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CLASSIFICATION OF THE REPRODUCTIVE PATTERNS OF AMNIOTES

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ABSTRACT: The classification of reproductive patterns inherited from the 19th century reflects mammalian biases and fails to capture our understanding of amniote reproductive diversity. Much more useful is a bipartite classification that fully distinguishes between two separate reproductive parameters: sources of nutrients for development, and state of the reproductive product at emergence from the mother. "Oviparity" and "viviparity" are used in their literal senses to refer to "egg-laying" and "live-bearing" reproduction. "Lecithotrophy" refers to provision of nutrients to the embryo via the yolk, and "matrotrophy" to provision by alternative means (e.g., a placenta, a pattern termed "placentotrophy"). Use of these terms has several advantages, including elimination of confusion associated with the archaic term "ovoviviparity". This system also recognizes commonality between patterns involving maternal provision of nutrients before birth or hatching (e.g., to eggs and embryos) and afterwards (to neonates). Growing consensus around the bipartite classification of reproductive patterns reflects recognition of the importance of a common biological vocabulary that applies widely across traditional methodological, disciplinary, and taxonomic boundaries.

Key words: Viviparity; Oviparity; Matrotrophy; Lecithotrophy; Squamates; Reproduction

VERTEBRATE REPRODUCTIVE DIVERSITY presents conceptual and terminological challenges to biologists interested in patterns that transcend taxonomic and disciplinary boundaries. Individual biologists commonly spend their careers applying specialized techniques to the study of particular organisms. Although biological journals and symposia potentially can promote cross-disciplinary communication, they often do the opposite, being focused on particular taxa or methodological approaches. As a consequence, biological disciplines historically developed divergent ways of conceptualizing reproductive diversity, and individual researchers have applied common biological terms in discrepant ways that have sometimes produced misunderstanding and confusion.

Methods of categorizing reproductive diversity not only affect our abilities to communicate, but affect the hypotheses we formulate and the observations we make. Unfortunately, comparative biology has inherited a 19th century reproductive classification that was developed for mammals, and which fails to reflect our current knowledge of reproductive diversity. Consequently, as shown below, we tend to overlook patterns that do not fit neatly into

the traditional mammalian scheme. Furthermore, discrepant usage of such common terms as "viviparity" and "oviparity" (as well as the archaic term "ovoviviparity") often make it difficult to tell what past researchers meant to communicate about the organisms they were studying (Blackburn, 1993*a*, 1994*a*).

Fortunately, the issues are easy to address and largely have been resolved. Since the early 1980's, a number of biologists working on vertebrate reproductive modes have reached a consensus on how to categorize and communicate about reproductive diversity. The terminology that has emerged is consistent with common usage and literal meanings, is easy to apply, and allows comparison of patterns between reptiles, mammals, amphibians, and fishes. Furthermore, clear criteria for recognition of the reproductive patterns have been established (Blackburn, 1993*a*, 1994*b*). For this series of volumes on neonatal biology, I have been asked by the conveners to present this classification of reproductive patterns and to summarize its rationale, in order to promote better understanding and communication about reproductive diversity in reptiles and other vertebrates.

Conceptual Confusion and Terminological Discrepancies

Dating to the writings of Aristotle, biologists have characterized animals according to two major reproductive parameters (Blackburn, 1992). One parameter is the type of reproductive product deposited by the mother, e.g., whether she lays eggs or gives birth to her young, sometimes referred to as "parity" mode. The other parameter is the source of nutrition for development, i.e., whether nutrients are provided to the embryo by the yolk or some alternative means. Traditionally, the terms "oviparity" and "viviparity" (and their equivalents in Latin, French, German, and other languages) have been applied respectively to the egg-laying and live-bearing reproductive modes. However, in the early 1800's, "viviparity" began to be used much more restrictively by some zoologists, to refer to mammals that provided nutrients to their embryos by a placenta (Home, 1802). Accordingly, some biologists adopted the word "ovoviviparity" to describe live-bearing animals that provided nutrients via the yolk. However, others applied this term to forms of egg-laying reproduction (see Blackburn, 1994a). Richard Owen (1834) was among those who labeled both marsupials and monotremes as ovoviviparous, on the grounds that neither forms a chorioallantoic placenta. Owen's perspective persists in more recent interpretations of marsupials as aplacental (Stonehouse, 1977) and essentially ovoviviparous (e.g., Eisenberg, 1981). Notwithstanding such interpretations, all marsupials do have placentae of the yolk sac variety and give birth to their young (Sharman, 1961; Tyndale-Biscoe and Renfree, 1987; Blackburn, 1993b).

The 19th century classifications of reproductive patterns were based on two mistaken but persistent assumptions: (1) that the chorioallantoic placenta is somehow more definitive than other types of placentas; and (2) that animals that provide extra-vitelline (non-yolk) nutrients are a subset of those that give birth to their offspring. Under these assumptions, a three-part classification ("oviparity", "ovo-

viviparity", "viviparity") may seem to exhaust the possibilities. The first assumption reflects a strong anthropocentric bias, by ignoring the fact that yolk sac placentas can be major sites of nutrient transfer in (non-primate) eutherians, as well as marsupials and other vertebrates. As for the second assumption, biologists have known for decades that female monotremes provide substantial quantities of nutrients to their eggs before oviposition, by means of oviductal secretions that are absorbed through the eggshell (Hill, 1933; Hughes and Carrick, 1978). During this period of nutrient absorption, the tiny 3 mm ovum of monotremes swells to about 15×17 mm in diameter before being oviposited. The reason this pattern often is overlooked may be that it cannot easily be expressed in the traditional taxonomy of patterns; it might be considered (on nutritional grounds) to be a form of viviparity, but monotremes do after all lay partially-developed eggs. Therefore, under traditional terminology, whether monotremes are to be classified as oviparous, ovoviviparous, or viviparous depends on the characteristics and terminological criteria one wishes to employ.

One legacy of the conceptual ambiguities is that individual terms are used in discrepant ways. This fact is commonly overlooked by biologists who deal with a restricted range of organisms or techniques. For example, in terminological systems that focus on reproductive products, the term "viviparity" is variously applied in the literature to (1) all cases of live-bearing reproduction (Fitch, 1970; Shine, 1985); (2) live-bearing reproduction in which no eggshell remnant is present during gestation (Weekes, 1930; Kasturirangan, 1951); (3) the deposition of partly-developed eggs (Turner, 1947) [a pattern seen in monotremes (Hughes and Carrick, 1978) and all squamates (Shine, 1983; Blackburn, 1995)]; and (4) all cases of internal fertilization (Nielsen, 1968). In systems based on sources of nutrients for development, the term has been applied to (5) all forms of extra-vitelline nutrient provision (Young, 1962; Orr, 1976); (6) all species in which parents feed the offspring; (7) pla-

cental species only (Amoroso, 1952; Matthews, 1955; Balinsky, 1975); and (8) eutherian mammals only (Eisenberg, 1981). The results can be highly problematic. In an international conference dealing with "viviparity" (one of six held in the past decade), not until the speakers arrived did it become apparent that they did not agree on the actual topic of the symposium. Time that could have been spent discussing reproductive diversity was expended in terminological confusion.

Because its past use has spawned so much confusion, discrepant usage of the archaic word "ovoviviparity" should be realized by anyone who deals with the older literature. This term has been applied indiscriminately to a remarkable range of reproductive patterns. Reviews of its usage have shown that "ovoviviparity" has meant different things to anatomists, physiologists, and field biologists, and to researchers who study fishes, amphibians, reptiles, and mammals (Blackburn, 1994a). The various applications of this term have little in common, although most writers assume that it represents a pattern that is somehow intermediate between "oviparity" and "viviparity", however defined. Some uses of the term are even mutually exclusive, for it has been applied to types of live-bearing as well as egg-laying reproduction, and to species with internal as well as external fertilization (Amoroso, 1952; Salthe and Mecham, 1974; Mackie, 1978; Wake, 1980; Blackburn, 1994a). In recognition of the confusion associated with the term, "ovoviviparity" is now seldom used, and is largely obsolete. Most biologists have abandoned it in favor of terms that are less-ambiguous and more descriptive (e.g., Bertin, 1952; Bauchot, 1965; Wourms, 1981; Guillette, 1982; Shine, 1985; Smith, 1986; Stewart, 1989, 1992; Blackburn, 1992, 1999a,b).

Bipartite Classification of Reproductive Patterns

Ambiguities in the reproductive literature of past decades largely can be traced to attempts to use a single set of terms for two distinct types of reproductive parameters. A simple, effective solution to the

problem was provided by Prof. John Wourms, who suggested use of separate terms to reflect reproductive products and embryonic nutritional patterns. Wourms (1981) proposed the use of "oviparity" and "viviparity" in their literal sense, to describe "egg-laying" and "live-bearing" reproduction respectively. To describe the sources of nutrients for development, he adopted the terms "lecithotrophy" and "matrotrophy". *Lekithos* is Greek for *egg-yolk*, and "lecithotrophy" refers to the provision of nutrients to the embryo by means of the yolk of the ovulated ovum. "Matrotrophy" refers to a provision of nutrients by some alternative means, such as oviductal secretions or placental organs. These two patterns are viewed as extremes of a continuum. In some species, embryos rely on both vitelline and non-vitelline sources of nutrients, in which case they can be characterized by the predominant source of developmental nutrients (Wourms et al., 1988; Blackburn, 1992, 1999c).

Using these terms in combination, we can simultaneously characterize any vertebrate species by reproductive product as well as embryonic nutritional mode (Table 1). For example, turtles, birds, and most squamates exhibit lecithotrophic oviparity, whereas most live-bearing squamates show lecithotrophic viviparity. Monotremes are recognized as matrotrophic and oviparous, a possibility not allowed for in the traditional classification (Blackburn, 1992). This bipartite classification has been widely adopted by zoologists interested in viviparity, because it is applicable to each of the major vertebrate groups. Accordingly, it has been applied successfully to reptiles, mammals, amphibians, osteichthyans, and chondrichthyans (e.g., Wourms, 1981; Wourms et al., 1988; Stewart, 1989, 1992; Blackburn, 1992, 1999a,c; Greven, 1998; Swain and Jones, 1997; Koob and Hamlett, 1998; Thompson et al., 1999).

Rationale and Refinements

The dichotomous classification of amniote species by their type of reproductive product emphasizes a long-standing distinction of fundamental importance. In vi-

TABLE 1.—Phylogenetic distribution of reproductive modes and embryonic nutritional patterns among amniotes.¹

	Oviparity	Viviparity
Lecithotrophy	Crocodylians, chelonians, birds, <i>Sphenodon</i> , most squamates	About 20% of squamates ³
Matrotrophy ²	Monotreme mammals	Therian mammals, three clades of scincid lizards

¹ Lecithotrophy and matrotrophy represent extremes of a continuum. Except for therian mammals, viviparous species lie between these extremes and are classified by the predominant source of nutrients for development.

² "Matrotrophy" refers here to substantial provision of extra-vitelline nutrients to the embryo prior to birth or hatching. In viviparous amniotes, such provision is largely placentotrophic. Arguably, the provision of nutrients via the albumen (a pattern found in chelonians, crocodylians, and birds) is a form of pre-paritive (pre-natal) matrotrophy. In addition, lactation and parental feeding of offspring can be considered as forms of post-paritive (post-natal) matrotrophy.

³ Sources of nutrients for development have been quantified in only a few viviparous squamates. The relatively large size of their ova suggests these species to be relatively lecithotrophic.

viviparity, newly emergent offspring potentially are able to feed, locomote, and otherwise interact freely with their environment. In oviparity, in contrast, the reproductive product is a developing egg whose interaction with the environment is essentially passive. These two patterns reflect the sequence of two important life history events, hatching and parturition (a term which subsumes oviposition + parturition: Smith, 1975). Thus, the distinction is inherently qualitative. When parturition precedes hatching, an animal would be considered oviparous, but when hatching precedes or accompanies parturition (or has been eliminated evolutionarily), the animal would be considered viviparous. One potential challenge to the distinction is the existence of occasional species in which females lay well-developed eggs that hatch after a relatively short incubation. For such species, the term "oviparous egg-retention" can be useful (Shine, 1983). Very few reptilian species (a few lizards) are known to exhibit this pattern, a fact that emphasizes the dichotomous nature of these reproductive patterns, and which may offer insight into the tempo of evolutionary change (Blackburn, 1995).

The classification of species by developmental nutritional pattern also upholds a fundamental distinction, one that is directly pertinent to the subject of this series of papers on neonatology. The means by which a female supplies nutrients to her embryos can affect the quantity of nutrients provided, and hence, the size and state of development of the offspring at emergence, regardless of whether repro-

duction is oviparous or viviparous. Moreover, in a broad sense, lactation (and other forms of maternal feeding) represent manifestations of matrotrophy (Blackburn, 1999c). Post-paritive (post-natal) matrotrophy is, of course, a major source of nutrients for development in birds and mammals. Thus, like pre-paritive matrotrophy, it is directly relevant to neonatal biology. For post-natal nutrient provision involving both parents, a pattern restricted among amniotes to most birds and a few mammals, the term "parentotrophy" could be appropriate. For pre-paritive nutrient provision involving a placenta, the term "placentotrophy" is available, and has achieved broad acceptance (e.g., Wourms, 1981; Wourms et al., 1988; Stewart, 1989).

As for application of the concepts to actual species, several criteria are available for distinguishing oviparity from viviparity in the field and the laboratory (Table 2). Likewise, multiple criteria exist for assessing whether embryonic nutrition in a given viviparous species is relatively lecithotrophic or matrotrophic (Table 3). In two recent reviews (Blackburn, 1993a, 1994b), these criteria were discussed and ranked by reliability and practicality in application to squamates. These criteria could easily be adapted for other vertebrate taxa that vary in reproductive and embryonic nutritional patterns.

Advantageous Features

The bipartite classification of reproductive modes offers several advantageous features. First, the use of terms that translate literally into their meanings minimizes

TABLE 2.—Criteria for the recognition of reproductive modes in squamate reptiles. Criteria are judged on a relative scale as to reliability (5 = highly reliable, 0 = unreliable) and practicality (5 = most practical, 1 = least practical). “Practicality” includes consideration of the number of squamate taxa to which the criterion is likely to apply. For details and justification, see Blackburn (1993a). O = oviparity, V = viviparity.

Evidence	Mode	Reliability	Practicality
Partition in the field	V, O	5	1
Developing eggs in the field ¹	O	5	2
Hatching of eggs of known history	O	5	2
Minuscule ova	V	5	1
Birth in captivity	V	4	5
Egg-laying in captivity	O	4	3
Egg-tending behavior	O	4 ²	1
Advanced oviductal fetuses	V	4	5
No visible shell membrane in moderately-developed embryos	V	3	3
Absence of advanced embryos in an extensive series of females	O	3	2
Thick shell membrane in moderately-developed oviductal eggs	O	3	3
Hatching of eggs of unknown history	O	2	3
Proximity of a female to some eggs	O	1	1
Thick shell membrane in early oviductal eggs	“O”	1	3
Unsubstantiated reports	O, V	1–3 ³	4
Developing oviductal eggs	“V”	0	—
No shell membrane in early eggs of unknown development	“V”	0	—

¹ Developing eggs that are identified to species from the hatchlings.

² Variable, depending on complexity of the observed behavior.

³ Variable, according to the nature of the report.

the chances of ambiguity. Second, the important distinction between reproductive product and source of nutrients for development is maintained. This distinction was obscured in past systems, which used the same terms for distinctly different parameters. Because reproductive mode and nutritional pattern are conceptually disengaged, the system allows recognition that viviparity and matrotrophy may evolve through different sequences and selective

pressures in separate lineages (Blackburn, 1992). Traditional systems assumed that what we now call matrotrophy only could evolve after viviparity, and thus presupposed a particular evolutionary sequence.

Third, the classification of reproductive patterns is applicable to all vertebrates, and allows recognition of common reproductive patterns across the broad spectrum of vertebrate diversity. The 19th century system was designed with a mammalian focus, hence the restriction of the term “viviparity” to eutherians and the persistent view that non-mammals cannot really be considered as truly viviparous. Fourth, a researcher using this terminological system can focus on the feature of interest (e.g., viviparity) without presupposing knowledge of others (e.g., nutrient sources). Under traditional classifications, workers had to make judgements about two sets of criteria simultaneously in describing an animal’s reproductive pattern, regardless of the availability of knowledge. In contrast, in the present system, an animal might be classified as viviparous (or even oviparous) without precise knowledge about the sources of nutrients for development. And finally, the functional re-

TABLE 3.—Criteria for the recognition of developmental nutritional patterns. Reliability is estimated on a relative scale (5 = highly reliable, 0 = unreliable), as is ease of use (5 = highly practical, 1 = difficult to apply). For details and justification, see Blackburn (1994b).

Criterion	Reliability	Practicality
Composition analysis	5	2
Dry mass changes	2 (5 ¹)	3
Wet mass changes	1 (4 ¹)	4
Size of ovum vs. neonate ²	1 (4 ¹)	4
Size of ovum vs. female ²	0	—
Timing of yolk sac depletion ²	0–3 ³	2
Placental morphology ²	0–3 ⁴	3
Transfer experiments ²	1	2

¹ Only in cases of extreme placentotrophy.

² Yields no quantitative data.

³ Depending on whether fetal lipid or residual abdominal yolk stores are determined.

⁴ Depending on the degree of cytological specialization observed.

lationship between nutrient provision to the offspring that precedes partion (e.g., placentotrophy) and that which follows partion (e.g., lactation) is maintained. This relationship is especially important to the present volume, given that pre- and post-partitive matrotrophy (or parentotrophy) offer two ways in which quality (and viability) of the offspring potentially can be modulated.

Concluding Remarks

Biological terminology changes slowly, in part because individuals are naturally reluctant to abandon the verbal tools with which they learned to conceptualize the world. What is striking about the classification of reproductive patterns is the rapidity of change; "ovoviviparity" has virtually disappeared from the literature, and a semantic distinction between reproductive mode and developmental nutritional pattern is now made routinely by anatomists, physiologists, and ecologists alike. Although much can be said for individual freedom when it comes to terminology, if we can uphold use of the same terms for the organisms we study, the use of a common vocabulary for reproductive diversity is a reasonable expectation, especially given past confusion and ambiguities. The growing consensus around the bipartite classification described herein reflects the benefits of communication between biologists working on different clades, and illustrates the increasingly integrative nature of the zoological sciences.

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