Ecological notes on Crowned Snakes *Elapognathus coronatus* from the Archipelago of the Recherche in southwestern Australia

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ABSTRACT

We collected 48 Crowned Snakes *Elapognathus coronatus* on Mondrain Island, in the Archipelago of the Recherche, in November 1999. Published data on the ecology of *E. coronatus* are based almost entirely on examination of museum specimens from mainland localities, and differ in several respects from our findings. Mondrain snakes are larger than their mainland conspecifics, and males grow much larger than females on Mondrain (mean adult snout-vent lengths of 456 vs 403 mm). In strong contrast, mainland snakes display little sexual size dimorphism (318 vs 321 mm SVL). Male crowned snakes on Mondrain differed from females in body shape as well as overall size, with males having relatively larger heads. The only prey items recorded on Mondrain were scincid lizards, whereas mainland conspecifics also feed frequently on frogs. Similar divergences between mainland and island populations have been reported in other snake species, suggesting that these peripheral populations represent a significant component of the overall ecological and morphological variation within each taxon.

Key words: elapid, food habits, island, reproduction, sexual dimorphism

Introduction

Despite a recent increase in herpetological research within Australia, detailed ecological information is available for only a small proportion of Australian reptile species. Unsurprisingly, taxa that are relatively rare, secretive or difficult to collect have attracted little attention in this regard. Most snakes fall into this category (Seigel 1993). For many Australian snake species, the only quantitative data on aspects such as mean adult body sizes, sexual size dimorphism, food habits and reproductive output have come from the examination of preserved specimens in museum collections (Shine 1991*a*; Greer 1997). Although this technique provides useful data, it is not a substitute for detailed single-population studies. The specimens within museum collections have been obtained over large areas and over many years, thus obscuring temporal and spatial variation in the traits under investigation. Both of these sources of variation can be important. For example, populations of the same snake species from different areas can differ dramatically in a wide range of morphological and ecological traits (e.g., dietary habits, activity patterns, reproductive output, mean body sizes, body proportions: Schwaner and Sarre 1990; Forsman 1991; Madsen and Shine 1993).

Detailed information from single-population studies of widely distributed species can clarify the degree to which local populations display traits believed to be typical of the species as a whole. On a recent fieldtrip to an island in the Archipelago of the Recherche, we obtained a large sample of crowned snakes, *Elapognathus coronatus*. These small (average snout-vent length approximately 300 mm) venomous snakes are widely distributed along coastal and near-coastal areas of southwestern Australia (Bush *et al.* 1995). The phylogenetic (and thus, taxonomic) affinities of this species have been controversial, and it has been allocated to different genera by different authorities (Storr 1982; Storr *et al.* 1986; Ehmann 1992). The species has traditionally been placed in the genus *Drysdalia* together with three species of crowned snakes from eastern Australia (Coventry and Rawlinson 1980; Cogger 1992). However, the western taxon differs from these species in internal anatomy (McDowell 1967; Coventry and Rawlinson 1980) and dietary habits (Shine 1981). Recent molecular studies unequivocally demonstrate a close relationship between *E. coronatus* and another Western Australian endemic, *E. minor* (Keogh *et al.* 2000).

Despite its wide distribution, *Elapognathus coronatus* has attracted little detailed study. The only quantitative published data on topics such as mean adult sizes, sexual size dimorphism, and reproduction are derived from examination of museum specimens (Shine 1981) plus observations of parturition in captive snakes (Bush 1992). Intraspecific geographic variation in such traits has been unstudied, despite the substantial morphological variation within this species. In his taxonomic review of *E. coronatus*, Storr (1982, p. 337) noted that "the most distinctive population is that of the Archipelago of the Recherche ... At first sight the Recherche population might seem to merit subspecific recognition". Our data suggest that the snakes on this island differ substantially from conspecific populations in mainland habitats in a series of other aspects also.

Methods

Study area

Mondrain Island (34° 08' S, 122° 00' E) is the second largest of around 200 islands that form the Archipelago of the Recherche (Nature Reserve A 22796). Mondrain Island lies 42 km SE of the town of Esperance and 10.5 km from the mainland. It is 6 km long, with a maximum width of 2.8 km and a maximum elevation of 222 m ASL. The island would have been physically connected to the mainland approximately 9,000 to 11,000 years ago during glaciation-associated falls in sea level (Main 1961; Dortsch and Morse 1984; Smith and Johnstone 1996).

The steep terrain is characterised by large granite domes and boulders, with thick intervening scrub dominated by *Melaleuca globifera*, *Acacia acuminata* and *Allocasuarina huegeliana*. In areas with deeper soils, low forests dominated by *Eucalyptus lehmanni* occur, typically with little undergrowth. Small open areas punctuating this low forest are vegetated with *Atriplex cinerea-Rhagodia baccata* shrubland and the low grasses *Poa australis* and *Stipa flavescens*. Sandy areas near the ocean are dominated by the low succulent *Caprobrotus virescens* and honeycombed by muttonbird burrows.

As part of an ecological study by the W. A. Department of Conservation and Land Management, we camped on the northern end of Mondrain Island (34° 06' 30" S, 122° 15' 00" E) from 16 to 20 November 1999. In the course of other work on the island fauna, we collected crowned snakes by hand whenever we encountered them. The snakes were then measured (snout-vent length [=SVL], tail length, head length from the snout to the posterior margin of the jaw), weighed, and palped to detect food items in the gut, or enlarged follicles or developing embryos in reproductive females. Sex was determined by manual eversion of hemipenes in males. Faecal items palped from the gut were preserved for later microscopic examination. Regurgitated prey items were also collected and identified. After processing, all snakes were released at the point of capture.

Results

We captured 48 specimens of *Elapognathus coronatus*. Several others were seen but eluded capture.

Behaviour

Most of the animals were found basking in direct sunlight in open areas among thick vegetation. Basking animals were seen throughout daylight hours, although during the hottest part of the day the animals usually exposed only a small part of their body to the sun's rays. Most snakes were captured between 0800 h and 1200 h; the earliest record of a basking snake was at 0730 h, and the latest at 1652 h. Typically, they were observed basking in a flat coil on the ground or stretched out across low *Caprobrotus*. When approached, most snakes retreated to nearby holes in the ground, or into dense vegetation. A few were observed basking on top of granite rocks, retreating rapidly into crevices. Even on cool overcast days, crowned snakes were observed basking in hazy sunlight when the air temperature was as low as 13°C. No active snakes were seen at night during spotlighting (2000 h to 2200 h).

Most snakes were encountered singly, although their concentration in particular areas (small openings among dense thickets) meant that on occasion, two or three snakes were found only 1 m apart. On at least five occasions, however, groups of two to four snakes were found sharing the same retreat site. They emerged to bask within centimetres of each other or even coiled together (Fig. 1), and retreated to the same burrow when disturbed. Three of these groups were captured (N = 2, 3 and 4 snakes per group), and were found to consist entirely of gravid females. When seized, the snakes vigorously attempted to bite. One of us (RS) was bitten on the finger, but without symptoms.

Sex ratio and body sizes

Of the 48 snakes captured, 34 were females and 14 were males. Thus, the sex ratio was significantly skewed away from 50:50 (χ^2 = 8.33, 1 df, $P < 0.01$). The mean SVL of the island snakes was much larger than has been reported for populations studied on the mainland. Our 48 samples included snakes up to 680 mm SVL, whereas 177 mainland snakes were all < 530 mm (Shine 1981). All of the snakes that we captured were above

Figure 1. Two gravid Crowned Snakes *Elapognathus coronatus*, photographed before collection on Mondrain Island. (see colour cover.) Photo: David Pearson.

the body size at maturation for this species as determined by dissection of museum specimens from mainland populations (228 mm SVL in males, 245 mm in females: Shine 1981).

Sexual dimorphism

Mean body size for males (mean SVL ± SD = 456.4 ± 99.3 mm SVL) was much greater than for females (403.4 ± 32.9 mm; one-factor ANOVA, $F_{1,39} = 6.70$, $P < 0.015$). Indeed, all of the largest snakes were males (Fig. 2). Males had significantly larger heads than did females (19.1 ± 3.7 mm vs 16.2 ± 1.1 mm; $F_{1,39} = 15.93$, $P < 0.001$). Males were heavier on average than were females (42.5 ± 21.3 g vs 35.5 ± 9.1 g) but the difference did not attain statistical significance ($F_{1,39} = 2.25$, $P = 0.14$).

Males and females also differed significantly in body proportions. We used single-factor analysis of covariance (ANCOVA) with sex as the factor and SVL as the covariate to compare the sexes after factoring out differences in snout-vent length. At the same body length, males had larger (longer) heads than did females (slopes were homogeneous - $F_{1,32} = 1.86$, $P = 0.18$, but intercepts differed - $F_{1,33} = 19.23$, $P < 0.0001$). Females (most of which were gravid - see below) weighed more than did males of the same snout-vent length (slopes were homogeneous - $F_{1,32} = 1.20$, $P = 0.28$, but intercepts differed - $F_{1,33} = 5.63$, $P < 0.03$).

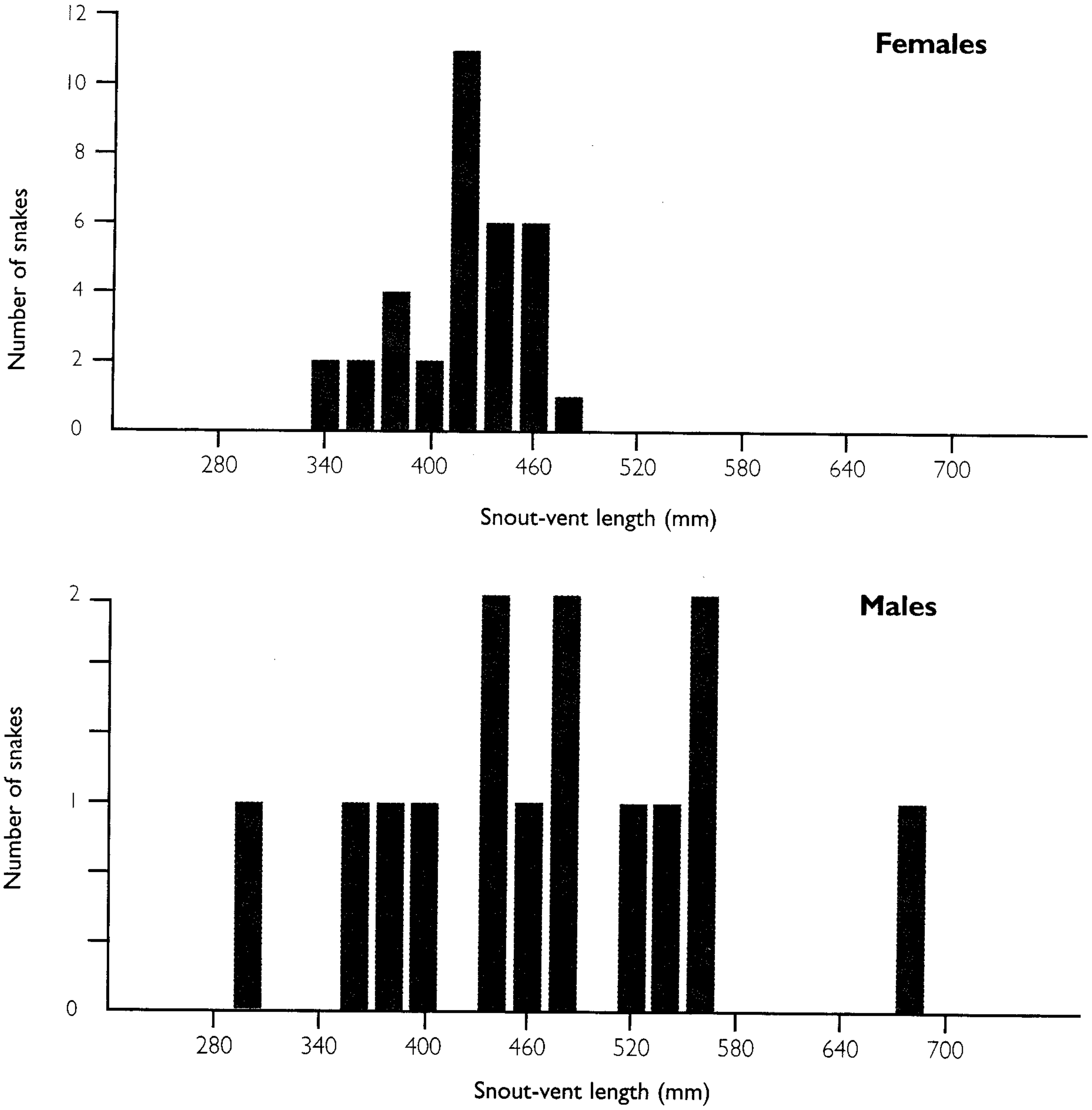

Figure 2. Frequency distributions of body sizes (snout-vent lengths) of male and female Crowned Snakes *Elapognathus coronatus* from Mondrain Island.

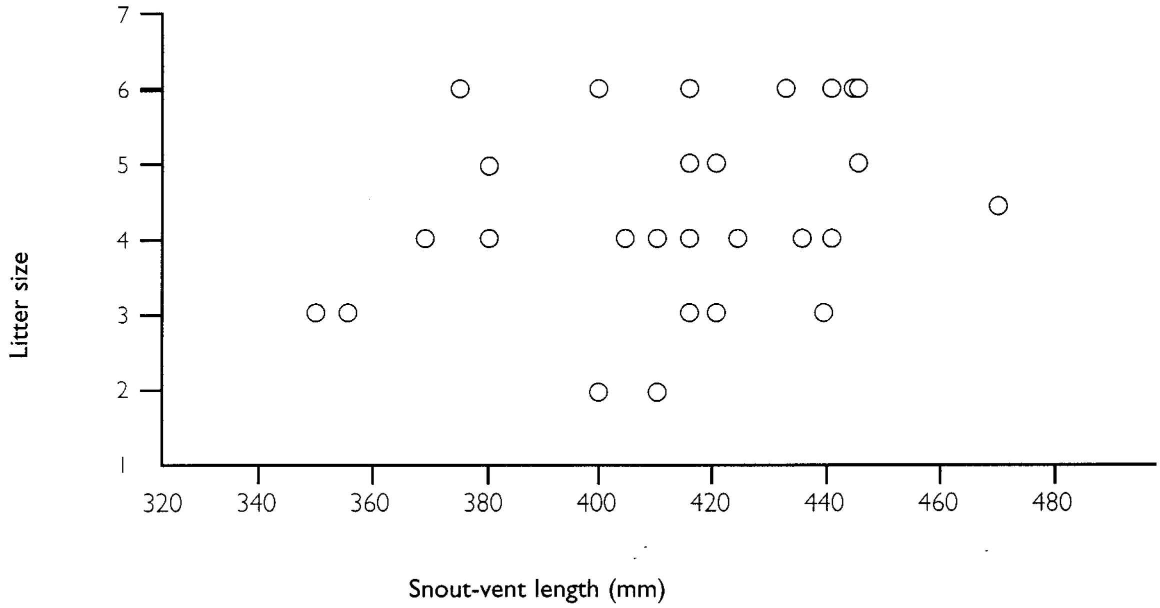

Figure 3. Litter sizes in relation to maternal body size (snout-vent length) in Crowned Snakes *Elapognathus coronatus* from Mondrain Island. See text for statistical treatment of these data.

Reproduction

Of the 34 females captured, 31 (91%) were reproductive (i.e., contained enlarged vitellogenic follicles or developing embryos). Two of the three non-reproductive females were the smallest examined (both with SVLs of 335 mm). Both of these animals may have been immature, although they were considerably larger than body sizes at maturation in mainland conspecifics (Shine 1981). Litter sizes were confidently detect-able by palpation; independent checks by different workers always yielded the same estimate of litter size. Litter size averaged 4.36 (SD = 1.23, range 2 to 6), and did not increase significantly with increasing maternal body size (Fig. 3; $r = 0.25$, $P = 0.18$).

Food habits

One male snake regurgitated two *Ctenotus labillardieri*, and another five snakes (four males, one gravid female) passed faeces containing scincid scales (*Ctenotus labillardieri*). Skinks (especially *Cryptoblepharus virgatus*, *Ctenotus labillardieri* and *Acritoscincus trilineatum*) were abundant in the habitats in which we found crowned snakes. The only other potential vertebrate prey type (frogs) are scarce on Mondrain. We found a single individual of *Crinia glauerti*. There is only one other record of a frog from this island (*Litoria cyclorhynchus*, Glauert 1954), presumably because there is no standing freshwater.

Parasites

Two male crowned snakes had ticks attached behind the neck, but all other *Elapognathus* that we saw were free of ticks. This situation offers a strong contrast to other snake species on the island. All of the 19 carpet pythons (*Morelia spilota imbricata*) that we captured on Mondrain had many ticks, as did three death adders (*Acanthophis antarcticus*).

Discussion

Although our results are very preliminary, they provide more detail about the ecology of crowned snakes than has previously been available for any single population. Several aspects of our results are concordant with previous findings based on mainland populations of the same species, but in other respects the island snakes are very different.

Points of similarity with previous work include the larger body size of Mondrain snakes than of mainland specimens (Storr 1982). Body-size differences between insular and mainland populations have been reported in several species of Australian snakes (reviewed by Greer 1997). Higher numbers of ventral scales in the Recherche animals than on the mainland (Coventry and Rawlinson 1980) are consistent with the body-size divergence: within and across snake species, higher ventral scale counts are usually associated with a greater mean body size (Lindell 1994). Our behavioural observations fit well with the description of *E. coronatus* as a "shuttling heliotherm" (Coventry and Rawlinson 1980), but do not accord with Cogger's (1992) statement that the species is nocturnal. Workers with extensive field experience have characterised *E. coronatus* as being active both diurnally and nocturnally (Bush *et al.* 1995); presumably, this aspect is sensitive to local weather conditions.

The insular crowned snakes resemble their mainland conspecifics in mean litter sizes (4.36 in our study, vs 4.3 from Shine 1981) and in the occurrence of a high proportion of reproductive animals among adult-sized females ($\geq$ 0.91 in our study, vs 0.88 in Shine 1981). Other aspects of our results also fit well with earlier reports. For example, female-biased sex ratios are commonly reported in viviparous snake species inhabiting cool climates, presumably because enhanced basking by reproductive females makes them more vulnerable to collection (Gibson and Falls 1979). Similarly, aggregation of gravid females (perhaps in response to scarcity of suitable basking/retreat sites) has been reported in other Australian elapids living in cool areas (Shine 1979), as well as in other snake species in other parts of the world (Fitch 1960). Thus, we suspect that the preponderance of females in our Mondrain sample was an artifact of sex differences in behaviour, and tells us nothing about the actual adult sex ratio in the population.

Nonetheless, there are three substantial disparities between our results and those of earlier studies. These are:

1. Male crowned snakes on Mondrain Island grow very much larger than females (Fig. 2), whereas females averaged slightly (but not significantly) larger than males in the sample (N = 76 males, 57 females) of mainland specimens examined by Shine (1981).
2. Litter sizes increased significantly with maternal body size within 22 litters of mainland snakes (r^2 = 0.62: Shine 1981) but not in the Mondrain animals (r^2 = 0.03, present study).
3. Frogs comprised 17 of 32 prey items in mainland snakes; most of the others were scincid lizards (Shine 1981). Our sample size from Mondrain is small: we obtained a total of seven prey records from six snakes. All comprised the scincid *Ctenotus labillardieri*. We doubt that frogs are sufficiently common on Mondrain to constitute a significant proportion of the snakes' diet. This is even more likely to be true on other islands of the Recherche. *Elapognathus coronatus* is distributed on at least nine islands, but frogs are known to occur on only two islands (Smith and Johnstone 1996).

The third of these points requires little explanation: there are many reports of local snake populations diverging in dietary habits in response to spatial variations in prey availability (e.g., Schwaner and Sarre 1988). However, the reasons for the other divergences are more problematical. A correlation between maternal body size and litter size (as seen in mainland *E. coronatus*) is the rule among snakes, although there are many exceptions (e.g., Seigel and Ford 1987). In particular, a common tradeoff between offspring size and litter size complicates body-size-associated shifts in reproductive output (Seigel and Ford 1987). It would be of great interest to know whether crowned snakes on Mondrain display a greater-than-usual degree of variation in offspring sizes. This is the case in some *Drysdalia* populations in eastern Australia (Shine 1981), suggesting that small Australian elapid snakes may provide interesting opportunities to explore the determinants of variation in fecundity.

The extreme male-larger sexual size dimorphism (SSD) in crowned snakes on Mondrain Island is undoubtedly the most surprising result from our study. Among snakes in general, male-larger dimorphism is significantly associated with the presence of male-male combat (Shine 1994). Such combat occurs in *E. coronatus*, even in mainland specimens (B. Bush, pers. comm.). Although the degree of SSD among male-combat taxa varies considerably, patterns of SSD in snakes are generally very conservative across species, and even across related genera (e.g., Shine 1994; Shine and

Fitzgerald 1995). To place the magnitude of this shift in *E. coronatus* into perspective, we calculated an index of sexual dimorphism in body size (Gibbons and Lovich 1990). This index is +0.01 for mainland snakes (Shine 1981) and -0.13 for the Mondrain snakes. If the 374 snake species reviewed by Shine (1994) are ranked in terms of the ratio of mean adult male SVL to mean adult female SVL, our Mondrain sample ranks in the 10th percentile whereas the mainland sample falls within the 36th percentile (Shine 1981). The two populations of *E. coronatus* thus span a significant proportion of the range in degrees of SSD exhibited by all snakes.

Although this level of intraspecific variation is exceptional, it nonetheless fits with several other cases. In a diverse array of lineages, snakes from islands differ from nearby mainland populations in SSD as well as in mean body size (e.g., Schwaner and Sarre 1988; Madsen and Shine 1993; D. Pearson, unpubl. data). Some of these cases are due to phenotypic plasticity, with prey resources restricting growth trajectories and thus, the degree of size dimorphism between the sexes (Madsen and Shine 1993). Other cases may reflect adaptation, whereby the lack of gene flow between island and mainland populations permits insular populations to evolve away from the usual situation in mainland conspecifics. The actual selective forces remain unclear, but may involve prey resources, thermal constraints, and/or mating systems (e.g., Schwaner and Sarre 1988). In keeping with the notion of sex-based partitioning of the prey resource, male *Elapognathus* on Mondrain have larger heads than conspecific females at the same body size. As in the case of overall SSD, the magnitude of the divergence in relative head size is greater in *E. coronatus* on Mondrain than in most other snakes: Shine's (1991*b*) review of 114 taxa detected only two other populations with a greater degree of head-size divergence between the sexes. In one elapid from eastern Australian (*D. coronoides*) that is morphologically similar to *E. coronatus*, there was no significant head-size dimorphism (Shine 1991).

Another possible explanation for SSD in the insular *Elapognathus* population involves allometry. Among snake species in general, the evolution of larger absolute body size is consistently accompanied by a shift in SSD towards a relatively large body size in males (Shine 1994). The same kind of allometry occurs in many other animal lineages (e.g., Clutton-Brock *et al.* 1977). Although the processes responsible for this allometry remain unclear, it is consistent with the simultaneous shift in Mondrain *Elapognathus* towards an increase in body size and in the degree of SSD.

In order to test between alternative possible explanations for the spatial variation in sexual dimorphism within crowned snakes, it would be of great interest to obtain information on the biology of the Mondrain snakes. In particular, we need to know more about topics such as reproductive biology (e.g., mating system, reproductive output) and feeding biology (prey types and sizes relative to the sex and size of the snakes). Data on other populations of *E. coronatus* would also be of value, to provide a more direct comparison with the situation on Mondrain. Given the extraordinary level of divergence associated with insular populations both in *E. coronatus* and in other snake species, it would be particularly interesting to quantify ecological attributes of crowned snakes from other islands. Our data reinforce the view that insular populations may often exhibit substantial ecological and morphological novelties, and hence may warrant special attention in conservation planning.

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