



成長する鳥類胚における心拍数解析： 成長モードと卵質量の効果

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Analysis of Heart Rate in Developing Bird Embryos : Effects of Developmental Mode and Mass

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Bird embryos may be regarded as developing in their thermo-neutral zone, at rest, and stay in the egg for a fixed period of time until hatching. It is therefore interesting to investigate if they follow the same "rule" set for adult homeotherms, which states that, within a taxonomically or functionally defined category such as mammals or birds, the number of heart beats throughout the life span (s_l) is more or less constant. This rule stems from the allometric relationships between heart rate (HR) and body mass (m_b) and between s_l and m_b .

As a step towards understanding the general allometric nature of avian embryonic physiology we analyzed the HR values of avian embryos in relation to their incubation span (s_i).

Data from 30 species were selected from the scientific literature for the analyses. Values obtained from invasive methods which were judged to grossly alter natural incubation conditions, or from undefined or unmatched temperature conditions were not used. These include most values obtained below the first 30% of the incubation. Also, data obtained after internal pipping were discarded since hatching activity influences them. Values for s_i and egg mass (m_e) as representative of embryonic mass were also collected.

Embryonic HR was normalized to 70.1-80% s_i . At 20.1-30% s_i it was only 85% of the value at 70.1-80% s_i and increased to a plateau at about 50.1-60% s_i . It was almost constant among species between 50.1-60% s_i and pre-internal pipping (PIP) time and thus, the mean HR value between 50.1-60% s_i and 90.1-100% excluding pipped eggs (MHR) was taken as a representative value for each given species. The MHR(bpm) and the corresponding s_i (d) values for the 30 species, scaled with m_e (g) as follows: $MHR = 371.1 \cdot m_e^{-0.112}$ and: $s_i = 12.29 \cdot m_e^{+0.209}$. Both powers were significantly different from 0. The product of MHR and s_i ($MHR \cdot s_i$), representing the total number of heartbeats throughout the incubation, scaled with m_e for the entire data set as follows: $MHR \cdot s_i = 6.565 \cdot 10^{-6} \cdot m_e^{-0.096}$, where the + 0.096 power is significantly different from 0.

Values for $MHR \cdot s_i$ from embryos of altricial birds tended to concentrate at the low m_e end of the plot while those of the precocial ones tended towards the high end. Separate analyses showed that the m_e power for the combined altricial and semi-altricial species (ASA), and the combined precocial and semi precocial species (PSP), of $\log MHR \cdot s_i$ against $\log m_e$ regressions, were both insignificantly different from 0. Thus, means of $MHR \cdot s_i$ for ASA and PSP were calculated. The mean ASA value of $7.27 \cdot 10^{-6}$ heartbeats for $MHR \cdot s_i$, was significantly different from the mean PSP value of $10.93 \cdot 10^{-6}$. The difference of $3.66 \cdot 10^{-6}$ (33.5%) heart beats can be attributed to either the more advanced stage of the PSP hatchlings at hatch, to the larger m_e values of these hatchlings, to the difference on water fraction of the hatchlings or all. The result of a linear regression of $MHR \cdot s_i$ (in d⁻¹

units) against the rate of s_1 completion (the inverse of incubation span, f_1 ; d^{-1}) was: $MHR \cdot 10^{-6} = 0.205 + 3.940 \cdot f_1$. Thus, the faster is the average rate of development accomplished per day (shorter incubation) the higher is daily heart rate. Data tended to cluster such that large eggs, mostly of the PSP type with relatively low MHR, complete 2 to 4% of their incubation per day, while small, ASA type eggs with relatively high MHR, complete 6 to 8% of their incubation time per day.

We conclude that, at this stage of knowledge, the data is insufficient to resolve whether the different modes of hatch stage alone can explain differences in the total number of heartbeats throughout embryonic life among all bird species, or egg mass and water content differences contribute variability. This should be investigated on a larger sample of species in more depth.

Keywords: Allometry, Altriciality, Avian Embryo, Avian egg, Development, Heart rate, Incubation, Precociality

1 RATIONALE

1.1 Homeotherms

The oxygen consumption rate per unit m_b in the thermo-neutral zone ($spVo_2$, an indicator of mass-specific resting metabolic rate), scales in both mammals and birds in the same way and is roughly in proportional to the -0.25 power of their m_b . For adult passerines (all altricial): $spVo_2 = 129 \cdot m_b^{-0.276}$, and for non-passerine (mostly precocial): $spVo_2 = 78 \cdot m_b^{-0.277}$ ⁽¹⁸⁾, where m_b is in kg and $spVo_2$ is in $kcal \cdot (d \cdot g)^{-1}$. Heart mass, blood volume and stroke volume (Q_s) are isometrically related to m_b ^(6,7,9,12,19). Cardiac output (Q) is well matched with $spVo_2$, at least for resting metabolic rate conditions. Since $Q = HR \cdot Q_s$, HR must scale roughly with $m_b^{-0.25}$ ⁽⁴⁰⁾. In fact, HR of birds in general is: $HR = 178.5 \cdot m_b^{-0.282}$ ⁽¹³⁾ where HR is in beats per minute. A similar equation was calculated for adult non-passerine birds: $HR = 155.8 \cdot m_b^{-0.23}$ ⁽⁹⁾, but in a different set of data ⁽⁶⁾ it was found that: $HR = 175.6 \cdot m_b^{-0.209}$, where in all cases m_b is in kg. The similar mass powers reported for $spVo_2$ and HR indicate that they may be directly correlated at any given m_b .

The life spans (s_1) of mammals and birds can be approximated as a function of their $m_b^{+0.25}$ although they differ in their proportionality constants. Somewhat lower powers have been reported for free living birds and when not separated to passerines and non-passerines ^(7,9,10,14,23,24,28,29). The general trend, however, indicates that on the average both mammals and birds survive a fixed amount of heartbeats since: $HR \cdot s_1 \approx k \cdot m_b^{-0.25} \cdot k' \cdot m_b^{+0.25} \approx K$, where k and k' are

the proportionality constants for the relationship between HR and s_1 to m_b respectively, and K is a constant number of heartbeats. The K value is a number, which describes a *similarity criterion* between species ⁽³⁹⁾. The value for adult mammals is $1.47 \cdot 10^{+9}$ heartbeats per life span ⁽⁴⁰⁾ and for adult birds it is: $2.32 \cdot 10^{+9}$ heartbeats per life span ⁽⁹⁾.

To speculate, it seems that life time in homeotherms lasts a given quantity of actions or events occurring in a mass unit. Life would have been longer if the rate at which these actions occur was slower and vice versa. However, the pace and/or life span are not arbitrarily set – they are strongly correlated with the animal's body mass.

1.2 Avian embryos

Bird embryos may be regarded as developing in their thermo-neutral zone, at rest, and stay in the egg for a given period of time in preparation for hatching. It is therefore interesting to investigate if they too follow the same allometric "rules" set for adult homeotherms and if *similarity criteria* may emerge within a taxonomically or a functionally defined category such as in bird embryos. In particular, it is of interest to elucidate if a similarity criterion, such as the K above, emerges from the allometric relationships between HR and fresh egg mass (m_E ; representing embryonic mass) and between s_1 and m_E .

1.3 Oxygen consumption rate.

The shape of the curve describing $spVo_2$ of a bird embryo with incubation time (s_1) is characteristic for each species. However, if s_1 is normalized to 100% and $spVo_2$ is either normalized to 100% at PIP time (ca 90% of s_1) or to mid-"plateau" value (a period during incubation starting

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shortly before PIP time and characterized by a sudden change in the slope of spVo_2 (vis a vis time), a pattern emerges which seems to be similar in all species and varies mainly in the duration of the above mentioned "plateau" stage^(18,29,50,51). Embryos of altricial species (and/or species possessing small eggs) tend to have short or even almost no plateau (lasting of up to 12.4% s_1) while precocials (and/or species possessing large eggs) tend to have a well pronounced plateau (lasting up to 16.9% s_1 ⁽³⁰⁾). The value of PIP spVo_2 was found to be allometrically related to m_E in the form of:

$\text{spVo}_2 = 22.2 \cdot m_E^{-0.228}$ (after ³⁴) and:
 $\text{spVo}_2 = 28.9 \cdot m_E^{-0.286}$ (after ¹⁸), where spVo_2 is in $\text{ml}[\text{STPD}] \cdot (\text{g} \cdot \text{d})^{-1}$ and m_E is in g.

The power values in the equations above fluctuate (depending on the sample) below and above those shown for the relation of spVo_2 at BMR and m_E of adult birds (~ -0.25). Note that bird embryos may be regarded as developing in their "thermo-neutral zone" "at rest" and in a quasi-steady state. This is because analysis shows⁽¹⁷⁾ that tissue maintenance accounts for about 70-80% of the total energy used up during development, even without taking into account the metabolism assigned to the extra embryonic membranes. However different models give estimates for maintenance cost, which are somewhat lower⁽¹²⁾.

1.4 Incubation duration and oxygen consumption

From literature data it is possible to show an inverse relationship between PIP spVo_2 and s_1 such that the product of the two averages ca 273 $\text{ml}[\text{STPD}] \cdot (\text{d} \cdot \text{g})^{-1}$ of O_2 for all bird embryos⁽³³⁾. During other equivalent fractions of incubation, hence in equivalent embryonic developmental stages, the normalized spVo_2 values ($\text{Vo}_2 / \text{PIP spVo}_2$) are also similar among species. (At least within altricial and precocial embryos). Thus, the areas under the curves, describing spVo_2 as a function of incubation time, are proportional, and it is justifiable to integrate the total amount of O_2 consumed per gram fresh egg mass during the entire incubation period ($\sum \text{spVo}_2 = \text{totVo}_2$, $\text{ml}[\text{STPD}] \cdot \text{g}^{-1}$) for comparing different species. The totVo_2 was indirectly estimated to be 90 $\text{ml}[\text{STPD}] \cdot \text{g}^{-1}$ of egg mass regardless of m_E and s_1 ⁽¹⁾. An average value of 102 $\text{ml}[\text{STPD}] \cdot \text{g}^{-1}$ was calculated for 34 species⁽¹⁸⁾. It appears that totVo_2 (which, when transformed into energy units per gram egg, describes the total energetic cost of converting m_E unit into an equivalent unit of chick mass) varies in a narrow range. Among altricial species it is

ca 0.3 to 1.1 $\text{kJ} \cdot \text{g}^{-1}$, and among precocial species - ca 0.4 to 2.1 $\text{kJ} \cdot \text{g}^{-1}$ ⁽⁵⁰⁾. From calculated values given in⁽¹⁷⁾ it can be concluded that the energetic cost of producing precocial hatchling (per gram of fresh egg mass) is ca 25% higher than that of altricial hatchling. This difference between altricials and precocials disappears when totVo_2 is expressed as a fraction of the energy utilized and transformed per gram egg (kJ/kJ) to form the (yolk-sac free) hatchling, because it disregards the higher water concentration in altricial hatchlings. It amounts at hatch, in all maturity forms, to an average of 35% of all energy utilized and transformed⁽⁴⁾. This fractional value seems to represent an embryonic similarity criterion as defined above. As Shown in the development above, it must be constant if s_1 scales with m_E the same way as s_1 scales with m_E . If this is the case, as suggested before⁽²⁹⁾, then a constant number of metabolic events, associated with totVo_2 , signify the embryonic development. One of these amounts could be the total number of heartbeats during the embryonic life, which represents the total number of oxygen pulses.

From studies, which show that growth time and time to sexual maturity in mammals are a fixed fraction of s_1 ^(10,37) it can be inferred that s_1 is proportional to s_1 of birds. More over, fledging time and time to first reproduction are also directly proportional to s_1 in birds⁽¹⁰⁾. Time spans of various variables in birds have been summarized⁽²⁹⁾. In 5 studies, m_E power values for s_1 , ranged from +0.16 to +0.24⁽²⁹⁾. The study concluded that the costs of embryogeny, ontogeny and maturity all scale with mass in the same way and are constants per unit mass, i.e. the durations of these stages are in a fixed proportion to each other⁽³⁰⁾. It is interesting to note that a difference was found between altricial and precocial birds in s_1 . In the same sample, the m_E powers for s_1 were +0.29 and +0.22 for altricial and precocial species respectively⁽⁵⁰⁾. Thus, a search for a K value of avian embryos, seems to be justified.

1.5 Cardiac functions

The proportions of m_E of the avian embryo at different developmental stages to both initial m_E and hatchling mass are rather fixed^(16,36). We have analyzed chick embryo data⁽³⁶⁾ and found that the fractional heart mass of the embryo stays constant throughout incubation (0.56%). Fractional heart mass of adult birds is about 1%⁽¹⁰⁾. Hence, Q_s at any embryonic stage must be also directly correlated with embryonic mass and thus with m_E .

Table 1. Averaged embryonic fH in different percentiles of incubation time for some avian species

No.	Species common name and mode of development	Latin name	Egg mass (g)	Incubation temp. (°C)	period (S/I)	Values are expressed in beats per minute and as percent of the 65% incubation time value ^{a)}														References				
						20.1-30 (%)	30.1-40 (%)	40.1-50 (%)	50.1-60 (%)	60.1-70 (%)	70.1-80 (%)	80.1-90 (%)	90.1-100 (%)	PIP (%)	f _H means (80-100%)									
<i>Altricial</i>																								
1	Bengalese finch	<i>Lonchura striata v.domestica</i>	1.061	38	16		81.52	300	91.85	338	96.20	354	101.4	373	105.0	368	108.7	400	104.1	383	117.1	431	376	27
2	Marsh Tit	<i>Parus palustris</i>	1.41	38	15		83.98	304	91.44	331	96.96	351	99.72	361	103.6	362	107.5	389	108.8	394	107.5	389	371	27
3	Bank swallow	<i>Riparia riparia</i>	1.42	38	13								96.19	278	99.65	289	103.1	298	108.7	314	108.7	314	295	48
4	Great tit	<i>Parus major</i>	1.49	38	13	85.30	296	297	93.08	323	97.69	339	98.56	342	101.4	347	104.3	362	110.7	384	104.3	362	355	27
5	Varied tit	<i>Parus varius</i>	1.7	38	15								95.81	343	97.21	348	101.8	350	106.4		106.4	361	358	27
6	Eurasian Tree sparrow	<i>Passer montanus</i>	2.08	38	12		86.65	305	89.49	315	97.16	342	102.3	360	101.8	352	101.4	357	102.6	361		102.6	361	27
7	Budgerigar	<i>Melopsittacus undulatus</i>	2.2	38	16				93.56	305	96.01	313	98.77	322	100.0	326	101.2	330	102.1	333		102.1	333	27
8	House martin	<i>Delichon urbica</i>	2.27	38	15		76.08	264	86.17	299	89.91	312	95.97	333	100.4	347	104.9	364		110.1	382	339	27	
9	Black-faced bunting	<i>Emberiza spodocephala</i>	2.56	38	13						82.67	291	85.23	300	93.04	352	100.9	355	98.68	374	98.68	374	374	27
10	Red-cheeked starling	<i>Sturnus philippenensis</i>	4.14	38	14								95.69	311	98.92	325	102.2	332	105.8	344	105.8	344	328	27
11	Brown-eared bulbul	<i>Hypsipetes amaurotis</i>	6.4	38	16								104.2	270	111.2	288	106.2	275	112.2	259	118.1	308	282	27
12	Collared turtle dove	<i>Streptopelia turtur</i>	6.5	36	13.5																		206	27
13	Domestic pigeon	<i>Columba domestica</i>	19.1	38	18		85.96	202	89.36	210	90.21	212	97.02	228	100.9	235	104.7	246	109.4	237	106.4	250	236	48
14	Lanner falcon	<i>Falco biarmicus</i>	41.2	36	32											227	93.83	213	94.7	215	92.07	209	218	27
<i>Semi altricial</i>																								
15	Barn owl	<i>Tyto alba</i>	20.1	36	28		107.7	211	106.1	208	104.6	205	105.6	207	103.3	196	101.0	198	112.8	221	103.6	203	205	27
16	Cattle egret	<i>Bubulcus ibis</i>	27.5	36	22.5				88.69	196	97.74	216	99.55	220	96.61	221	93.67	207	93.67	207	104.5	231	214	27
<i>Semi precocial</i>																								
17	Brown noddy	<i>Anous stolidus</i>	37.9	36	36								97.35	257	98.48	264	98.62	263		99.24	282	261	47	
18	Hermann's gull	<i>Larus hermanni</i>	53.4	36.7	25	120																	5	
19	Wedge-tailed shearwater	<i>Puffinus pacificus</i>	57.2	36	50								100.0	214	100.7	214	101.4	217	100.5	215		215	49	
20	Laysan albatross	<i>Diomedea immutabilis</i>	208	36	65											188	103.7	195	105.9	199	108.5	204	194	49
<i>Precocial</i>																								
21	King quail	<i>Colurnix chinensis</i>	5.96	38	16		92.07	302	95.12	312	95.73	314	96.95	318	100.3	328	103.7	340	96.0	315		323	26	
22	Japanese quail	<i>Colurnix colurnix japonica</i>	10.7	38	17				93.52	303	92.90	301	95.37	309	97.07	324	98.77	320	104.3	338		318	46	
23	White-tailed ptarmigan	<i>Lagopus leucurus</i>	18.7	35.2	25											292	100.0	202				292	44)	
24	Chicken	<i>Gallus domesticus</i>	64.9	37.8	20.8	85.04	233	270	101.1	277	98.54	270	97.45	267	98.72	274	100.0	274	96.35	264		270	8,15,21,32,45,46	
25	Pekin duck	<i>Anas platyrhynchos</i>	79	38	28				103.2	258	102.4	256	98.80	250	95.20	238	93.20	233				247	46	
26	Turkey	<i>Meleagris gallopavo</i>	82.9	38	28				97.55	239	95.92	235	95.71	245	95.51	234	95.92	235				238	46	
27	Peafowl	<i>Pavo cristatus</i>	111.3	38	28				94.21	244	96.14	249	99.03	259	101.9	264	94.98	246				252	46	
28	Chinese goose	<i>Anser cygnoides</i>	158.3	38	30				107.8	248	105.7	243	102.2	230	98.70	227	116.5	268				243	46	
29	Emu	<i>Dromiceus novaehollandiae</i>	560	36	50						98.21	105	94.64	168	91.07	153	87.50	147				158	43	
30	Ostrich	<i>Struthio camelus</i>	1362	36.3	42				108.8	186	108.8	186	106.4	182	95.61	171	84.80	145	70.70	121		161	42,43	

^{a)} See details in text^{**)} Ar, Paganelli & Carey, unpublished

On this basis we hypothesize that Q , and thus HR, would be proportional to the same m_e power as s_i with a negative sign, and that the integrated heart beat number throughout the incubation span would yield a K constant which represents a *similarity criterion* for the total number of heart beats of avian embryos during incubation.

2 MATERIALS AND METHODS

Egg masses, incubation durations, incubation temperatures and heart rate data were collected from scientific publications (Table 1). Care was taken to ensure that individual species values of s_i and HR correspond to the incubation temperatures given, whether in nature or in the laboratory. Only HR values, which were obtained using methods, which did not alter the physiological state of the embryo, were used. Thus, methods, which involved opening of the eggshell, which may change dramatically the gas pressures over the chorioallantoic membrane, or those incubated at uncontrolled temperature, were eliminated. For this reason we could not use data of embryonic ages below the 20.1-30 percentile of the incubation duration.

The final list of 30 species, which was subjected to our analysis, is given in Table 1. Species were arranged according to their maturity rank at hatching following the conventional classification (³, after ²⁵). Within each group, species were arranged in ascending order of their fresh egg mass.

Conventional statistical methods were employed using STATISTICA/W 5.0⁽⁴¹⁾. Model I regression was preferred for the allometrical relations. This model permits direct comparison with most published data. Also, our data is interspecific and the small number of data points did not permit sub-divisions into lower taxonomic levels, and the performance of nested ANOVA. Regressions were compared using ANCOVA tests and slope comparison tests. The error variance in heart rate was considered much greater than in egg mass, and at any rate, the same egg mass was used for both the analysis of heart rate and incubation span. The standardized major axis method did not fit here because it is reliable at powers close to 1.0 and the non-linear regression analysis is reasonable only at powers below 0.2.

3 RESULTS AND DISCUSSION

3.1 Heart rate and egg mass

From inspection of the data sets that were chosen for the analysis (references in Table 1), it became obvious that, in many species, young embryos have some what lower heart rates than more mature ones by about

16-20%^(27,42-50). Towards the end of the incubation, some species increased in HR while some decreased, but no consistent pattern was found^(27,42-50). In order to try and choose a representative HR for any given species, all HR values were grouped according to their relative occurrence during the incubation. Thus, values between 20.1 and 30% of s_i (assigned the value 25% of s_i), 30.1 and 40% (assigned the value 35% of s_i) etc. were grouped, and when necessary averaged for each species. These HR values are given in Table 1. They are also given in percent of their respective values of the 75% s_i group. The 75% s_i percentile group was chosen as a reference of 100% HR since it represented, by inspection, a plateau value for embryonic HR (Fig. 1). Since all HR values of the 75% s_i group were assigned the value 100% as a reference value, we interpolated the HR of the 65 and 85% s_i groups for each species in order to estimate the variability within the 75% group. The group of 95% includes only values for non-pipped eggs. The PIP values were discarded from analysis since they may represent activity HR.

A Kruskal-Wallis one-way ANOVA by ranks and single factor ANOVA tests showed that there was no significant difference in percent HR between the 45 and 95 percentiles of incubation. However, since LST and χ^2 tests showed that the 45% s_i group is significantly different from the others, a mean representing the plateau in HR was taken for every species between 55 and 95% s_i . This mean HR (MHR) is given in Table 1. The relationship between HR and m_e of our data set was:

$$\text{MHR} = 371.1 \cdot m_e^{-0.112};$$

$$\text{SE} = \times 1.116; r^2 = 0.812; n = 29.$$

where the symbol \times (representing multiplication or division) becomes \pm in the log form of the equation. Thus $\pm \log \text{SE}$ is the standard error of estimate. The antilog of $2 \cdot \log \text{SE}$ is the factor by which a value of MHR, calculated using a given m_e , has to be multiplied and divided in order to estimate its 95% confidence limits. As can be noticed, the m_e power of $-0.112 (\pm 0.010 \text{ SE})$ is low when compared with the initially expected value of -0.25 .

Previously published work found differences between the altricial and precocial allometry (see above). We speculated that separating the MHR data into maturity groups could yield different powers. Due to the limited number of data values, we subdivided our values into 2 groups - (a) precocial and semi-precocial species (PSP), and (b) altricial and semi-altricial (ASA).

Hence, much in the same way, we have calculated, for MHR of the above 2 maturity

at hatch categories as a function of their m_E , the following:

$$\text{MHR (PSP)} = 439.1 \cdot m_E^{-0.140};$$

$$\text{SE} = \pm 1.089; r^2 = 0.871; n = 13,$$

and:

$$\text{MHR (ASA)} = 383.7 \cdot m_E^{-0.163};$$

$$\text{SE} = \pm 1.093; r^2 = 0.838; n = 16.$$

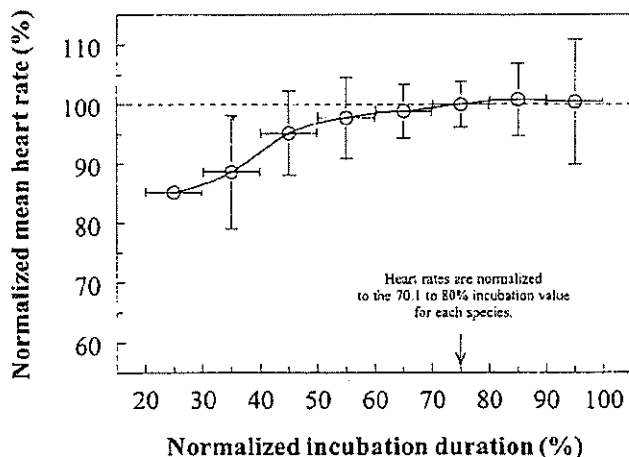


Fig. 1. Mean heart rates of avian embryos (Table 1). Species values were grouped, averaged and presented as percent relative to their intraspecific value at the 75% incubation interval. The normalized heart rate values at different percentiles of incubation were averaged among species. Vertical bars are among-species SD. Horizontal bars are the percent incubation zones from which individual species values were grouped and averaged (e.g. 70.1 - 80% is given as 75%).

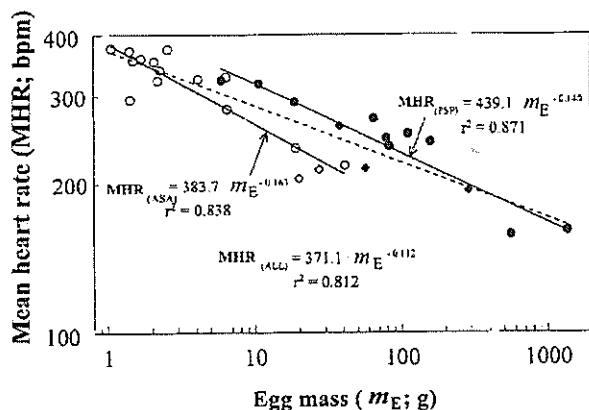


Fig. 2. Mean heart rate of avian embryos (MHR) as a function of their initial egg mass (EM) presented on log-log scales. Broken line is the regression line for all the data (ALL). Solid lines are for precocial + semiprecocial (PSP) and for altricial + semi-altricial (ASA) embryos. Closed circles - precocial eggs; closed diamonds - semi-precocial eggs. Open circles - altricial eggs; open diamonds - semi-altricial eggs.

Both negative powers were higher and significantly different from zero ($p < 0.0001$). There was no difference between the slopes (variance test for slopes; $p = 0.3665$). ANCOVA test gave $F_{1,26} = 3.3022$ and $p = 0.0807$. This means that when the effect of m_E is removed there is no difference in MHR between the PSP and the ASA groups. Noticeable increases in r^2 and decreases in SE were evident, in spite of smaller n values as compared with the overall equation. This indicates that the separation of the MHR data into PSP and ASA groups was justified (Fig. 2).

An equation similar to the one above for PSP has been obtained⁽⁴⁶⁾ on 6 precocial species with a lower m_E power value, of -0.106 . The same paper cites unpublished works⁽⁴⁶⁾; Tullett and Deeming; Rahn and Paganelli both with low m_E powers (-0.107 ; $n = 6$ and -0.11 ; $n = 9$ respectively). This is understandable considering the smaller n values and the scatter of the data. (It has been shown⁽³⁵⁾ that such regressions tend to underestimate the slopes of linear relations. In our cases: the power functions translate into linear relationships between $\log \text{MHR}$ and $\log m_E$ where the powers are the slopes of these regressions). A power value of -0.12 was found for 3 semi-precocial species⁽⁴⁶⁾, and of -0.08 for 2 altricial species⁽⁴⁸⁾.

3.2 Incubation duration and egg mass

The relationship between s_I and m_E of our data set was:

$$s_I = 12.282 \cdot m_E^{+0.207};$$

$$\text{SE} = \pm 1.254; r^2 = 0.769; n = 30,$$

and is similar to that obtained on a much larger data set⁽³²⁾:

$$s_I = 12.03 \cdot m_E^{+0.217};$$

$$\text{SE} = \pm 1.237; r^2 = 0.860; n = 475.$$

However, since a difference was found between the altricial and precocial s_I allometry⁽⁵⁰⁾ and in order to be able to analyze the relationship between MHR and s_I , we subdivided again our values into PSP and ASA groups, and obtained:

$$s_I(\text{PSP}) = 12.286 \cdot m_E^{+0.209};$$

$$\text{SE} = \pm 1.332; r^2 = 0.552; n = 14,$$

and:

$$s_I(\text{ASA}) = 12.532 \cdot m_E^{+0.187};$$

$$\text{SE} = \pm 1.194; r^2 = 0.632; n = 16.$$

There were no significant differences in the slopes ($p = 0.7526$) and intercepts between the equations for the PSP and the ASA groups (Fig. 3). ANCOVA test gave $F_{1,27} = 0.0905$ and $p = 0.7662$, showing that,

after removing the egg mass influence, there are no differences in s_i between the PSP and the ASA groups.

3.3 Total number of heart beats during incubation

The product $MHR \cdot s_i$ of each species in our data set may be regarded as representing an estimate of the total amount of heartbeats of an avian embryo throughout its embryonic development:

$$MHR \cdot s_i = 6.565 \cdot 10^{+6} \cdot m_E^{+0.096};$$

$$SE = \pm 1.248; r^2 = 0.434; n = 29.$$

Although both the power and the r^2 values are low, they are significantly different from 0 ($p < 0.0001$), indicating that there is a residual m_E power of $+0.096 \pm 0.021$ SEE in the equation and thus $MHR \cdot s_i$ is not constant among all embryos in our sample. Furthermore, inspection of the data (Fig. 4) reveals that $MHR \cdot s_i$ of small eggs tends to be low,

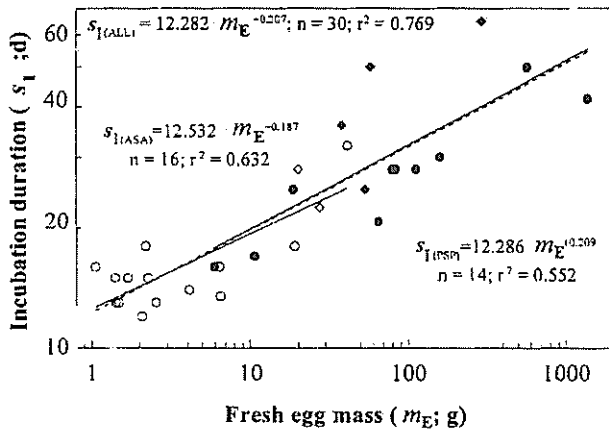


Fig. 3. The relationship between log incubation duration (ID) and log fresh egg mass for the entire data set, for precocial + semiprecocial and altricial + semi-altricial embryos. Abbreviations and symbols are as in Fig. 2.

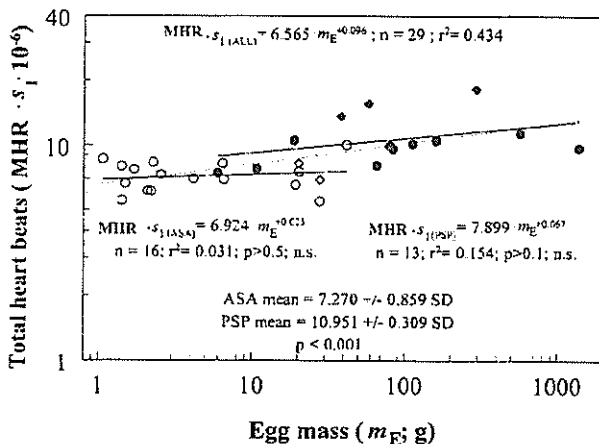


Fig. 4. The total number of heart beats of avian embryos during incubation (HRID) as a function of their initial egg mass, presented on log-log scales. Broken line is the regression line for

all the data. Solid lines are for precocial + semiprecocial and for altricial + semi-altricial embryos. Abbreviations and symbols are as in Fig. 2.

but apparently independent of mass, as compared with relatively large eggs. It was also noted that most ASA eggs of our sample are small (range: 1-41 g) in comparison to PSP eggs (range: 6-1362 g).

The inspection of the two sets of equations of s_i and MHR as a function of m_E for the PSP and ASA groups indicated that the hypothesis of a constant $MHR \cdot s_i$ should be tested separately for each group according to their maturity. The regressions of $MHR \cdot s_i$ on m_E yielded (Fig. 5):

$$MHR \cdot s_i(PSP) = 7.899 \cdot 10^{+6} \cdot m_E^{+0.067};$$

$$SE = \pm 1.285; r^2 = 0.154; n = 13,$$

and:

$$MHR \cdot s_i(ASA) = 6.924 \cdot 10^{+6} \cdot m_E^{+0.025};$$

$$SE = \pm 1.187; r^2 = 0.031; n = 16.$$

The powers were not significantly different from 0 ($p = 0.185$ and 0.517 ; $SEE = \pm 0.048$ and ± 0.037 respectively). Since $m_E^0 = 1$ there is no significant effect of m_E on the $MHR \cdot s_i$ values within each group. Thus, we felt justified to average $MHR \cdot s_i$ within each group as:

$$MHR \cdot s_i(PSP) = 10.951 \cdot 10^{+6};$$

$$SD = \pm 0.309 \cdot 10^{+6}; n = 13,$$

and:

$$MHR \cdot s_i(ASA) = 7.270 \cdot 10^{+6};$$

$$SD = \pm 0.859 \cdot 10^{+6}; n = 16.$$

Both one-tailed and 2-tailed t-tests for unequal variances showed significant differences at the $p = 0.001$ level. (Note that the values presented here are probably over estimating the real values because of the relatively low HR values at the early stages of the development.) The difference between the PSP group and the ASA group in $MHR \cdot s_i$ is $3.682 \cdot 10^{+6}$ heartbeats. The 34% higher $MHR \cdot s_i(PSP)$ value is in accord with the group's maturity state at hatch and its corresponding higher totVo_2 . It was found that the precocial group is ca 25% higher in totVo_2 than the altricial one^(17,50). Fresh egg content energy stores (per g) of altricial species are smaller in comparison with precocial species by ca 60 to 90 %^(2,4,11,38,50).

Hence, each of the 2 maturity groups can be characterized by a particular similarity criterion - a constant total number of heartbeats throughout incubation. This finding indicates that our initial hypothesis should be modified. It seems to

hold only within a more homogeneous group, and indicates substantial differences in $MHR \cdot s_i$ between the maturity groups tested.

3.4 Egg water content

While the totMo_2 and energy content values per gram fresh egg mass differ between the maturity groups, the difference tends to disappear when they are recalculated on the basis of dry egg mass^(4,50). This may indicate that egg water content may play a role in differentiating the embryonic pattern of development between PSP and ASA embryos.

So far, egg water content per se is not known to be a factor, which can influence either s_i or MHR among species. The differences in $MHR \cdot s_i$ between the two groups appear to be linked to the maturity state at hatching which, however, is also linked to both egg (and hatchling) water content and egg (and hatchling) mass^(3,11). It would thus be premature or impossible at this stage to conclude that the $MHR \cdot s_i$ of bird embryos is dependent on developmental mode only. Water content may play a role as well. We need more data on e.g. large altricial and small precocial bird eggs of different water contents to draw more definite conclusions.

3.5 Heart rate and developmental rate

If the total amount of heartbeats during incubation as estimated by $MHR \cdot s_i$ is fixed within each of the maturity groups irrespective of m_e or s_i , then the time interval between 2 heartbeats should be directly proportional to s_i , and MHR - to an estimate of the rate at which embryonic development proceeds.

We have compared MHR, but this time expressed in per day units ($MHR; d^{-1}$), with the developmental rate per day of avian embryos. An estimate of the average developmental rate of avian embryos can be obtained as s_i^{-1} . Namely, the embryonic development accomplished per day. Since we expected a simple correlation between f_H per day and s_i^{-1} , a linear regression was used. The regression equation for all our data was:

$$MHR \cdot 10^{-6} = 0.205 + 3.940 \cdot s_i^{-1} \\ SE = \pm 0.050; r^2 = 0.729; n = 29,$$

where MHR is per day. The significant slope indicates that MHR and s_i^{-1} are positively correlated (ANOVA test: $F_{1,27} = 72.67; p < 0.0001$; Fig. 5). Analysis of the individual regressions for the ASA and PSP groups showed that both the slopes and the intercepts are significantly different from 0 but are not significantly different from each other ($p = 0.5852$ and 0.2813 , respectively). Separation into two groups is not justified at this time.

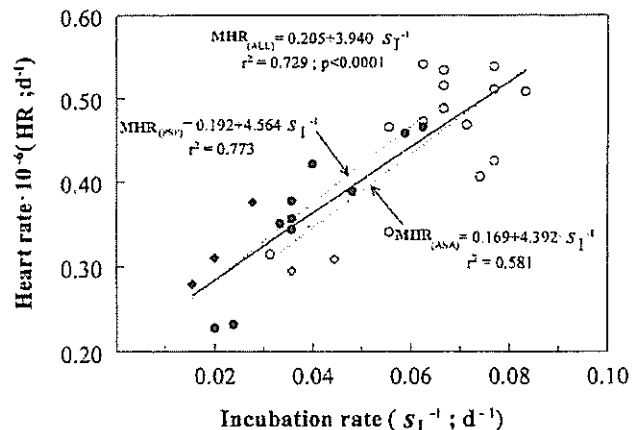


Fig. 5. Mean heart rate of avian embryos expressed in per day units (HRD) plotted vs their developmental rate, the reciprocal value of their incubation period (IR). Solid line is the regression line for all the data. Dotted lines are for precocial + semiprecocial and for altricial + semi-altricial embryos. Abbreviations and symbols are as in Fig. 2.

Thus, on an inter-specific basis, an increase in the average rate of development among avian embryos (= shortened incubation) is associated with an increase in the number of heartbeats per day.

4 CONCLUDING REMARKS

The analysis of log-log relationships between various structural, functional and temporal parameters of avian embryonic development and fresh egg mass, representing the embryo, reveals that they may be regarded as allometrically linked such that some biologically explainable constants or similarity criteria emerge.

In the particular case of the present paper we show that, within functionally linked sub-groups of avian embryos, an estimate for the total number of heartbeats during the entire embryonic development is constant. The magnitude of this constant correlates either with the maturity state at hatch, (which in turn is related to a taxonomic state) or perhaps to egg mass and/or egg water content.

The relatively little data available at this stage makes it difficult to draw final cause and effect conclusions and more information needs to be gathered before final statements can be made.

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成長する鳥類胚における心拍数解析：成長モードと卵質量の効果

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概要

鳥類胚は安静状態でかつ一定範囲の温度環境で成長し、孵化するまで一定期間卵内に留まっている。従って、恒温動物の成体で見られると同じ法則；即ち、一生を通した心拍数の総数は哺乳類にしても、鳥類にしても多かれ少なかれほぼ一定であるという法則に従っているかを検証することは興味のある。この法則は心拍数と体重、それに一生の期間と体重との間のアロメトリー特性に由来している。

鳥類胚生理機能の一般的なアロメトリー特性をまず理解するために、鳥類胚心拍数を孵卵期間に関連して分析した。データは文献から選んだ 30 種であり、自然の孵卵条件を変えてしまうと判断される侵襲による計測結果及び温度条件が記載ないかあるいは不都合な条件による結果は除いた。これらの多くは孵卵期間の最初の 30%におけるデータである。又孵化行動は心拍数に影響を与えてしまうので内嘴打ち中のデータも除いた。孵卵期間と胚質量に代わるデータとして卵質量を使った。

胚心拍数は孵卵期間 70.1-80%に規格化した。孵卵期間 20.1-30%で 70.1-80%の値の 85%になるとし、孵卵期間 50.1-60%でプラトーに達するとした。孵卵期間 50.1-60%と内嘴打ち前との間で一定値になるとし、孵卵期間 50.1-60%と外嘴打ちを除く孵卵期間 90.1-100%間の平均心拍数値を任意のそれぞれの種の代表値とした。30 種の平均心拍数と孵卵期間を卵質量に対してプロットすると、

$$\text{平均心拍数} = 371.1 \cdot (\text{卵質量})^{-0.112}$$

$$\text{及び 孵卵期間} = 12.29 \cdot (\text{卵質量})^{0.145}$$

となり、それぞれの果乗値は 0 と有意の差があった。孵卵期間中の心拍総数を表す平均心拍数と孵卵期間の積を全てのデータについて卵質量に対してプロットすると

$$\text{心拍総数} = 6.565 \cdot 10^{14} \cdot (\text{卵質量})^{-0.096}$$

となり、果乗値+0.096 は 0 と有意の差があった。

晩成種胚の心拍総数値は卵質量の小さい領域に集まり、早成種胚の心拍総数値は大きい領域に集まる傾向を示した。晩成種及び半晩成種における卵質量の対数値に対する心拍総数の対数値、及び早成種と半早成種における卵質量の対数値に対する心拍総数の対数値の回帰式は共に 0 と有意の差はなかった。そこで両グループに対して心拍総数の平均値を計算した。前者のグループの心拍総数の平均は $7.27 \cdot 10^4$ 回、後者については $10.93 \cdot 10^4$ 回で、両者の差は有意である。その差、 $3.66 \cdot 10^4$ 回 (33.5%) は孵化時の早成種の雛がより成熟していることによる、これらの雛を孵した卵質量がより大きいことによる、雛の含水量の差によるあるいはこれら全てによるものと思われる。

しかし、結論を出すにはまだデータは十分であるとは言えず、より多くの鳥類胚における心拍数計測が求められる。

キーワード：アロメトリー、晩成性、鳥類胚、鳥類卵、成長、心拍数、孵卵、早成性

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