19	10.2
Native lizards marked in 2002 as juveniles	30	4	13.1

[a] Since three more lizards were captured in 2003, at least 29 lab-bred animals of the 2001 cohort (16.3%) survived for 1 year. Additionally, five lizards captured in 2002 were recaptured in 2003. Thus, at least eight individuals of the 2001 cohort (4.5%) survived for 2 years.

Table 3
Differences between native and introduced juveniles (mean ± SE, with sample size in parentheses) in indices of intra-season field survival, activity, and dispersal. ANOVA results are shown in the last two columns.

	Native	Introduced	*F*	*P*
No. of days between 1st and last capture	45.8 ± 7.8 (18)	53.7 ± 7.0 (24)	0.53	0.472
Date of last capture	7 July ±5.7 (47)	25 July ±4.6 (45)	5.92	0.017
No. of days a lizard was seen	1.9 ± 0.23 (47)	2.6 ± 0.30 (45)	3.13	0.080
Sum of distances moved between observations (m)	28.8 ± 8.08 (17)	33.9 ± 8.01 (24)	0.19	0.662
Distance moved among fragments (m) (range in parentheses)	108.6 ± 61.4 (2) (47.3–170)	217.3 ± 31.3 (8) (115.5–400)	2.43	0.158

was much higher for introduced (8 of 48 lizards: 16.7%) than for native lizards (2 of 112: 1.8%; Fisher exact $P = 0.0011$).

3.4. Growth and body size

Native juveniles grew faster than introduced ones (relative growth rate of native lizards: 0.0059 ± 0.0006 days^{-1}, introduced lizards: 0.0041 ± 0.0006 days^{-1}), although the difference was marginally non-significant ($F_{1,30} = 4.09$, $P = 0.052$) and vanished when statistically controlling for the fact that the size at first capture was larger for introduced lizards, because the size-specific growth rate is larger for smaller individuals (ANCOVA; introduced vs. native: $F_{1,29} = 1.50$, $P = 0.231$; SVL at first capture: $\beta = -0.636$, $F_{1,29} = 21.39$, $P < 0.001$). In fact, the size advantage of introduced juveniles was evident throughout the first half of their first growing season (ANCOVA with the data in the bottom left corner of Fig. 2; introduced vs. native: $F_{1,50} = 77.95$, $P < 0.001$, date of capture: $F_{1,50} = 113.93$, $P < 0.001$). This size difference was one of the clearest results of our study.

3.5. Success and costs of captive breeding

Hatching success and hatchling survival in the lab were high in both breeding seasons: 0.924 and 0.913 in 2001 ($n = 178$ juveniles released), respectively, and 0.869 and 0.827 in 2002 ($n = 187$ juveniles released).

The study was funded by the Spanish Ministry of Education and Science (Project BOS 2000-0556) with a total budget of 32,380 € (28,910 € of direct costs, plus 3470 € overheads). A major fraction (55.3%) of these funds was spent in a study of the distribution and habitat selection of lizards in our study area (Santos et al., 2008). The remainder (14,467 €) was spent in field and lab work that produced the data presented here and in a previous report of the effects of fragmentation on reproductive investment of lizards (Díaz et al., 2005). More precisely, we spent 2346 € in captive breeding, 10,570 € in field work, and 1551 € in overheads (Table 4). Additional costs not shown in Table 4 include 23 weeks of use of two incubators funded by an associated project (10,904 €, to be written off over >10 years of use), plus some small scientific equipment (one binocular microscope, two digital calipers, and four digital balances), and the use of Faculty facilities at the Department of Zoology, Universidad Complutense de Madrid (a 72-m^2 lab housing adult terraria during 20 weeks, and a 136-m^2 lab housing nursery terraria during 26 weeks).

4. Discussion

Our results indicate that the release of captive-bred juvenile lizards was successful in the short-term, since we introduced individuals of apparently higher phenotypic quality than the native ones. Thus, captive-bred individuals were larger, dispersed more frequently among nearby fragments, and showed similar, if not higher, values of survival and activity than native ones. Captive-breeding programmes are commonplace in current conservation practice, but their utility for reptile conservation has long been viewed as highly variable among species and difficult to evaluate (Dodd and Seigel, 1991; Burke, 1991). More recently, relocation procedures, with or without captive breeding, have been advocated or used to recover some small-sized, endangered lacertids and skinks (Brito et al., 1999; Towns and Ferreira, 2001; Capula et al., 2002; Germano and Bishop, 2008). Although more time would be necessary to demonstrate the ultimate success of reintroductions, our study not only confirms that captive breeding lacks undesirable effects in *P. algirus*, but it also suggests that introduced lizards are given an advantage over native ones, two circumstances that

Table 4
Costs of captive breeding and field monitoring funded by project BOS 2000-0556. Mean distance between lab facilities and study area is 230 km.

Component	Amount (€)
Lab costs	
Captive breeding (terraria, egg containers, heating and UV lamps, etc.)	1346
Food (crickets, mealworms, waxworms) and vitamins, vermiculite	1000
Subtotal	2346
Field costs	
Capture and transport of adults, release of captive-bred juveniles (20 days)	3020
Field monitoring (50 days)	7550
Subtotal	10,570
Overheads	1551
Total costs	14,467

clearly show the viability of relocation programmes based on captive breeding in this species.

4.1. Survival, activity and dispersal

Annual survivorship was similar between captive-bred and native lizards, and at least eight of 178 lizards released in 2001 survived until their third (2003) activity season, a survival rate which is not much lower than the one previously reported for a population in Central Spain (Civantos and Forsman, 2000). Moreover, data on activity levels and intra-year survival also pointed out an advantage of introduced juveniles, which were active more frequently and until later dates than their native counterparts. These results might also be due to the high investment of captive-bred juveniles in exploring new microhabitats for home-range acquisition (Massot et al., 1994; Tweed et al., 2003), but even in that case their greater activity did not cause higher mortality.

Introduced lizards showed a higher propensity to disperse among fragments than native ones, covering distances up to 400 m (i.e. much larger than the 39 or 142 m required to move between V-1 and V-2 or between B-30 and B-32). Thus, captive-bred juveniles were able to cross through adverse farmland, which is consistent with an apparent advantage of juveniles in relocations (Reinert, 1991; Tweed et al., 2003). Long-distance dispersal from release sites is a sound indicator of reintroduction success (Ausband and Foresman, 2007), and the ability to move among patches of suitable habitat is clearly advantageous in fragmented landscapes (Hanski, 1998; Fahrig, 2003; Driscoll and Weir, 2005). Nevertheless, increased dispersal of introduced lizards could also be the result of competition with native residents (Mathews et al., 2005; Burns, 2005) until they managed to settle in a vacant territory (Burns, 2005). However, such a competitive disadvantage is unlikely because introduced juveniles were larger than native ones (see below), and body size is a significant predictor of survivorship and dominance in this and other lizard species (Tokarz, 1985; Díaz et al., 2005; Iraeta et al., 2008). The ability of captive-bred juveniles to disperse among nearby fragments should allow them to colonize the numerous unoccupied fragments in the landscape studied (Santos et al., 2008). This highlights the utility of reintroductions with captive-bred stocks as a conservation strategy in fragmented landscapes.

4.2. Body size advantage of captive-bred juveniles

The body size advantage of captive-bred juveniles relative to native ones was one of the clearest results of our study (Fig. 2). Thus, introduced juveniles (with mean SVL at release of 36.2 and 36.3 mm on 18 September 2001 and 26 September 2002, respectively) were larger than native juveniles from B-32 (28 and 28.9 mm on 7 and 25 September 2003). Such difference in body size could be explained by the advantage of early hatching (in the laboratory) or by better rearing conditions in captivity, two non-mutually exclusive possibilities which we cannot distinguish with our data. However, we can shed light on this issue by comparing our study population with another population from a montane oak forest in central Spain (Iraeta et al., 2006). Thus, the lizards we introduced in Lerma reached larger sizes than central Spanish juveniles, either if the latter were born in the field (mean capture date = 17 September 2005, mean SVL = 28.7 mm, $n = 35$) or if they were born in captivity and released in the field the day after hatching (mean hatching date = 27 July, mean recapture date = 13 September, mean SVL = 31.6 mm, $n = 14$; Iraeta et al., 2006). The size difference between field-born and lab-born juveniles in central Spain can only be attributed to the advantage of hatching early, because lab-born juveniles were released the day after hatching. This suggests that our introduced lizards (mean SVL > 36 mm) benefitted not only from early hatching, but also from a head start due to better rearing conditions in captivity, because they were fed *ad libitum* during an average period of 57.2 days (range = 27–74) before being released.

Moreover, the body size advantage of introduced juveniles was still clear after emergence from hibernation (see also Iraeta et al., 2008), and it was maintained throughout their second calendar-year (Fig. 2). Because body size greatly determines maturity in lizards (Bauwens and Díaz-Uriarte, 1997), a further advantage derived from captive breeding could be that reintroduced lizards may take shorter to mature because they are given a head start in terms of body size, compared to field-born conspecifics of a similar age. In fact, we made casual observations supporting this interpretation. Thus, on 18 July of 2003 we recaptured a gravid female in B-32 which had been released there as a juvenile in September of 2002 (SVL = 68 mm, age = 358 days). On 26 June 2003, we observed a male introduced in B-32 in 2002 (SVL = 69 mm, age = 345) copulating with a 69-mm long native female in B-31 (a fragment amid B-30 and B-32). These observations demonstrate that introduced lizards can mature in their second calendar-year, which is 1 year earlier than reported in other populations of this and other lacertid species (Bauwens and Díaz-Uriarte, 1997; Civantos and Forsman, 2000). Such an early maturation, remarkable because our study area is close to the northern edge of the species' distribution range (Díaz et al., 2007), might facilitate the settlement and long-term survival of introduced lizard populations.

4.3. Long-term survival and establishment of introduced populations

In spite of the short-term success of stocks of captive-bred juveniles, our reintroductions lack the ultimate test of the establishment of a viable self-sustaining population, which is a recognized criterion to judge the efficiency of *ex situ* conservation programmes (Fischer and Lindenmayer, 2000). Although we lack unequivocal evidence of reproduction in the formerly vacant fragment V-1, the search carried out in 2006 strongly suggests the presence of an established lizard population in V-1, supporting an increased achievement of our reintroductions over time. Thus, there were remarkable differences between our first and last visits in the time needed to capture the first native lizard (39 h in 2001 vs. 17 min in 2006), the number of lizards captured per unit of searching time (0.03 lizards/h in 2001 vs. 0.70 in 2006), and the proportion of adults seen (0 of 3 in 2001 and 2002 vs. two of six in 2006).

4.4. Success and costs of captive breeding

Captive breeding was successful and cheap and it was easily implemented in our Faculty facilities. Thus, 84% of the eggs laid in 2001 and 72% of those laid in 2002 developed into healthy juveniles which were released into the field. This is a satisfactory outcome, especially because captive breeding problems are frequent in many vertebrate species (Snyder et al., 1996).

Total cost of the whole procedure (excluding salaries) was very low: ca. 14,500 € in 2 years field work included, plus the use of small scientific equipment and a lab space of 210 m^2 during 2.5–3 months each breeding season. This amount was enough to release 365 juveniles. Specifically, our lab breeding program amounted to ca. 2500 €, a negligible quantity if it is considered that 20 years ago the average cost of captive-breeding programmes was about 500,000 $ per species and year (Snyder et al., 1996). In fact, such cost would be low even if salaries were included (ca. 18,000 € to cover the staff requirements in the lab: 3 months × 2 part-time lab technicians × 2 years). Also, the space and time requirements for developing successful vertebrate breeding programmes are usually much greater (Rahbek, 1993; Earnhardt et al., 2001; Tenhumberg et al., 2004).

5. Conclusions

It is common wisdom that the cost of captive breeding increases with body size and generation time of target animals, whereas release failures increase with domestication risk and persistence of the factors causing population decline (Snyder et al., 1996; Fischer and Lindenmayer, 2000). As a consequence, the best potential candidates for successful reintroductions with captive-bred stocks are small species easy to breed in captivity and lacking parental care (Snyder et al., 1996). These features decrease the costs of captive breeding and avoid disadvantageous behaviours in the wild, such as inefficient foraging and predator avoidance (Snyder et al., 1996; Mathews et al., 2005; Seddon et al., 2007). Clearly, the large *Psammodromus* fits well into this category and constitutes an appropriate model to develop this kind of conservation programme. Species like the above have two additional advantages in conservation practice. Firstly, they can be used as 'substitute species' to investigate the potential responses of endangered populations to relocation procedures (Fischer and Lindenmayer, 2000; Caro et al., 2005). Secondly, they can facilitate the study of life history traits which are critical for the success of both captive breeding and reintroduction in the wild (Rakes et al., 1999; Seddon et al., 2007).

Finally, it should be emphasized that our study was carried out in a fragmented landscape in which *P. algirus* has a meta-population structure composed by small sub-populations isolated from one another by distances that range between a few tens and hundreds of metres (Santos et al., 2008). Because dispersal among habitat patches is crucial to the long-time persistence of populations in fragmented landscapes (Hanski, 1989), the ability of captive-bred lizards to disperse among fragments further supports the success of our reintroductions. Moreover, our study has practical implications for the conservation of this and perhaps other similar species at a regional scale. Previous results on the distribution pattern of the species suggest that no lizard populations persist westwards of the motorway A-I, despite the existence of numerous woodland fragments of a high habitat quality and a more than suitable surface area (Díaz et al., 2000; Santos et al., 2008). The loss of these potential sub-populations is likely associated with historical effects of fragmentation (Díaz et al., 2000) combined with severe isolation caused by the motorway, which would have prevented the recolonization of the western fragments by lizards dispersing from eastern woodlands. Thus, conservation planning should carefully consider reintroducing captive-bred lizards from the eastern side of the motorway, given the low cost and high success of the procedures reported in this study.

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