

The relationship of neonate mass and incubation temperature to embryonic development time in a range of animal taxa

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Abstract

Embryonic development time has been of long-standing interest to physiologists and ecologists because of its importance in understanding the behaviour and ecology of reproduction, and the evolution of reproductive strategies in animals. Yet, the relationship of embryonic development time to both neonate mass and incubation temperature remains poorly understood for most taxonomic groups. Here we define the relationship of embryonic development time to neonate mass (embryo mass at birth) and incubation temperature for a broad range of animals, ectothermic and endothermic, invertebrate and vertebrate, microscopic and gigantic. We begin by establishing the relationship of embryonic development time to neonate mass for a broad array of zooplankton, fishes and amphibians for temperatures from 5 to 20 °C. Next, we compare the relationships of embryonic development time to neonate mass in these aquatic ectotherms to those for terrestrial ectotherms (reptiles) and endotherms (birds and mammals) in terms of degree-days. The similar nature of these relationships allows us to define embryonic development time as a function of neonate mass for many of the species considered here with a single equation in terms of degree-days for incubation temperatures ranging from 5 to 38 °C. This relationship establishes a basis by which to compare differences in embryonic development time among species.

Key words: incubation, temperature, embryo, development time, hatching, mass, size, egg, zooplankton, fish, amphibian

INTRODUCTION

Embryonic development time is generally studied in individual species either as a function of temperature (as with ectotherms) or size (as with endotherms), with differences between species attributed to their unique taxonomic status. While embryonic development time (time from fertilization to birth) is thought to be under metabolic control in animals (McLaren, 1965; Rahn, Paganelli & Ar, 1974; Sacher & Staffeldt, 1974), no general relationship for embryonic development time has been defined such as the 'mouse to elephant curve' for metabolic rate. In endotherms, embryonic development time is known to scale positively to egg mass in birds (Heinroth, 1922) and maternal mass in mammals (Sacher & Staffeldt, 1974), but incubation temperature is rarely considered. Among ectotherms, embryonic development time is generally recognized as inversely related to incubation temperature in individual species (fishes, Pepin, 1991; zooplankton, Bottrell, 1975; Vijverberg, 1980; reptiles, Deeming & Ferguson, 1991), and has often been expressed in terms of cumulative thermal units (i.e. degree-days (°C days) (fishes, Ricker, 1979; insects, Pritchard, Harder & Mutch, 1996). Yet,

while it has been recognized that embryonic development time is related to egg or neonate size in ectotherms (e.g. fishes, Ware, 1975; zooplankton, Bottrell, 1975), the relationship has only been described in two ectotherm taxonomic groups at a single incubation temperature (i.e. amphibians, Bradford, 1990; reptiles, Birchard & Marcellini, 1996). Thus, it remains unclear how embryonic development time varies with neonate size across a range of incubation temperatures within and across ectotherm taxonomic groups.

In this paper, we compare the relationship of embryonic development time to neonate mass and incubation temperature for several taxonomic groups spanning a broad range of neonate sizes and incubation temperatures (5–38 °C). We first establish the relationship of embryonic development time to neonate mass at four different temperatures (5, 10, 15, 20 °C) for aquatic ectotherms, and evaluate differences in this relationship within and across taxonomic groups. Next, we define the relationship of embryonic development time to neonate mass as a function of degree-days to account for differences in incubation temperature. We conclude with a comparison of the relationship of embryonic development time to neonate mass and incubation

temperature in aquatic ectotherms to the relationship for terrestrial ectotherms (reptiles), oviparous endotherms (birds) and viviparous endotherms (mammals). Among these taxonomic groups, we also include animals with unusual reproductive strategies (e.g. monotremes, marsupials, and viviparous ectotherms) to examine if they are exceptional for embryonic development time. Together, these relationships provide a basis for the evaluation of differences among species in embryonic development time, the most basic of life-history processes.

MATERIALS AND METHODS

Data for this study were obtained from published studies that are listed in the appendices at the following website: <http://www.wisc.edu/zoology/grads/james.htm>. Data used in the analyses of embryonic development time in aquatic ectotherms (marine and freshwater) were collected from studies of zooplankton, amphibians (aquatic breeders) and fishes across a broad range of neonate sizes and incubation temperatures (zooplankton: 2 phyla, 7 orders, 29 species; fishes: 7 orders, 21 species; amphibians: 2 orders, 10 species) (Appendix 1). The relationship of neonate mass and incubation temperature to embryonic development time in aquatic ectotherms was evaluated for neonates ranging in mass from the rotifer *Filinia pejeri* (2.9×10^{-8} g) to the salmon *Oncorhynchus tshawytscha* (0.15 g). Embryonic development time across this size range was assessed for aquatic ectotherm eggs at 2 or more of 4 constant temperatures (5, 10, 15, and 20 °C). For species incubated across this temperature range at constant temperatures other than 5, 10, 15 or 20 °C, embryonic development times were estimated at 1 or more of these temperatures from the lines fitted to the relationship of embryonic development time to temperature.

The fresh egg mass of all oviparous species in this study was used as an estimate of neonate mass because it was not possible to convert egg mass to neonate mass in 3 of the 5 taxonomic groups. Although neonate mass is a similar fraction of egg mass in birds and reptiles (Vleck & Hoyt, 1991), the relationship of neonate mass to egg mass is not known for the 3 aquatic taxonomic groups (i.e. zooplankton, amphibians, fishes). Egg sizes for zooplankton, fishes and amphibians were most often obtained from general reference texts and synthesis papers (amphibians, Stebbins, 1951; fishes, Scott & Crossman, 1973; zooplankton, Lynch, 1980; Maier, 1994) because egg or neonate sizes were rarely recorded in studies of embryonic development time (an indication of the degree to which the importance of mass is overlooked). Where only the egg radius size was recorded for a species, fresh egg mass was estimated from the egg radius by first calculating egg volume (volume of a sphere), and then converting volume to mass assuming a density of 1.0. Published reports of egg mass values in each taxonomic group suggest this approximation generally falls within

10% of the empirically determined egg mass (amphibians, Brown, 1977; fishes, Fleming & Ng, 1987; zooplankton, Trubetskova & Lampert, 1995).

The similarity of the relationships of embryonic development time to neonate mass in different taxonomic groups of aquatic ectotherms led us to consider how these relationships compared to those for terrestrial ectotherms and endotherms. The relationship of embryonic development time to neonate mass in aquatic ectotherms was compared to those of reptiles (Appendix 2), as well as birds and mammals (Appendix 3) ranging in size from a small lizard *Anolis carolinensis* (neonate mass = 0.024 g) to an elephant *Loxodonta africana* (neonate mass = 1.20×10^5 g). Data relating embryonic development time to neonate mass in all species were analysed by performing least squares linear regression on log-transformed data. Differences in the slopes and intercepts of regression lines were compared using analysis of covariance (Zar, 1996). Data (and corresponding relationships) for reptiles (12 crocodylians, 28 testudines, 103 squamates (36 snakes, 68 lizards)) were obtained from a single source (Birchard & Marcellini, 1996), with the exception of data for the viviparous lizard species *Leiopisma coventryi* (Shine, 1983). The reptile groups crocodylia and testudines were evaluated separately from squamate reptiles because they differ in their relationship to neonate mass (Birchard & Marcellini, 1996). Mean incubation temperatures of 30.7 ± 0.9 , 30.0 ± 0.7 , and 29.9 ± 0.9 °C were used for crocodylians, testudines and squamates, respectively (Birchard & Marcellini, 1996). Embryonic development time and neonate mass data in birds (13 orders, 172 species) and mammals (16 orders, 94 species) were obtained from 2 sources (birds, Heinroth, 1922; mammals, Sacher & Staffeldt, 1974), with the exception of data for the monotreme *Tachyglossus aculeatus* (Griffiths, 1978) and the procellariiform birds (Williams & Ricklefs, 1984) (Appendix 2). For all birds, the mean incubation temperature of 35.7 °C (SD = 1.7 °C, $n = 101$) (McNab, 1966) was used to convert embryonic development time to degree-days because incubation temperatures were not available for most species. For mammals, incubation temperatures of 32.5 °C for the monotreme (Griffiths, 1978), 35 °C for the marsupial, and 38 °C for all other mammals were used to convert embryonic development time to degree-days (Schmidt-Nielsen, 1997).

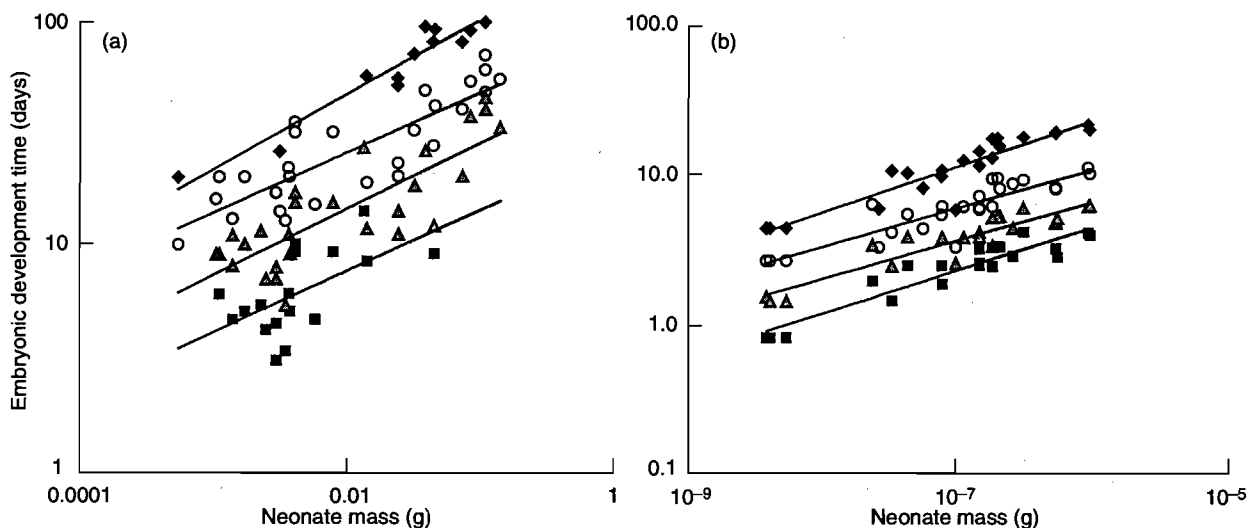
RESULTS

Zooplankton, fishes and amphibians

Embryonic development time in aquatic ectotherms scales to neonate mass across a range of temperatures much as it scales to neonate mass in endotherms (Fig. 1a, b). Embryonic development time (days) scaled to neonate mass in zooplankton, fishes and amphibians at each of four temperatures (5, 10, 15 and 20 °C). There were no distinguishable differences in the relationship of

Table 1. Relationship of embryonic development time (degree-days) to neonate mass for amphibians, fishes, zooplankton, reptiles, birds and mammals (Fig. 2)

Incubation temperature (°C)	Taxonomic group	Equation (EDT =)	n	P	r ²	95% CI			
						Slope		Intercept	
						Low	High	Low	High
5.0	Amphibians, fishes	$1037.53x^{0.32}$	16	<0.0001	0.93	0.27	0.38	847.23	1270.57
5.0	Zooplankton	$3475.36x^{0.30}$	23	<0.0001	0.87	0.25	0.35	1686.55	7161.43
10.0	Amphibians, fishes	$895.36x^{0.27}$	28	<0.0001	0.73	0.20	0.34	642.69	1244.51
10.0	Zooplankton	$2018.37x^{0.25}$	26	<0.0001	0.81	0.20	0.31	979.49	4149.54
15.0	Amphibians, fishes	$862.98x^{0.30}$	28	<0.0001	0.68	0.22	0.39	642.69	1244.51
15.0	Zooplankton	$1879.32x^{0.26}$	26	<0.0001	0.89	0.22	-0.29	1137.63	3111.72
20.0	Amphibians, fishes	$799.83x^{0.34}$	17	0.0170	0.34	0.07	0.62	172.19	3723.92
20.0	Zooplankton	$2004.47x^{0.26}$	25	<0.0001	0.90	0.23	0.31	1164.13	3459.39
29.9	Lizards, snakes	$1534.62x^{0.15}$	102	<0.0001	0.36	0.11	0.19	1377.21	1706.08
30.7, 30.0	Crocodylians, testudines	$1093.96x^{0.18}$	40	<0.0001	0.56	0.13	0.23	909.91	1318.26
35.7	Birds	$412.10x^{0.21}$	174	<0.0001	0.75	0.20	0.23	385.48	441.57
38.0	Mammals	$805.38x^{0.28}$	94	<0.0001	0.83	0.26	0.31	680.77	955.00
***	All groups but birds	$1030.39x^{0.24}$	386	<0.0001	0.95	0.23	0.25	988.55	1071.52

**Fig. 1.** Embryonic development time vs neonate mass for: (a) fishes and amphibians and (b) zooplankton incubated at four constant temperatures (◆, 5 °C; ○, 10 °C; △, 15 °C; ■, 20 °C). Lines fitted to a log-log scale using power law equations (Table 1). Data sources listed in Appendix 1.

embryonic development time to neonate mass and incubation temperature between fishes and amphibians at each of these temperatures, although limited data prohibited statistical comparisons between groups. Similarly, no differences were observed between the freshwater and marine fish species among these data. Thus, all data for fishes and amphibians were pooled to express the relationship of embryonic development time to neonate mass with a single equation at each of the four temperatures (Table 1). At each temperature, embryonic development time was positively correlated ($P < 0.0001$) to neonate mass ($r^2 = 0.93, 0.73, 0.68, 0.34$ for 5, 10, 15 and 20 °C, respectively; Table 1). The increasing variability in embryonic development time with temperature is partially explained by the inherent increase in experimental error with embryonic development rate, and by the decrease in the range of neonate

sizes with increasing temperature in these relationships, particularly at 20 °C. Data for larger size neonates at higher temperatures were scarce because at these higher temperatures development is problematic for many of these larger egg species (e.g. salmonids).

Embryonic development time scaled to neonate mass in zooplankton at each of the four incubation temperatures much as it did for fishes and amphibians (Fig. 1a, b). The relationship of embryonic development time to neonate mass for zooplankton was homogeneous in slope to those of fishes and amphibians at each of the four temperatures, but differed in intercept (Table 1). The differences in intercept were small relative to the differences in body size between these groups. Among the three major groups of zooplankton (i.e. copepods, rotifers and cladocerans), however, no differences in the relationship of embryonic develop-

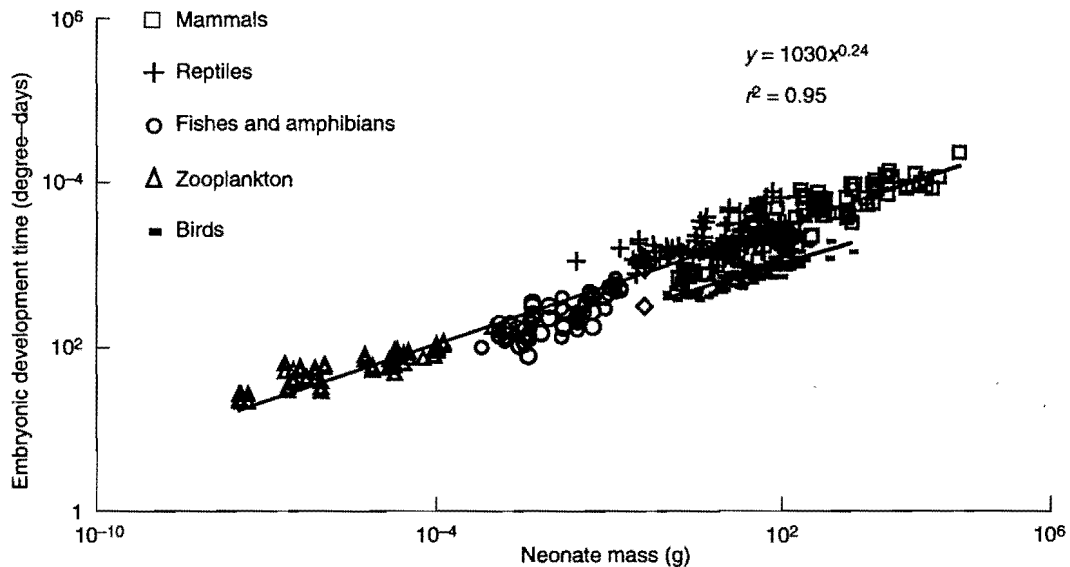


Fig. 2. Embryonic development time vs neonate mass for zooplankton ($n = 73$), amphibians ($n = 19$), fishes ($n = 53$), reptiles ($n = 143$), birds ($n = 174$) and mammals ($n = 94$). Zooplankton, fishes and amphibians were incubated at 5, 10 and 15 °C. Lines fitted to a log-log scale using power law equations (Table 1). Data sources noted in Methods.

ment time to neonate mass and incubation temperature were observed, despite the differences in life history and morphology between groups (see Allan, 1976). At each temperature embryonic development time in zooplankton was positively correlated ($P < 0.0001$) to neonate mass ($r^2 = 0.87, 0.81, 0.89, 0.90$ for 5, 10, 15 and 20 °C, respectively) (Table 1).

When embryonic development time at each temperature (5, 10, 15 and 20 °C) was redefined in terms of degree-days, embryonic development time relative to neonate mass was nearly equivalent at all temperatures for zooplankton, fishes and amphibians. The relationships of embryonic development time to neonate mass for fishes and amphibians, and for zooplankton, did not significantly differ in slope at 5, 10, 15 and 20 °C ($P > 0.50$ in both cases), or in intercept at 5, 10 or 15 °C (zooplankton, $P > 0.10$; fishes, $P > 0.05$). For fishes and amphibians, as well as zooplankton, the intercept of the line describing embryonic development time (degree-days) as a function of neonate mass for neonates incubated at 20 °C was significantly different from the other lines ($P < 0.05$), but the differences were small. For example, in zooplankton, the intercept for neonates incubated at 20 °C (2004) fell between the intercepts for neonates incubated at 10 °C (2018) and 15 °C (1879) (Table 1). Thus, the relationships of embryonic development time to neonate mass expressed in degree-days at each of these four temperatures for fishes and amphibians, and zooplankton, may be used to estimate embryonic development time across this range of temperatures (5–20 °C).

Zooplankton, fishes and amphibians vs reptiles, birds and mammals

The relationships of embryonic development time to neonate mass and incubation temperature in aquatic

ectotherms are similar to those of reptiles, birds and mammals – including for the unusual species (monotremes, marsupials and viviparous ectotherms; Fig. 2). A comparison of the relationships of embryonic development time (degree-days) to neonate mass in fishes and amphibians at 5, 10 and 15 °C (temperatures with no significant differences in development time in degree-days), to those of terrestrial ectotherms (reptiles) and endotherms (birds and mammals), revealed that differences between groups were small relative to the differences in body size. The slopes of the lines describing the relationships of embryonic development time (degree-days) to neonate mass fell between 0.15 and 0.34 for all groups (Fig. 2, Table 1). The slopes of many groups such as fishes and amphibians, crocodylians and testudines, and mammals were not significantly different from each other ($P > 0.20$). The slope of the relationship for zooplankton did not differ from those of reptile groups ($P > 0.50$), and the slope of the relationship for birds did not differ with that of crocodylians and testudines ($P > 0.20$).

The intercepts of the lines relating embryonic development time (degree-days) to neonate mass among many of these taxonomic groups were also similar. Across many groups, including fishes and amphibians, crocodylians and turtles, and mammals, the intercepts of the lines did not differ significantly ($P > 0.50$). The three unusual species among these taxonomic groups (monotreme, marsupial, and viviparous ectotherm) were indistinguishable from the general pattern. Thus, the time to birth adjusted for size and temperature was the same whether the organism was a fish, frog, turtle or human mother. However, the lines relating embryonic development time (degree-days) to neonate mass in birds and squamate reptiles (particularly lizards) were significantly different in intercept from other groups. On average, for a given neonate mass, squamate reptiles

required more development time than other groups, while birds required less time to develop. If all taxonomic groups except birds are included, the relationship of embryonic development time to neonate mass may be expressed in terms of degree-days with a simple power law equation ($EDT = 1030 * (\text{neonate mass})^{0.24}$) that explains 95% of the variability in this relationship ($P < 0.0001$, $r^2 = 0.95$).

DISCUSSION

Zooplankton, fishes and amphibians

The relationship of embryonic development time to neonate mass in fishes and amphibians and zooplankton, transcends obvious differences in the morphology and life history of species in these two groups. These differences, and the tendency of researchers to study life-history traits of one or more similar species, have often led to the assumption that traits such as embryonic development time are specific to a species or taxonomic group. For example, within zooplankton, the development time of copepods (which undergo complete metamorphosis) and cladocerans (which are born as miniature adults), have long been considered distinct, given their very different developmental paths to maturity (Hutchinson, 1967; Allan, 1976). Yet, we found no such differences in the relationship of embryonic development time to neonate mass between any of the three major groups of zooplankton (i.e. rotifers, cladocerans and copepods). Certainly, the relationships between embryonic development time and neonate mass in zooplankton, fishes and amphibians described here may explain variability in embryonic development time among species previously attributed to 'species-specific' differences. We speculate that these relationships have not been previously described because the size ranges used in interspecific comparisons have been too small to view this broad pattern.

The relationships of embryonic development time as a function of neonate mass in aquatic ectotherms (Table 1) provide an expression for the combined effects of neonate mass and incubation temperature. These relationships may be useful as tools for estimating the embryonic development time of aquatic ectotherms in natural systems with variable temperature regimes. Previous empirical relationships and mathematical models of embryonic development time describe either the effect of neonate size (e.g. Blueweiss *et al.*, 1978), or the effect of incubation temperature on individual species (Humpesch & Elliot, 1980; Elliot, Humpesch & Hurley, 1987), but never both. These results demonstrate that embryonic development time scales to neonate mass in the same manner across a range of temperatures, and that the change in development time with temperature is relatively constant for zooplankton, fishes and amphibians from 5 to 20 °C. For all aquatic ectotherms, embryonic development time approximately doubled with an increase of 10 °C. As such, the

relationship of embryonic development time to neonate mass from 5 to 20 °C could be expressed with a single equation in terms of cumulative thermal units (degree-days). These results support the hypothesis that embryo development requires a fixed number of degree-days over a limited temperature range, a hypothesis that was first proposed in 1735 for fishes by Réaumur (Ricker, 1979).

Observations from natural systems point to the increase in embryonic development time imposed by greater neonate (egg) mass as a constraint that may explain long-standing mysteries of ectotherm ecology, behaviour and evolution, respectively. The increase in embryonic development time with increasing neonate mass is significant at all temperatures, but especially at colder temperatures because the relationship of embryonic development time is expressed on a log-log scale in degree-days (Fig. 1a, b). For example, the difference in development time between the relatively small neonate of the rotifer *Filinia pejeri* and the relatively large neonate of the salmon *Oncorhynchus tshawytscha* is about 30 days at 15 °C, whereas at 5 °C, the difference is > 100 days (Fig. 1a, b). These longer development times for larger-size neonates may constrain successful reproduction in colder climates if development time approaches the duration of the summer season. Ectotherms challenged by this constraint must avoid colder regions, adjust their reproductive behaviour, or develop a new mode of reproduction. Evidence of strategies that serve to circumvent development time constraints in colder climates include the rare occurrence of ectotherms with large neonates, the relatively early reproduction of ectotherms with large neonates that do occur in colder regions (e.g. salmon), and the evolution of viviparity (Gans & Pough, 1982). So, while a species egg or neonate size is often considered a consequence of the interaction of parental life history with the environment, neonate size may also influence the life history and environment of a species.

Zooplankton, fishes and amphibians vs reptiles, birds and mammals

The relationship of embryonic development time to neonate mass and incubation temperature presented here (Fig. 2) provide new insights into the similarities and differences between terrestrial and aquatic ectotherms and endotherms for this life-history process. These results demonstrate that embryonic development time scales to neonate mass in much the same way for a broad assortment of animals. Despite the obvious morphological and developmental (i.e. precocial vs altricial) differences between animals, these results indicate that embryonic development time largely depends on neonate mass and incubation temperature. The broad applicability of the relationship is especially notable as traditionally aquatic and terrestrial organisms, endotherms and ectotherms, and oviparous and viviparous species, have been treated as distinct in most

respects including embryonic development time. The similarity in the relationship of embryonic development time to neonate mass across taxonomic groups further suggests the process (e.g. metabolic rate) controlling the rate of embryonic development is the same for all animals. Indeed, the slope of the line relating embryonic development time to neonate mass (degree-days) for these animals (0.24, Fig. 2) is very close to the 0.25 slope predicted by processes controlled by metabolic rate (Peters, 1983). However, the similarity in the relationship of embryonic development time for endotherms and ectotherms is not consistent with a process controlled by metabolic rate given the large difference in metabolic rates between these groups (Peters, 1983).

The relationship between embryonic development time and neonate mass presented here accounts for differences in incubation temperature, and thus provides a standard by which to examine differences in embryonic development time between species or taxonomic groups with different incubation temperatures. For example, these results indicate that birds require substantially less time for embryonic development than most other animals, an observation that requires further investigation. Comparisons of this relationship to the many animal groups not included in this study (e.g. insects, terrestrial-breeding amphibians) may provide further insights as to the similarities and differences between animals. This relationship may also help in assessing the relative influence of numerous other factors (e.g. geographical location, competition and predation, evolutionary history) which may affect embryonic development time in individual species (Gans & Pough, 1982; Kamler, 1992). Indeed, the relationship of embryonic development time to neonate mass presented here poses many new questions for ecologists and physiologists.

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