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Communal egg-laying in oviparous *Zootoca vivipara louislantzi* of the Central Pyrenees

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Communal egg-laying, or communal nesting, has been observed in reptiles, amphibians, insects and birds (Doody et al., 2009). Different hypotheses may explain its evolution and maintenance (Doody et al., 2009; Graves and Duvall, 1995). Prevalent hypotheses are: low availability of adequate habitat for egg-laying (Pleguezuelos et al., 2004), attraction of gravid females by freshly laid eggs or old hatched eggshells (i.e. conspecific attraction or cueing, Brown and Shine, 2005; Elphick et al., 2013; Radder and Shine, 2007), and increased egg survival of aggregated eggs in stressful environments (Marco and Díaz-Paniagua, 2008; Marco et al., 2004). Radder and Shine (2007) and subsequently Doody et al. (2009) classified the diverse explanations for the existence of communal nesting into two main non-mutually exclusive hypotheses: the 'constraint hypothesis' states that a low availability of suitable habitat or environmental conditions (e.g. specific and rare temperature or moisture range) favours communal egg-laying. On the other hand, the 'adaptive hypothesis' implies the existence of direct or indirect fitness benefits for females that lay eggs in communal nests. According to these two hypotheses, a high frequency of communal nests would be predicted in habitats with few suitable laying sites and/or in places where eggs have been previously laid (either fresh clutches or old eggshells), since this provides evidence for quality of and success at a laying site.

On 11 July 2012, close to El Portalet (Sallent de Gallego, Huesca, NE Spain; 42° 48' 2.96'' N, 0° 24' 48.24'' W; 1.720 m a.s.l.; Fig. 1A), the authors turned over a medium sized rock (approximate measure of the stone: 40 cm in length and 20 cm in width) in an intensively surveyed common lizard population and discovered a communal nest and an adult female common lizard *Zootoca vivipara* (Lichtenstein, 1823), which were hidden below the rock (Fig. 1B). The study population belongs to the NE Spain clade (Milá et al., 2013) of the oviparous *Z. vivipara louislantzi* Arribas, 2009 and it is located in a wet heathland adjacent to a bog, which is the species' preferred habitat (Pilorge, 1987). The population gently slopes down from north-west to south-east. To the south-west it is bordered by the Gállego River, to the north-east by the slope of an asphalted parking, and to the south by the junction of a rill and the Gállego River. Vegetation mainly consists of hydrophilic grasses *Carex davalliana*, *Carex lepidocarpa* and *Carex nigra* on the eastern side and it is herbaceous on the west. No shrubs are present and rocks represent an area of less than 10 % of the total surveyed area (3872 m^2). The communal clutch consisted of a cluster of at least 80 fresh and calcified eggs (Fig. 1B-D) and an additional 6 eggs that were laid nearby (1.4 cm apart). The fresh eggs were surrounded by at least 37 eggshells from previous years (Fig. 1D). We measured the size of a sub-sample of the eggs (mean ± standard error) using Adobe Photoshop and a reference distance of known length. Eggs were on average 11.7 ± 0.2 mm long and 8.7 ± 0.2 mm wide (n = 10). In the Cantabrian populations clutch size ranges from 2 to 11 eggs with a mean of 6.35 eggs per clutch, and a mean egg size of 12 mm in length and 9 mm in width (Bea, 1978; Braña, 1986; Braña and Bea, 1987). In populations of southern France average clutch size is 5.3 eggs and mean egg size is 10.3 mm in length and 6.7 mm in width (Heulin, 1988). Eggs of the same clutch are normally glued together by oviductal secretions, and eggs laid by different females and on different dates generally

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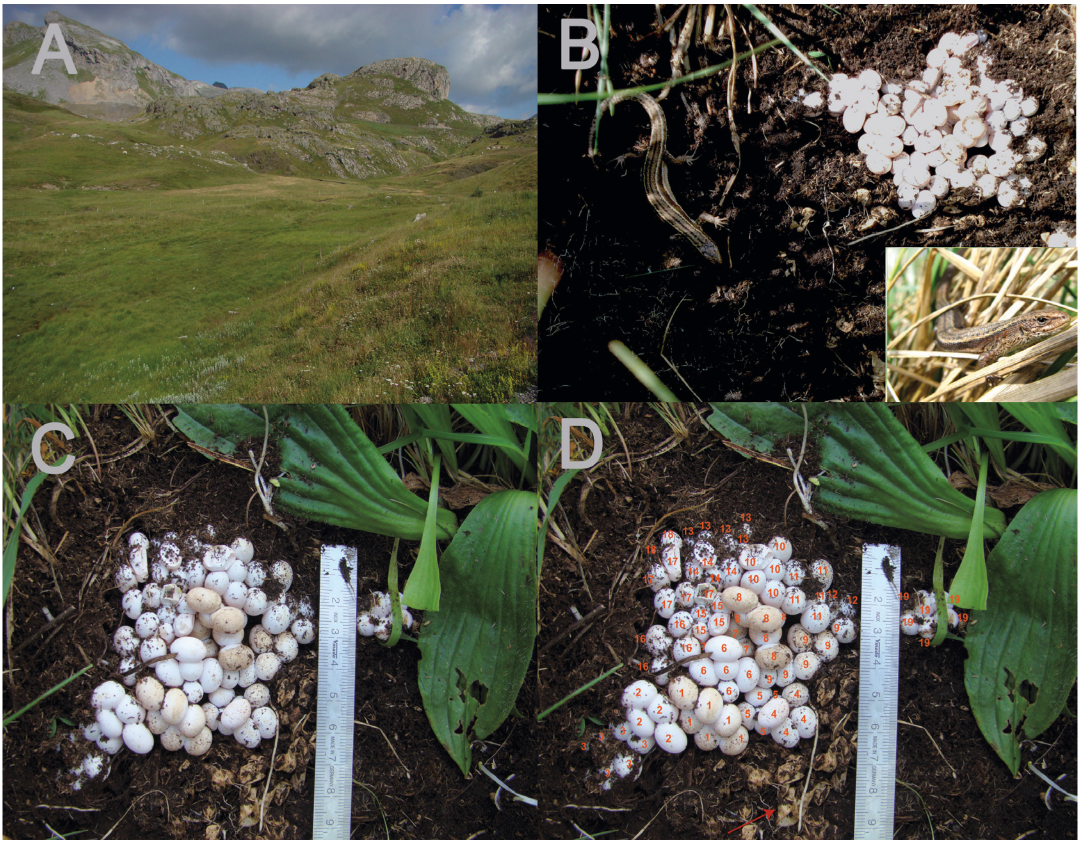

Figure 1. A) Photograph of the habitat where the communal nest was found (population close to El Portalet, Sallent de Gállego, Huesca, Spain). B) Communal clutch photographed on 11 July 2012, right after its discovery. An adult female common lizard was hidden below the rock, near the oviposition site. Lower right corner: adult female *Z. vivipara*. C-D) Communal nest of *Z. vivipara*. Eggs have been assigned to different clutches and numbers in D) so that eggs with the same number belong to the same clutch (see text). The red arrow points to one representative old eggshell. (Photos: A, B: C. Romero-Diaz, B: (adult female) M. C. Breedveld, C, D: M. Peñalver-Alcázar).

have a different coloration, orientation, and size. Taking these characteristics into account, we estimated that the detected communal nest consisted of at least 18 clutches laid by different females (Fig. 1D and Table 1; note that eggs were laid on top of other eggs and thus not all eggs and clutches are visible on the photograph), whereas the 6 nearby eggs probably belong to the clutch of a single female. The average clutch size was 4.5 eggs ± 0.3 SE (Table 1). Both the egg size and the clutch size are within the range of the eggs and clutches produced by *Podarcis muralis* (Ji and Braña, 2000), another lacertid which lives in sympatry with *Z. vivipara* in some locations of the Central Pyrenees. Intensive population censuses performed by the authors during 30 hours along 3 months, revealed only 4 individuals of *P. muralis* at the borders of the study area (88 x 44 meters). All *P. muralis* observations were located at a minimum distance of 28 meters from the rock, in plots exhibiting much lower humidity than the plot where the communal clutch has been found and in none of the censuses were other lacertids observed. The clutch and egg characteristics, the detected high abundance of *Z. vivipara* in the rock's vicinity, the presence of an adult *Z. vivipara* female when detecting the communal clutch (Fig. 1B), the absence of *P. muralis* observations, and the low suitability of the habitat surrounding the rock

Table 1. Clutch number and number of eggs per clutch of the communal clutch shown in Fig. 1B-D. The clutch number corresponds to the clutch number indicated in Fig. 1D.

Clutch Nº	Nº Eggs
1	6
2	4
3	6
4	4
5	4
6	5
7	3
8	6
9	6
10	5
11	5
12	2
13	5
14	4
15	4
16	4
17	5
18	2
19	6
Total eggs	86

for *P. muralis,* guaranteed the correct attribution of the eggs to *Z. vivipara* (Ji and Braña, 2000; Van Damme et al., 1992).

In Spain, southern France, Slovenia, Croatia, southern Austria, and northern Italy the reproductive mode of *Z. vivipara* is oviparous, while in the rest of its distribution (i.e. from Ireland to Japan, and from Finland to the Alps) it is viviparous (Surget-Groba et al., 2006). Previous cases of communal egg-laying have been reported for *Z. vivipara* in the Cantabrian Mountains (Mellado, 1981; Braña, 1986) and in the Pyrenees (Lantz, 1927), but no observations exist from the viviparous clades. The most detailed report of a communal clutch stems from Braña (1986) and was located in Señales-Tarna (Caso, Asturias). This clutch (Braña, 1986, page 281) consisted of at least 33 eggs from 6 different clutches (numbers based on personal counts, 3 well defined clutches, and one cluster of eggs seemingly made up of 3 aggregated clutches). Our observation thus is the biggest documented example of communal egg-laying in *Z. vivipara*.

The location of the communal clutch suggests that females may have selected to lay the eggs below the rock due to its favourable microclimate, which is in line with the 'adaptive hypothesis'. The rock under which the communal clutch was found was the only big rock present in the adjacent areas, which are usually flooded and where only very few visible small stones exist. Thus the 'constraint hypothesis' may also explain the existence of the communal clutch.

To disentangle among the two hypotheses, in 2012, we allowed 3 females to lay eggs in a semi-natural population of a size of 100 m^2 and located at 'el Boalar de Jaca', Jaca. The population consisted of 4 stone piles with plenty of stones, bark, natural plants, and 2 water ponds (Cote et al., 2008; Fitze et al., 2008; Le Galliard et al., 2008; Le Galliard et al., 2005; San-Jose et al., 2014). After egg-laying, clutches were searched in the entire population and a communal clutch consisting of two clutches was found below one stone. Given that a lot of different stones existed in the population, it is unlikely that nesting sites under stones were a scarce resource. Thus, the 'constraint hypothesis' cannot explain the existence of the communal clutch. Furthermore, in previous years females were never allowed to lay eggs in this population, and thus attraction by old hatched eggshells can be discarded as well as philopatric female behaviour, given that none of the females was born in this population. This suggests that favourable microclimate and/or attraction by conspecific eggs, and thus the 'adaptive hypothesis' may explain the occurrence of communal egg-laying in the wild. The high humidity of the soil below the stone where the communal nest was found, assures that eggs will not dry out. The clutch's location under a rock moreover exposes the eggs to prolonged periods of heat, since rocks of this size heat up rapidly and act as heat reservoirs, when ambient temperatures are lower, which accelerates the egg development time (Shine, 1999). This could explain why no clutches were found under smaller stones, where microclimatic conditions are not the same (e.g. smaller stones do not act as heat reservoirs for as long as intermediate sized rocks). Moreover, clutches laid below a stone may also be protected from avian and above-ground dwelling predators. These lines of evidence suggest that laying clutches below stones might provide advantages, and thus that the 'adaptive hypothesis' may explain the occurrence of communal egg-laying.

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