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AN ENCLOSURE DESIGN ALLOWING QUANTIFICATION OF DISPERSAL IN LIZARD POPULATION STUDIES

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SUMMARY

Dispersing common lizards were trapped in pitfall traps buried along both sides of an enclosure that fenced the study area. Local movements across the fence comprised about half of the captures made. An estimated 25% of the movements were not recorded by the traps. Less than 10% of the emigrants were detected by searching the surroundings of the plot. Use of the method described resulted in a tenfold increase of the accuracy of the emigration estimates compared to estimates obtained by searching the surroundings of the area.

INTRODUCTION

Dispersal is not often measured in population studies especially in lizards. The paucity of investigations of dispersal processes in lizard populations is well illustrated in a recent review of the dynamics of squamate populations (Turner, 1977), in which no special attention to dispersive movements could be given. This is unfortunate but not surprising since dispersal is undoubtedly very difficult to investigate. For this reason investigators usually assume dispersal to be negligible, or that immigration and emigration rates are equal. Although studies of dispersal are laborious and often difficult, they may provide important insight in the dynamics of population structure and in components of life history strategies (Horn, 1978).

In lizard population studies, estimates of dispersal may be obtained by intensive search for marked individuals beyond the margins of the study area (Tinkle, 1967; Ballinger, 1973). This method is however extremely laborious and therefore often impracticable. Attempts to estimate dispersal in lizard population studies are therefore rarely made (Turner, 1977).

In a population study of the common lizard, *Lacerta vivipara*, we initially attempted to quantify dispersal by an intensive capture–recapture programme both within and beyond the margins of the study plot. In addition to being very time consuming, the method proved to be unsuccessful since we could show that the observed emigration rate underestimated the actual dispersal rate (Bauwens & Verheyen, 1980). Although a rather high number of lizards marked within the plot were subsequently recaptured outside the study area, the majority, if not all of them, were animals whose home ranges were located on both sides of the margins of the plot. Lizards considered as dispersers were only occasionally captured, probably because the majority of them moved to areas that were not visited by us. Intensive search in a larger area would possibly reveal more dispersal, but was impracticable within the time available. In order to overcome this problem, we designed an enclosure allowing quantification of dispersal. The reliability of the estimates obtained by this method is discussed here.

MATERIALS AND METHODS

A population of common lizards, *Lacerta vivipara*, was studied in a 52 m × 36 m study plot located in the Belgian national nature reserve "de Kalmthoutse heide" (Kalmthout (51°25′N, 4°25′E), Province of Antwerp, Belgium).

The vegetation of the study area is characteristic of moist heathland. Dominant plants are cross-leaved heath (*Erica tetralix*), purple moor-grass (*Molinia caerulea*) and bog asphodel (*Narthecium ossifragum*). A part of the study site is flooded temporarily (Fig. 1). Birch (*Betula pendula*) and pine (*Pinus sylvestris*) stand isolated and form small bushes. A long side of the plot borders on a sand dune. On the lee-side the dune is overgrown by birch and some pine (Fig. 1). The top and the weather-side of the dune form a zone of bare sand of about 50 m wide which acts as a natural barrier for the lizards.

Lizards were captured by hand. We gave each lizard a unique and permanent mark by toe-clipping. A corresponding colour mark was painted on its back, allowing future identification by sighting.

Three age classes could readily be distinguished in the field: juveniles (young born during the current activity season), subadults (lizards born during the preceding activity season) and adults (animals being at least in their third activity season).

Within the study plot, lizards were captured and/or identified by sightings daily, weather permitting, from March through to October. A 30 m wide zone surrounding the plot was visited weekly from March to June and daily from July to September 1979.

During the winter of 1978–79 an enclosure was placed at 5 m distance from the margins of the study area (Fig. 1). The enclosure was constructed of aluminium sheets (2.5 m × 0.6 m × 0.8 mm) and supported by wooden stakes which extended about 20

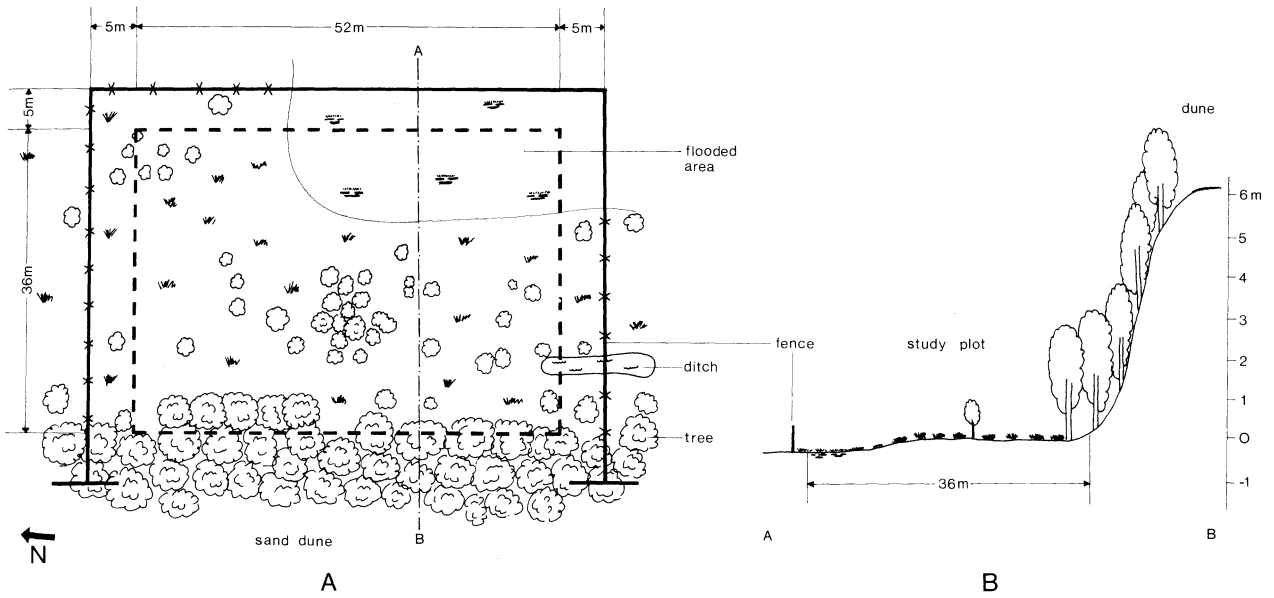

FIG. 1. (a) Map of the study area showing boundaries of the plot (dashed line), location of the enclosure (solid line) and characteristics of the vegetation. The position of the pitfall traps along the fence is indicated by crosses (a persisting high water table prevented burying of traps in the flooded area). (b) Cross section of the study area through the line A–B.

cm aboveground (see also Medica, Hoddenbach & Lannom, 1971). The metal sheets were placed in the ground to a depth of about 15 cm and extended 45 cm aboveground. Approximately every 4 m a gap of about 35 cm wide was left in the fence. On both sides of every gap we placed a plastic box (45 cm × 15 cm × 15 cm) as a pitfall (Fig. 2). Previous tests indicated that the lizards could not escape from these traps. Within the traps we placed small boxes of white plastic as a shelter against possible avian predators and to allow the lizards to thermoregulate. Preliminary tests demonstrated predation by nocturnal carabid beetles (mainly *Carabus clathratus* and *C. violaceus*) on the lizards in pitfalls. To avoid such artificial predation, traps were removed at night and during periods of abscence, and the gaps were closed so that dispersal was prevented. The 19 pairs of pitfall traps were examined at least twice daily.

Lizards attempting to enter the plot were trapped in one of the outer boxes, toe-clipped and placed within the study area. Lizards trapped in an inner box were identified and placed outside the study area.

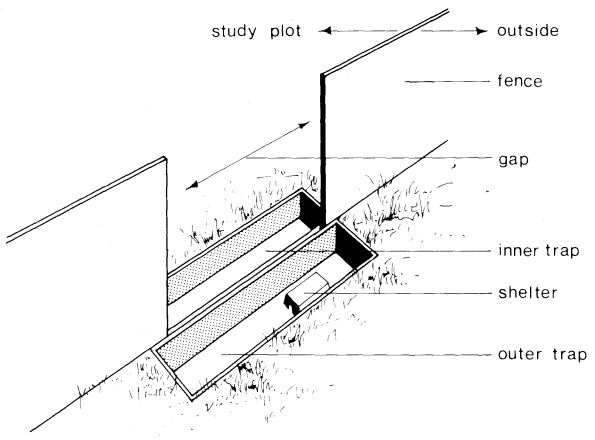

FIG. 2. Detail of the enclosure which allows trapping of dispersing lizards.

The gaps in the fence are perhaps not a necessary device for the method. Gaps were left to allow possible directional orientation toward visible objects such as trees, forest-edges and other objects in the landscape.

Lizard movements across the enclosure traps were classified into five categories (according to definitions of Caughley, 1977):

(i) dispersal: one way in- or outward movements of lizards which were not known to have occupied a home range near the margins of the plot before and after the movement.
(ii) non-permanent migration: in- or outward movement followed, after an interval of at least one month, by a movement in the reverse direction. During their temporary presence or absence in the plot, these lizards did not occupy a home range near the margins of the plot. This category includes movements from an animal's summer home range toward its hibernation site and vice versa.
(iii) nomadism: movements of lizards which enter and subsequently leave the plot, within an interval of one month, at localities (traps) that are at least 30 m apart.
(iv) local movements: movements across the fence of animals which occupied a home range near or at both sides of the enclosure.
(v) unclassifiable movements: movements that, due to a lack of information before and after it, could not be assigned to one of the former categories.

RESULTS AND DISCUSSION

In order to provide accurate estimates of dispersal, the method described here must meet two major requirements. Firstly, only dispersing or migrating animals should be trapped in the enclosure-traps, or

TABLE I. Number of animals trapped and number of captures made during 1979 in the enclosure traps. Movements of lizards across the fence were classified into five categories according to the capture–recapture history of the individual animals (see text for definitions)

	Number of animals trapped	Number of captures
Dispersal	52 (27%)	52 (19%)
Non-permanent migration	21 (11%)	28 (10%)
Nomadism	13 (8%)	20 (7%)
Local movements	69 (36%)	139 (51%)
Unclassifiable*	33 (17%)	33 (12%)
Total	191	272

* Includes three animals killed in the traps by carabid beetles.

one should be able to distinguish between dispersive and local movements. Secondly, all dispersing and migrating lizards should be trapped in the boxes.

It is obvious from the data shown in Table I that not only dispersing or migrating animals are trapped in the enclosure-boxes. About half of the captures relate to local movements. This may not be surprising since the enclosure acts as a drift fence on lizards with home ranges near or along both sides of it. Since these animals are captured repeatedly as they move back and forth across the gaps in the fence and/or at both sides of the enclosure, they are distinguishable from migrating animals. Omission of these movements reduces, to a large degree, the bias that would result if we would estimate dispersal by counting the number of animals trapped in the pitfall traps. However, it remains possible that a number of local movements were erroneously considered as dispersive because the lizards involved were missed when we inspected the surroundings of the study plot or died shortly after they crossed the fence. This would result in an overestimate of the actual dispersal rate. Since our capture–recapture programme was very intensive (about 40% of the minimum number of lizards alive in the plot were captured daily) it is likely that the resulting bias is small.

In spite of repeated attempts to prevent lizards leaving or entering the enclosure via routes other than by the traps, some lizards were known to escape through the enclosure wall. Estimates of the number of these "escapes" can be made more accurately for the process of immigration than for emigration because animals moving into the study area will usually be detected while the reverse is not necessarily true. Adult lizards which avoided the pitfall traps could be recognized since all resident adults and subadults were marked during 1978 (Bauwens & Verheyen, 1980). Since only a fraction of the juveniles present during 1978 were marked, we could not always distinguish between resident subadults (the juveniles of the preceding activity season) and subadults avoiding the pitfall traps during 1979. For the subadult age-class, an indirect method had to be used. Figure 3 shows the cumulative number of marked and unmarked subadults captured in the study area during 1979. By the end of May we had captured all surviving marked subadults, whereas the curve for unmarked lizards only levels off by the end of June. We estimate the minimum and maximum number of clandestine immigrants in this age-class as the number of unmarked lizards captured respectively from July and June onwards. These figures were compared to the actual number of immigrants trapped in the enclosure boxes (Table II). Table II also shows the minimum number of illegal local movements across the fence. These could be detected by analysing the successive capture localities of the individual lizards. According to the data in Table II we estimate that approximately 25% of the movements across the enclosure were uncontrolled. Assuming that this figure also applies for movements out of the plot, it is possible to correct the obtained estimates for emigration rate. Nevertheless, the number of "escapes" remains high and some elaboration is needed here. Repeated attempts to prevent the lizards from escaping by stopping

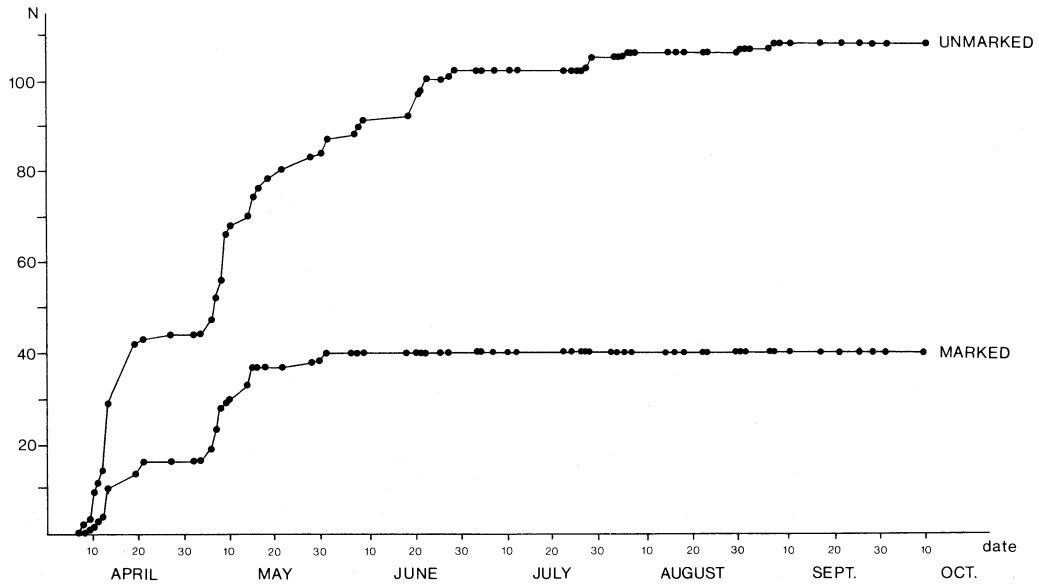

FIG. 3. Cumulative number of different subadults trapped during 1979 within the study plot. Distinction was made between subadults that were marked during 1978 (as juveniles) and unmarked subadults.

TABLE II. Number of captures made in the enclosure traps and estimated number of uncontrolled movements across the fence assigned to the processes of immigration and travelling within a home range

	Number of captures made	Estimated (minimum and maximum) number of "escapes"	% "Escapes" (minimum and maximum) of total number
immigration*	47	7–22	13–32
local movements	141	33	19

* Includes dispersive, migrating and nomadic movements.

up small crevices at both sides and under the metal sheets as well as by joining the sheets tightly were unsuccessful. As the possibility existed that lizards could get through the gaps without actually falling into the pitfalls by climbing over the joined side-walls of both traps, we placed a plate between the pitfalls that extended about 7 cm above them. This modification did not completely prevent "escapes". Hence, we suppose that the alternative ways still remaining which were used by the lizards to cross the enclosure include small crevices and perhaps burrows of small mammals that remained undetected by us. In building a similar enclosure, care should thus be taken to place the metal sheets as deep as possible and to make every attempt to stop up all visible crevices.

Since we also visited the surroundings of the study plot, we compared the estimates of emigration rate obtained by both the enclosure- and the search-method. Of 41 animals that were known to have left the plot during the processes of dispersal, non-permanent emigration or nomadism, 5 were recaptured in the surroundings of the area. Taking into account that an estimated 25% of the actual number of dispersing lizards avoid the pitfalls (none of which was recaptured out of the area), less than 10% of the emigrants were detected out of the plot. In view of these findings, it is not surprising that we underestimated the actual emigration rate during 1978 when only the search method was employed.

Although a rather high number of movements across the enclosure were uncontrolled, the method described seems to provide estimates of dispersal rate which are less biased compared to estimates obtained by searching beyond the boundaries of an unfenced area. In addition, the timing of dispersal can be determined exactly and the occurrence of nomadic movements can be demonstrated. We therefore conclude that the enclosure method is currently the most accurate and least time consuming for use in lizard population studies.

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