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Life tables are an insufficient reference in the ontogenetic evaluation of the lizard skeleton

ABSTRACT

The main problems of using life tables as the only reference in ontogenetic studies are discussed and exemplified with the data of the genus *Liolaemus* (Squamata:Tropiduridae). The embryo data that must be included, in order to make comparative different studies, are listed.

Life tables are mainly employed for the indicative discrimination of discontinuous maturity stages in studies of various kinds. Most of them are based on the embryonic external morphology.

The investigation of the skeletal development often reveals substantial modifications despite the absence of any change in the external morphology. If reference is made to the tables, therefore, embryos may be regarded as in the same stage even though there is a one-week difference in their ages.

Our recent investigation of the skeletal development of two oviparous *Liolaemus* species: *L. scapularis* (Lobo *et al.* 1995) and *L. quilmes* (this paper) has revealed that life tables are not sufficient for this purpose. The literature comprises a study of the intrauterine development of the ovoviviparous *L. tenuis tenuis* by Lemus & Duvauchelle (1966), a life table for this species (Lemus *et al.*, 1981) and another for the viviparous *L. gravenhorsti* (Lemus, 1967).

The incubation period for *L. scapularis* and *L. quilmes* was 44-45 days, compared with 60 intrauterine and 72 extrauterine days for *L. tenuis tenuis* (Lemus *et al.*, 1981). It is evident that the biology of our two species is very different from what was used to compile the tables. The first difficulty, therefore, is that there are no tables for all species as a whole. The same difficulty also arises for genera.

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Moreover, as we shall see, the problem remains even when the employment of a table is confined to the study of its exact species, since tables are constructed from the scattered information offered by the embryonic external morphology. It is true that some internal anatomy characters are used by both Lemus (1967) and Lemus *et al.* (1981) to define each stage. Their skeletal data, however, are very general and poorly informative.

Our examination of two *L. scapularis* embryos, whose external morphology was much the same, so that they could be placed in stage 34 according to Lemus's table for *L. gravenhorsti* (1967) despite their one-week difference in age (14 and 21 days after laying), disclosed marked differences in the maturity of their skeletons (Lobo *et al.*, 1995, table I & II). The following features, in fact, were only present in the older embryo:

1. initial ossification of the prootic, exoccipital, basioccipital, basiparasphenoid, columella and quadrate bones;
2. appearance of the scapula and coracoid centres of ossification;
3. fusion of the two halves of the sternum, and contact of another rib with the sternum;
4. appearance of the distal carpal 1 and the pisiform bone;
5. ossification of the shafts of metacarpals, metatarsals and phalanges;
6. median fusion of the ischium, and development of the hypoischium;
7. appearance of the centres of ossification of the three components of the pelvis;
8. initial ossification of the atlas and the median region of the ribs.

The table for *L. tenuis tenuis* (Lemus *et al.*, 1981), on the other hand, identified other stages, some of which partly overlapped those of the first table. Stage 33 of the *L. gravenhorsti* model, for example, corresponds to stage 39 of the *L. tenuis tenuis* model, while its stages 34A and 35B (our division on the basis of the skeletal data) and stage 35 correspond to the other's stage 40. Three stages of the skeletal development, therefore, fall within a single external morphology stage.

Stage 35 displays the following features that are not included in stage 34B (see also Lobo *et al.*, 1995, Table I & Table II):

- 1 Initial ossification of the supraoccipital and the articular, i. e. the last bones to ossify in the neurocranium and lower jaw respectively.
- 2 Initial ossification of the transverse processes, the talus and the fifth metatarsal.

The *L. scapularis* embryo at stage 35 was at day 36 of its 44 to 45-day incubation period, whereas in *L. gravenhorsti* this stage is typical of the newborns. In *L. t. tenuis*, stage 35 of *L. gravenhorsti* corresponds to stage 40 (day 42 of the 72 ± 3 days incubation period).

The 14-day-old *L. quilmes* embryo was at stage 33 on the *L. gravenhorsti* table because it displayed interdigital membranes, whereas its skeletal picture corresponded to stage 34B for *L. scapularis*. It also had some of the characteristics of stage 33 for *L. scapularis*, namely a divided sternum and the pelvic girdle only fused anteriorly by the pubis.

CONCLUSIONS

The age of an embryo and (if oviparous) the incubation conditions must be specified in ontogenetic studies, since the incubation period is influenced by environmental factors, such as temperature (Rieppel, 1994). Many workers, however, describe embryos they have not incubated and are thus confined to a limited amount of information.

When the age of an embryo is not known, reference must be made to precisely defined maturity stages. Life tables are one type of yardstick. As mentioned earlier, however, one is not obliged to use them when investigating questions of internal anatomy, especially when the species concerned is not that for which the table was elaborated. In cases of this kind, it is preferable to combine a description of the external morphology using the character commonly included in life tables with that of any other character allowing the differentiation of maturity stages.

Many papers on species development simply use the total or snout-vent length of any embryo. Size, however, has little to say with regard to age or maturity, and many more characters are included in all life tables.

The tail lengths, in fact, of two embryos of different age, but with the same body size, may not be the same. By the same token, two embryos of the same size and tail length may differ because only one has scales and claws.

Provision of the following information is thus essential in development studies:

1. Age (in hours or days) and reference measurements.
2. Incubation conditions (at least temperature and humidity).
3. The preservation fluid. Instructions for the fixation of embryos are provided by Alberch (1985). The main points are separation of the embryo from the membranes and fixation in 10% buffered formalin. It is also necessary to have several individuals from the same clutch as a guarantee of correct species identification.
4. Stage, as shown by the life table for the species concerned, or
5. Stage, as shown by the life table for related species or genus. All discrepancies observed must be clearly indicated.
6. In the absence of any appropriate life table, a brief account of the embryo's external morphology must be provided.

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RIASSUNTO

I "Life Tables" sono insufficienti negli studi sullo sviluppo embrionale dello scheletro nelle lucertole.

Gli autori elencano i principali problemi collegati all'uso dei "life tables" come unico riferimento per lo studio dello sviluppo embrionale e li esemplificano con i dati sullo sviluppo di alcune specie di *Liolaemus* (Squamata: Tropiduridae).

E' presentata, inoltre, una lista di informazioni supplementari sull'embrione da utilizzare negli studi per permettere la comparazione dei risultati.

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REFERENCES

- ALBERCH P., 1985. Museum collections and the evolutionary study of growth and development. 29 - 41 pp. En: (E.H. Miller Ed.) "Museum collections: their roles and future in biological research". - British Columbia Provincial Museum, Occasional Paper N° 25, 222 pp.
- LEMUS D.A., 1967. Contribución al estudio de la embriología de reptiles chilenos II. Tabla de desarrollo de la lagartija vivípara *Liolaemus gravenhorsti* (Reptilia: Squamata: Iguania). - *Biologica* 40: 39 - 61.
- LEMUS D.A., DUVAUCHELLE R., 1966. Desarrollo intrauterino de *Liolaemus tenuis tenuis*. - *Biologica* 39: 80 - 98.
- LEMUS D.A., ILLANES J., FUENZALIDA M., PAZ DE LA VEGA Y., GARCIA M., 1981. Comparative Analysis of the Development of the Lizard, *Liolaemus tenuis tenuis*. II A Series of Normal Postlaying Stages in Embryonic Development. - *Journal of Morphology* 169: 337 - 349.
- LOBO F., ABDALA F., SCROCCHI G., 1995. Desarrollo del esqueleto de *Liolaemus scapularis* (Iguania: Tropiduridae). - *Boll. Mus. Sci. Nat. Torino*. 13 (1): 77 - 104.
- RIEPEL O., 1994. Studies on skeleton formation in reptiles. Patterns of ossification in the skeleton of *Lacerta agilis exigua* Eichwald (Reptilia, Squamata). - *J. Herpetol.* 28 (2): 145 - 153.