

Decrease in litter size in the shrew *Crocidura suaveolens* (Mammalia, Insectivora) from Corsica (France): Evolutionary response to insularity?

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Abstract: Populations of the lesser white-toothed shrew, *Crocidura suaveolens* (Pallas, 1811), from Corsica show an increase in adult body size associated with a decrease in litter size. The average number of embryos in wild Corsican females is smaller (mean 2.6, $n = 62$) than in mainland females (mean 4.6, $n = 173$). A breeding experiment was run for 4 years, yielding three generations. Under standard breeding conditions, the differences between island and mainland populations were maintained and were significant (median litter size was 2 for Corsica and 5 for the mainland). These differences in life-history traits were therefore proved experimentally to be genetically determined. Hypotheses concerning the mechanisms responsible for these differences are discussed.

Résumé : Les populations corses de Musaraigne des jardins, *Crocidura suaveolens* (Pallas, 1811), sont affectées de gigantisme et le nombre de jeunes par portée y est réduit. Le nombre moyen d'embryons chez les femelles sauvages corses est plus bas (moyenne 2,6, $n = 62$) que chez les femelles du continent (moyenne 4,6, $n = 173$). Des expériences d'élevage en laboratoire durant une période de 4 ans ont donné trois générations. Dans des conditions ordinaires d'élevage en captivité, la différence entre les populations insulaires et continentales s'est maintenue et est restée significative (taille médiane des portées : Corse, 2; continent, 5). Ces différences reflètent un déterminisme génétique propre. Les hypothèses sur les mécanismes qui ont abouti à ces différences font l'objet d'une discussion.

Introduction

The evolution of island populations has been extensively studied since the pioneer work of MacArthur and Wilson (1963, 1967). The Royal Society of London has recently published a symposium "Evolution on islands" (Clarke and Grant 1996), which is presumably the most up-to-date discussion of the subject. This interest stems from the fact that a species colonizing an island is subject to new environmental conditions, which Blondel (1986, 1995) terms the "syndrome d'insularité." Changes on islands include, for example, a decrease in the diversity of predators and competitors, which is generally associated with an increase in population density of the colonizing species (Stamps and Buchner 1985; Granjon and Cheylan 1988) with broadening of their ecological niches. But colonization may also lead to

a situation in which, under island conditions, previously unimportant predators and competitors become important. Moreover, the body sizes of island vertebrates may show important changes. Though there are many exceptions, large mammals such as elephants or hippopotami usually become smaller, whereas small mammals tend towards gigantism (Case 1978; Heany 1978; Abbott 1980, 1983; Lawlor 1982; Lomolino 1985; Libois and Fons 1990; Libois et al. 1993; Michaux et al. 1996). Litter size is known to increase with body size among continental mammals smaller than 1 kg (Tuomi 1980), but adaptation to insularity is expected to lead to a decrease in fecundity (Lack 1948; Blondel et al. 1992).

Although many studies have provided examples of changes in life-history traits on islands, few have provided clear evidence of corresponding genetic evolution (Blondel et al. 1990). In this respect, the shrew model seemed to be a particularly interesting one to study in Corsica because most of the prey, predator, and competitor species found in the shrew's environment around the Mediterranean basin are missing from this island. For example, 13 species of Insectivora and 14 species of Carnivora live on the mainland. Of these, three Insectivora (*Erinaceus europaeus*, *Suncus etruscus*, *Crocidura suaveolens*) and four Carnivora (*Vulpes vulpes*, *Mustela nivalis*, *Martes martes* (?), *Felis silvestris*) remain in Corsica (Fayard 1984; Fons 1987; Cheylan 1987).

Two species of *Crocidura*, the greater white-toothed shrew, *C. russula*, and the lesser white-toothed shrew, *C. suaveolens*, live in southern France. The former is a relatively large-bodied species weighing 6–12 g, whereas the latter is small and weighs 3.5–5 g. Corsican shrews look like *C. suaveolens* but are similar in size and mass (6–13 g) to the continental *C. russula* (Poitevin et al. 1987; Fons 1988). This explains why the name of the Corsican shrew has changed seven times

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in the last 50 years, depending on whether emphasis is given to biometry or to morphology. Finally, analysis of the Corsican populations by electrophoresis, karyology, and morphology has shown that these shrews are in fact "giant" *C. suaveolens* (Catalan and Poitevin 1981).

Is this increase in body size of *C. suaveolens* associated with larger litters, as on the mainland? Does insularity lead, on the other hand, to a decrease in fecundity? The observations and breeding experiments reported here are aimed at answering these questions.

Material and methods

Fecundity is determined by two parameters, the number of pups born in each gonotrophic cycle and the number of reproductive cycles. Counting the embryos in each female captured in the field gives an estimate of the first parameter. The second parameter is impossible to determine in the field because longitudinal analyses of shrew populations are difficult and, in any case, would be of little interest because uterine scars are almost invisible in *Crocidura* spp. (Jeanmaire-Besançon 1985).

Moreover, litter size variability is under genetic and environmental control (Land 1985). To determine the relative contributions of genetic and environmental variance to total phenotypic variance, two methods can be used: (i) estimating correlations (h^2) between related individuals; and (ii) comparing different populations under standard breeding conditions, allowing the genetic component of the individuals to be fully expressed. We used the second method, which has been successfully employed to establish the genetic component of egg laying in Corsican blue tits (Perret et al. 1989).

Using Sherman or pitfall traps, 714 *C. suaveolens* were collected from mainland France (336 males and 378 females, 173 of them pregnant) and 285 from Corsica (148 males and 137 females, 62 of them pregnant). On the mainland and the island, habitats representing the different types of vegetation were sampled from sea level to 1000 m elevation. Sampling of animals over the whole annual cycle was repeated for 7 years in Corsica and 10 years on the mainland. The embryos in each female captured in the field were counted after dissection. The results show that the breeding season lasts from March to October and is similar in both regions. The existence of postpartum oestrus was observed in the two populations bred at the laboratory, where the number of pups per litter varies from 1 to 4 for both populations. These results correspond to previously known data on the Crocidurinae (Fons 1988). In the laboratory, the animals were placed in 50 × 30 × 70 cm glass vivaria. The ground was covered with 10 cm of soil or sawdust litter. Artificial burrows in blocks of plaster linked to the vivaria by maze-like pipes were at the disposal of the shrews. A glass partition allowed direct 24-h observation of the animals in their nests. The vivaria were subjected to the natural photoperiod, with temperatures ranging from 12 to 30°C (median 20°C). The animals were fed ad libitum with larvae, pupae, and adults of the flour worm *Tenebrio molitor*, adult crickets *Acheta domestica*, and cow spleen. Water was provided ad libitum (Fons 1974).

Results

Field observations

The distributions of embryo numbers observed in the two populations (Fig. 1A) were not symmetrical and did not fit Gaussian distributions (for normal distribution, $p = 0.004$ and $p = 0.005$, respectively). Therefore, nonparametric statistics were used for all further analyses. These comparisons showed that these distributions were significantly different ($\chi^2 = 138$, $df = 4$, $p < 10^{-4}$) and that the median

of the Corsican data (2) was lower than that of the mainland data (5) (median test, $\chi^2 = 89$, $df = 1$, $p < 10^{-4}$), which was, in turn, similar to that reported by Vlasak (1989) in Czechoslovakia.

Breeding experiments

The breeding experiment was run for 4 years; 30 island females and 36 females from the mainland were bred in the laboratory, yielding 75 and 66 litters and 181 and 289 pups, respectively. The observed distributions of the number of pups per litter on the island and on the mainland (Fig. 1B) were both skewed (normality, $p = 0.03$ and 0.004 , respectively). They did not differ from those observed in the wild (Corsica: $\chi^2 = 1.6$, $df = 2$, $p = 0.4$; mainland: $\chi^2 = 1.93$, $df = 3$, $p = 0.5$). However, the number of pups born in the laboratory was slightly lower than that observed in the wild; the median test showed that this reduction was significant ($\chi^2 = 5.99$, $df = 1$, $p = 0.02$). The differences between island (median = 2) and mainland populations (median = 5) were maintained and significant (Fig. 1) ($\chi^2 = 21$, $df = 2$, $p < 10^{-3}$).

Discussion

Rood (1965) noticed that in the Scilly Islands, *C. suaveolens* contained 1–5 embryos (mean 2.97). In the absence of other observations, and disregarding the island origin of Rood's data, Vlasak (1989) concluded that "in the area of distribution of *Crocidura suaveolens*, the average size of an embryonic set increases apparently in eastward direction."

The results from southern France challenge this conclusion, since the difference between the two mainland populations studied by Vlasak and ourselves is not significant ($\chi^2 = 6.9$, $df = 3$, $p > 0.05$), whereas these two populations differ clearly from all known island populations of *C. suaveolens* (Table 1).

From our results with laboratory-born animals, we may conclude that (i) the increase in body size of *C. suaveolens* in Corsica is associated with a decrease in litter size; (ii) this change correlates with an increase in the size of the pups at birth; they are almost twice as heavy as those of mainland shrews (mainland: 0.42–0.65 g; Corsica: 0.9–1.0 g; accuracy ± 0.01 g) (Fons 1988). Moreover, in Corsican shrews there is a considerable decrease in the energy allocated to gestation: the total mass of a litter is 50% of that of the mother on the mainland versus only 18% in Corsica; (iii) these changes, which are genetically controlled, occurred recently, since, according to Vigne and Marinval-Vigne (1990), *C. suaveolens* colonized Corsica only 4000 years ago. Two pieces of evidence suggest that the selective pressures affecting body size and litter size are relatively independent (Batten and Berry 1967; Genoud and Perrin 1994). First, the relationship between these two characters is positive on the mainland and negative on islands. Second, the pattern observed in Corsica, large body size and low fecundity, is not general; not every island population of *C. suaveolens* is characterized by large size, although their fecundity is always reduced. This discrepancy has also been observed in species of Muridae (Granjon and Duplantier 1989; Adler and Levins 1994). For instance, an increase in body size of the black rat, *Rattus rattus*, occurred only on Mediterranean

Fig. 1. Litter sizes of wild-caught (A) and laboratory-bred female *Crocidura suaveolens* (B) on the mainland of France (Banyuls-sur-Mer) and on an island (Corsica). The reduction in litter size observed in nature (A) is maintained under standard breeding conditions (B).

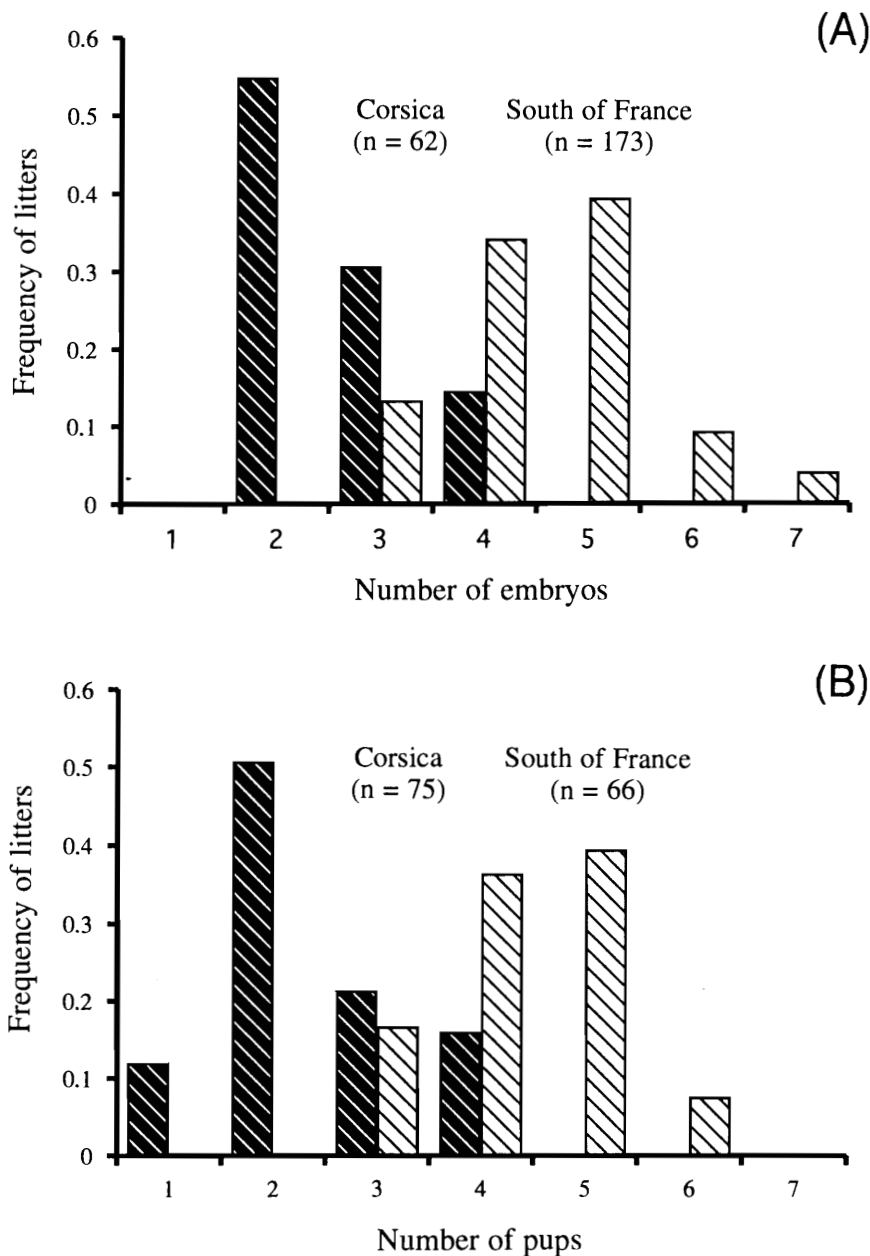


Table 1. Comparison of litter sizes in mainland and island populations of *Crocidura suaveolens*.

Populations	Median	Range	Mean	<i>n</i>	Source
Mainland					
Bratislava	5.0	3–7	4.9	40	Vlasak 1989
Banyuls-sur-Mer	5.0	3–7	4.6	173	This study
Islands					
Minorca	3.0	1–3	2.4	5	S. Mas Coma (personal communication)
Scilly	?	1–5	2.97	31	Rood 1965
Porquerolles	3.0	2–4	3.0	17	This study
Corsica	2.0	2–4	2.6	62	This study

Note: Embryos were counted after dissection of animals from the field.

islands smaller than 1500 ha, while the decrease in litter size was constant and not related to the size of the islands (Cheylan 1986).

However, the mechanisms that led to changes in these traits remain hypothetical; in vertebrates, the size of offspring correlates with that of the future adult, whose fitness is strongly influenced by this factor (Perrins 1965; Albon et al. 1987; Clutton-Brock 1988; Richner 1989; Sinervo 1990; Tinbergen and Boerlijst 1990; Stearns 1992; König 1993; Genoud and Perrin 1994). However, among mammals and birds, most of the reproductive investment occurs after birth. It is modulated through interactions between the young and their parents so that the young partly control this investment (Trivers 1985). The resulting compromise is dependent on the phenotype ("quality") of the female, particularly her mass, as well as factors that control the size and number of young. For a particular level of maternal investment, the mean number and mass of young are negatively correlated, but among species like *C. russula*, the variation in litter mass, which depends on the combination of these two factors, can affect the survival of the young and the contribution of the adults to reproduction (Genoud and Perrin 1994). In the Soricidae, whose metabolic rate is already very high (Fons and Sicart 1976; Bartels et al. 1979; Genoud and Vogel 1991), reproduction entails a threefold increase in energy demand.

In *C. suaveolens* from Corsica, the increase in adult size, combined with the decrease in the number of young per litter, leads to the production of larger pups than on the mainland (mass of the island animals: 6–13 g; mass of the mainland animals: 3–5.4 g) (Fons 1988). There are two ways to interpret this original response. The first one is based on ultimate factors and the second on proximate ones.

The first one postulates that, like the blue tit at the beginning of the breeding season (Blondel et al. 1990), at some period of the year, *C. suaveolens* in Corsica has difficulty in meeting its energy requirements and is obliged to attack larger prey, which in turn selects for an increase in its own size. In this hypothesis, the observed evolutionary changes would result from adaptation to disadvantageous conditions of life.

The second hypothesis considers that the absence of the competitors usually encountered on the mainland allows *C. suaveolens* to reach a large size in Corsica and reduce the energy allocated to gestation by minimizing the parent-offspring conflict. The observed evolutionary changes would then have arisen from the new social interactions that appear in mammal populations when the density is high and stable over time.

These two hypotheses may be correct, and they are not mutually exclusive: ecological factors could play a major role during colonization, while the behavioural mechanisms of regulation could balance the selective advantage of the more prolific individuals in settled island populations.

The second hypothesis suggests that the social structure is more complex in less prolific island populations. The comparative ethology and physiology of animals from different situations in the field may help to answer these questions (investigations are in progress). So the shrew model from Corsica seems to be particularly interesting for analyzing how selective mechanisms can operate at different levels and lead to the emergence of more complex systems.

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