INCUBATION AND FLEDGING DURATIONS OF WOODPECKERS[1]

YORAM YOM-TOV AND AMOS AR[2]
Department of Zoology, Tel Aviv University, Tel Aviv 69978, Israel

Abstract. The relatively long fledging duration of cavity-nesting birds has been related to the relative safety of their nesting sites (Lack 1968). We compared the relationships between body and egg masses and incubation (I) and fledging (F) times of 39 species of woodpeckers and wrynecks (Picidae) to those of altricial birds in general. We found that Picidae have shorter incubation and longer fledging periods in the comparable range of altricial birds' body and egg masses. However, the total development duration (I + F) is similar to that of other altricial birds. The representative F/I ratios of altricial birds within the size range of Picidae are 1.21–1.26, while for 32 picid species they are 2.09 ± 0.09 SE. Similar trends appear to exist in other cavity-nesters.

We suggest that the short incubation of Picidae is an adaptation to the apparently poor gas exchange around the eggs under the incubating parent in the nest chamber, where oxygen and carbon dioxide levels may be low and high, respectively, and early transition to pulmonary respiration associated with an increase in nest ventilation is of advantage. The relatively short incubation may indicate a relatively immature state of hatching that requires compensation by a prolonged hatching to fledging duration.

Key words: Woodpeckers; hole-nesters; incubation; fledging; allometry.

INTRODUCTION

The study of allometric relationships between various life history parameters and body parameters is useful, as it may uncover broad generalizations (Schmidt-Nielsen 1984). Residual variations in allometric relations must be attributed to other factors, and clear exceptions to generalizations might raise questions as to which factors these are. For example, Rahn et al. (1975) showed that throughout the class Aves there is a highly significant relationship between log body mass and log initial egg mass. However, different taxa may have different slopes and intercepts that represent different evolutionary trends. A significant relationship also exists between initial egg mass and incubation duration for birds in general (Rahn and Ar 1974), but the Procellariiformes have, for example, a significantly longer incubation duration for their egg mass (Rahn et al. 1984). This may be attributed to their long periods of nest neglect (Boersma 1982). The incubation duration of woodpeckers (Picidae) is remarkably short (Short 1982), while the time between hatching and fledging of hole-nesters such as woodpeckers is relatively long (Martin

and Li 1992). Lack (1968) attributed this long duration to the relative safety of the nest chamber in cavity-nesters. However, little work has been carried out on the general relationships between incubation duration and time until fledging in Picidae, taking into account body mass and egg mass.

We report here the above allometric relationships in woodpeckers and suggest an explanation for our results.

METHODS

We gathered data on female body mass (Mb), incubation (I) and time between hatching and fledging (F = fledging period or nesting period) from Short (1982), Fry et al. (1988), and on egg mass (Me) from Schönwetter (1967). Some complementary data on North American species were taken from Ehrlich et al. (1988), and Martin and Li (1992). Data on the Syrian Woodpecker are from Barnea (1982). Ordinary Least Squares regression equations and their statistics were calculated for the relationships between log Mb or log Me and log I, log F or log (I + F) for 39 species and 12 genera of Picidae. Use of multiple species within a taxon for comparative analyses of animal variables has been criticized, since such species share some common genetic information and therefore they do not provide independent values (Harvey and Mace 1982). Ideally, the most satisfactory comparative analysis should be based

on comparing phylogenies. However, since accurate evolutionary histories of species are rarely available, taxonomic classifications can form an ad hoc basis of comparative studies (Harvey and Purvis 1991). Here, we analyze data allometrically at both the species and genus levels. Since most published analyses are based on species, we compare the results within the general avian trends mainly at the species level. However, a nested-ANOVA test (Sokal and Rohlf 1969) was conducted to account for the relative variation at the species and genera levels.

RESULTS AND DISCUSSION

We obtained data on Mb, Me, I, F, and the ratio F/I for 2 species of wrynecks and 37 species of woodpeckers (Table 1).

Relationship of egg mass to body mass. Picid species have significant positive correlations between egg mass and body mass (Table 2). The relationship between egg mass and body mass is similar to that given for Piciformes (including 3 Bucconidae) by Rahn et al. (1975), and for a larger sample of mainly African Picidae by Payne (1989). Our relationship has, however, one of the lowest slopes (on log-log scales; Table 2 vs. Rahn et al. 1975) among all avian orders tested. Therefore, in spite of the similar intercepts of the relationship between the logarithm of egg mass and that of body mass in birds in general, Picidae have small eggs in relation to their body mass. This means they have relatively small hatchlings which may take longer to reach final size and fledge. The nested-ANOVA test shows that most of the variation in either body mass or egg mass is explained as differences among genera rather than of species within genera (Table 3).

Relationship of incubation duration to body and egg masses. Egg and body masses in picid species are significantly correlated with either incubation duration or the sum of incubation and fledging times (Table 2). However, incubation duration seems to depend little on body mass (Table 2), when compared to the equation for birds in general: $I = 9.105 \cdot Mb^{0.167}$ (Rahn et al. 1975). Incubation durations of Picidae are shorter than those of similar-sized altricial birds, especially among larger species (Table 2; Fig. 1). The same is revealed when analyses are based on egg mass. Large eggs (from large species; Tables 1, 2) tend to have shorter-than-expected incubation when compared with the general avian trend (Rahn and Ar 1974). The relatively small egg size of the

Piciformes can not solely account for the very short incubation period, since incubation is short even for the size of these small eggs. Most of the variation in incubation duration is also explained at the generic level, suggesting very little independence among individual species (Table 3).

Time between hatching and fledging. Time from hatching to fledging (F) in Picidae is not significantly correlated either with egg mass or body mass (Table 2), and the variation explained at the generic level is 53% (Table 3). We found no published relationship between F and body mass for altricial birds in general, but by using the F vs. incubation duration (I) relationship (Ar and Yom-Tov 1978; $F = 1.053 \cdot I^{1.061}$; $r^2 = 0.632$), and the relationship of body mass to egg mass (Rahn et al. 1975), we estimated the general equation to be: $F = 10.97 \cdot Mb^{0.177}$.

Fledging vs. incubation durations. From the equation of Ar and Yom-Tov (1978), altricial birds, within the range of incubation durations of woodpeckers, should have F/I ratios of 1.21–1.26. Fledging and incubation periods in Picidae are essentially uncorrelated ($r^2 = 0.042$ for the species level and 0.072 for genera level; Table 2). The F/I ratio for the 32 species of Picidae in Table 1 averages 2.09 ± 0.49 ($\bar{x}$ ± SD). On the genus level, it averages 1.96 ± 0.39 (Table 2). However, only 41% of the variation is explained on the generic level (Table 3). Note that the incubation durations of some other cavity-nesting birds are also substantially shorter in relation to their fledging periods. An example is provided by Australian parrots, where F/I = 1.96 ± 0.41 in 53 species. All of these are cavity-nesters, whereas the only parrot nesting in the open (*Pezoporus wallicus*) has an F/I ratio of 1.14 (Saunders et al. 1984). Similarly, the mean F/I ratio among 8 African hornbill species (Bucerotidae) is 2.15 ± 1.12 (Yom-Tov and Ar, unpubl. data). From data given by Martin and Li (1992) we calculated average F/I and SD values for open-nesters, non-excavators and excavators as 0.9 ± 0.1, 1.2 ± 0.2, and 2.0 ± 0.4, respectively.

Time from laying to fledging. The combined development period (I + F) in Picidae correlates significantly with body mass and egg mass, and the correlations are closer at the generic level (Table 2), although only 23% of the variation in (I + F) is explained (Table 3). The slope of (I + F) vs. body mass on log-log scales (0.072 ± 0.020) does not differ significantly from the slope for I

TABLE 1.   Female body and initial egg masses (Mb and Me, respectively), incubation and fledging durations (I and F, respectively) of wrynecks and woodpeckers. For sources of the data see text.

Species and mean of genus	Mb (g)	Me (g)	I (d)	F (d)	F/I ratio
Wrynecks					
Jynx torquilla	36	2.9	12	21	1.75
J. ruficollis	52	3.0	13	25	1.92
Jynx mean	44.0	2.95	12.5	23.0	1.84
Woodpeckers					
Picumnus minutissimus	13	1.30	13		
P. olivaceus	13		14	25	1.79
Picumnus mean	13.0	1.3	13.5	25	1.85
Melanerpes lewis	110	5.6	13	31	2.38
M. erythrocephalus	80	5.3	12	28	2.33
M. formicivorus	76	5.1	11	31	2.82
M. chrysauchen	56	4.3	10	35	3.50
M rubicapillus	44	4.7	10	32	3.20
M. uropigiallus	65	4.8	13		
M. aurifrons	84	5.0	13	30	2.31
M. carolinus	79	4.6	13	25	1.92
Melanerpes mean	74.5	4.93	11.9	30.3	2.55
Sphyrapicus varius	49	3.7	12	27	2.25
S. thyroideus	54	3.8	13	24	1.85
Sphyrapicus mean	51.5	3.75	12.5	25.5	2.04
Dendropicos fuscescens	27	2.7	11		
Picoides moluccensis	16	1.8	12		
P. canicapillus	26	2.8	12		
P. minor	21	2.3	11	21	1.91
P. mahrattensis	37	3.2	13		
P. medius	57	4.3	12	23	1.92
P. leucotus	121	7.0	15	27	1.80
P. syriacus	72	5.1	11	25	2.27
P. major	84	5.2	13	21	1.62
P. nuttallii	37	3.1	14	29	2.07
P. pubescens	28	3.2	12	21	1.75
P. borealis	47	4.3	11	25	2.27
P. stricklandi	42		14		
P. villosus	66	4.4	14	29	2.07
P. albolarvatus	64	4.4	14	26	1.86
P. tridactylus	61	4.4	13	24	1.85
P. arcticus	75	4.8	13	25	1.92
Picoides mean	53.4	4.02	12.7	24.7	1.94
Colaptes auratus	142	6.8	13	28	2.15
Celeus brachyurus	70		13		
Dryocopus pliaetus	290	11.0	18	27	1.50
D. martius	330	11.8	12	28	2.33
Dryocopus mean	310.0	11.40	15.0	27.5	1.83
Campephilus principalis	448	13.0	14	35	2.50
Picus viridis	205	9.1	18	21	1.17
P. canus	140	7.5	18	24	1.33
Picus mean	172.5	8.30	18.0	22.5	1.25
Chrysocolaptes lucidus	160	7.5	15	25	1.67

alone (0.077 ± 0.025). Hence, it is not surprising to find that F does not correlate significantly with body mass (Table 2; Fig. 1). By using the equations of Rahn et al. (1975) for the relationship between incubation duration and body mass, and assuming $1.23\mathrm{I} = \mathrm{F}$ after Ar and Yom-Tov (1978),

an equation for the relationship between $(\mathrm{I} + \mathrm{F})$ and body mass for altricial species in the appropriate mass range is calculated as $\mathrm{I} + \mathrm{F} = 20.304 \cdot \mathrm{Mb}^{0.167}$. A similar equation, $\mathrm{I} + \mathrm{F} = 19.338 \cdot \mathrm{Mb}^{0.167}$, was calculated by Yom-Tov (1987) for 58 species of Australian passerines. Comparing

TABLE 2.   Values for Ordinary Least Squares regression equations relating breeding parameters in Picidae in the form of log y = log a + b·log x. Values are for species; values in parentheses are for genera.

Independent variable, x	Dependent variables, y			
	Egg mass, g	Incubation, d	Fledging, d	Inc. + Fledg., d
Body mass, g				
a ± SE	0.362 ± 1.097 (0.291 ± 1.129)	9.373 ± 1.110 (9.734 ± 1.160)	20.312 ± 1.155 (19.813 ± 1.199)	28.761 ± 1.073 (30.190 ± 1.097)
b ± SE	0.603 ± 0.022 (0.639 ± 0.027)	0.077 ± 0.025 (0.072 ± 0.033)	0.058 ± 0.033 (0.063 ± 0.039)	0.072 ± 0.020 (0.063 ± 0.020)
n	36	39	31	31
N	(11)	(12)	(10)	(10)
r^2	0.958 (0.985)	0.209 (0.247)	0.098 (0.248)	0.305 (0.563)
P	0.0001 (0.0001)	0.003 (0.052 n.s.)	0.087 n.s. (0.143 n.s.)	0.001 (0.012)
Egg mass, g				
a ± SE		10.485 ± 1.072 (11.320 ± 1.100)	21.738 ± 1.110 (22.756 ± 1.114)	31.051 ± 1.065 (34.566 ± 1.058)
b ± SE		0.134 ± 0.044 (0.106 ± 0.055)	0.114 ± 0.062 (0.090 ± 0.060)	0.145 ± 0.038 (0.092 ± 0.032)
n		36	30	30
N		(11)	(10)	(10)
r^2		0.217 (0.297)	0.106 (0.217)	0.348 (0.516)
P		0.004 (0.083 n.s.)	0.079 n.s. (0.175 n.s.)	0.0006 (0.0192)

these equations with the equation we calculated for Picidae (Table 2) indicates that overall development from laying until fledging tends to be longer in small woodpeckers, and shorter in large ones, when compared to the general trend in altricial birds (Fig. 1). However, this can also be partially explained by the effect of the variability on the slope (Riggs et al. 1978) in the narrower range of ordinates of our data set. Body mass explains only about 31% of the variation in (I + F) among species and about 56% among genera (Table 2). The "average" picid in our data set has a body mass of 89 g and a developmental period (I + F) of 40 days, similar to the value of 41 days calculated from the equation of Yom-Tov (1987). Little of the variance in (I + F) can be explained as a genuine difference among the different genera (26%; Table 3).

Concluding remarks. The main difference between altricial birds in general and the Picidae is that the point in time at which picids hatch within their total, normal developmental period (I + F) occurs earlier, even for the relatively small size of their eggs. Therefore, their fledging time is relatively extended.

Lack (1968) suggested that the apparently long fledging time of cavity-nesters relates to the relative safety of their nest sites. However, this may not apply to Picidae because the sum of I and F does not differ appreciably from altricial birds in general (Fig. 1). We suggest an alternative explanation, that the shorter incubation of woodpeckers may represent an adaptation for breeding in cavities. In such cavities, gas exchange may be poor, oxygen concentrations are low, and carbon dioxide levels may rise considerably (Withers 1977, Birchard et al. 1984, Boggs et al. 1984, Howe et al. 1987, Ar and Piontkewitz 1992), especially at night when the incubating bird does not leave the nest. During late incubation, when

TABLE 3.   Results of 2 level nested-ANOVA test (level 0—species; level 1—genera; level 2—subfamilies) showing variation explained on the genus level.

Variable	Variation*	df	F	P
Body mass	0.94	10.1	45.77	≪0.001
Egg mass	0.88	9.1	21.79	≪0.001
Incubation	0.98	10.0	276.18	≪0.001
Fledging	0.53	8.7	4.05	<0.005
Fledg./Inc.	0.41	8.9	2.86	<0.05
Inc. + Fledg.	0.26	8.5	2.33	<0.05

* Expressed as the fraction of the total taxonomic variation accounted for at the generic level.
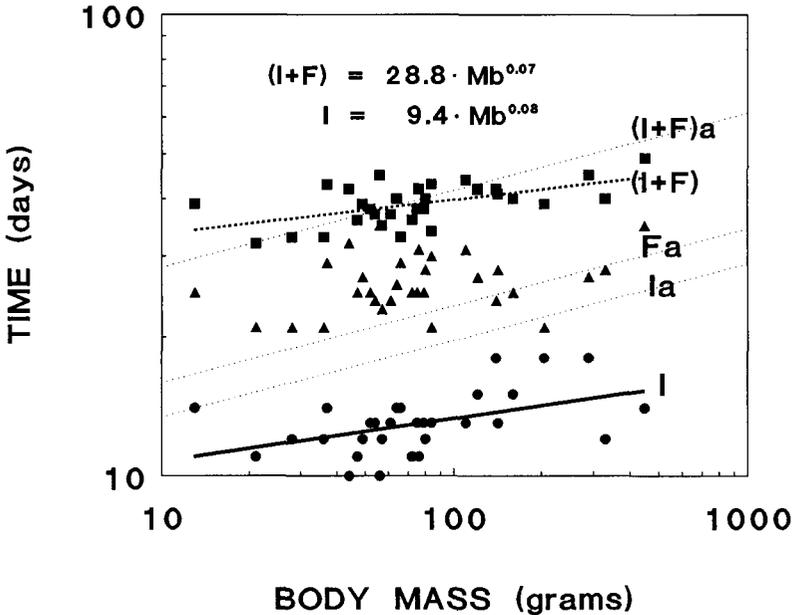
FIGURE 1.   A comparison of the relationships between incubation durations (dots, solid heavy line, I), hatching to fledging durations (triangles), the sum of the two (squares, broken heavy line, [I + F]), and species mass in Picidae to the general trend of altricial birds (dotted fine lines marked Ia, Fa and [I + F]a for incubation, fledging and their sums). Equations are for picid species. See text for details.

the needs of the developing embryos for oxygen increase and add to that of the incubating parent in the nest, the poorly ventilated atmosphere in the deeper part of the nest below the incubating parent may stress the embryos. A hypoxic and hypercapnic nest atmosphere reduces the diffusive gradients for respiratory gases between the nest and the respiratory organ of the embryo, and may restrict the oxygen uptake because the embryo does not have a mechanism for ventilatory compensation (Ar et al. 1991, Tazawa et al. 1992). A solution might be to shorten incubation and, therefore, shift as soon as possible from diffusive respiration across the eggshell and the parallel, relatively inefficient, embryonic circulation to convective respiration of the hatchling, using lungs, and to serial-type circulation. Thus, perhaps excluding the respiratory system, the chick hatches relatively immaturely as may be judged from the extreme altriciality the hatchlings exhibit (naked, eyelids fused, low thermoregulatory capacity; Weathers et al. 1990). Compensation may be achieved by increasing the time of development up to fledging. During this period, any departure of a parent from the nest to provide food or climbing by the hatchlings up the nest cavity would force ventilation in the nest

and aid respiratory gas exchange (Howe et al. 1987, Ar and Piontkewitz 1992). Rahn et al. (1974) suggested an inverse relationship between incubation duration and oxygen uptake rate during pre-internal pipping, provided that total oxygen uptake and the degree of development at hatching are the same in all cases. The only pre-internal pipping value reported for Picidae is that of the Great Spotted Woodpecker (*Dendrocopos major*). It amounts to 132 ml O_2 [STPD]/day (Berger et al. 1992), compared to the predicted value of 80–90 ml O_2/day (Hoyt et al. 1978, Hoyt 1987). However, it is not known whether the total amount of oxygen consumed during embryonic development, which may represent the degree of altriciality at hatching (Vleck and Vleck 1987), is different in Picidae from other altricial species. Data presented by Carey et al. (1980) indicate such a pattern. The Northern Flicker (*Colaptes auratus*) egg contains only 3.3 kJ/gram of energy, compared with eggs of altricial birds in general (5.0 kJ/gram), and the Eurasian Wryneck (*Jynx torquilla*) has only 16% yolk compared with the 23.5% average for the eggs of altricial birds. In sum, egg respiration represents only a small fraction of total oxygen consumption rate in the nest (Ar and Piontkewitz 1992).

Interestingly, in all the above-mentioned hole-nesters, incubation starts after the laying of the first egg, and hatching and fledging are asynchronous. This spreads the overall rate of oxygen uptake of the nest population over time during incubation and fledging, reducing peak consumption (Mock and Schwagmeyer 1990). Further comparative analyses of I and F in groups where both open- and hole-nesters exist, direct measurements of metabolic parameters of eggs and embryos, and nest atmosphere composition might support or refute our hypothesis.

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