Wilson Bull., 92(2), 1980, pp. 169–176

THE INCIDENCE OF RUNT EGGS IN WOODPECKERS

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Little is known about "runt" or "dwarf" eggs in birds. Physiologically, runt eggs are often produced by a temporary disturbance to the reproductive organs; a minority are laid by birds with permanent abnormalities (Pearl and Curtis 1916). Runt eggs do not develop; their yolks are generally abnormal or missing. Although reported in many species, runt eggs are of uniformly low incidence (Table 1). This suggests that the disturbances responsible for the production of a runt egg are accidental, occur rarely in most or all species, and are not affected by nutritional or behavioral factors.

As part of a study of the ecology of the Acorn Woodpecker (*Melanerpes formicivorus*), I discovered a high occurrence of runt eggs in this species. The purpose of this paper is thus twofold: (1) to compare the incidence of runt eggs among North American picids, and (2) to examine hypotheses which may explain the frequency of egg dwarfism in the Acorn Woodpecker.

METHODS

Data were collected in 3 ways. (1) Museum egg sets were examined for unusually small, possibly runt eggs. Maximum length and width for a large sample of Acorn, Red-headed (*M. erythrocephalus*) and Lewis' (*M. lewis*) woodpeckers' eggs were measured. Sets of other species were measured only when inspection revealed 1 or more eggs which might be a runt. When possible, the original data cards were examined for Acorn Woodpecker sets and the stage of incubation noted. (2) Information on the presence of runt eggs in Acorn, Red-headed and Lewis' woodpeckers was requested from curators of several major oological collections. (3) Sets of Acorn Woodpecker eggs were measured in the field at Hastings Reservation, Monterey Co., California, between 1976 and 1978.

Runt eggs are those whose relative volume (length $\times$ width^2 $\times$ $\pi/6$) is: (1) $<75\%$ of the average of all larger eggs in the set and (2) smaller than 3.10 SD below the mean of eggs not meeting criterion (1) of that species. For rationale of these criteria see Koenig (1980).

A comparison of the 3 sets of data for Acorn Woodpeckers indicates a bias towards a higher frequency of runts in museum collections (Table 2). However, these differences are not significant. Thus, data from all sources are lumped when possible.

In total, data were collected on 1845 sets (9136 eggs) of 18 species of woodpeckers. Statistical testing was made by either the 2-tailed Fisher exact test (Bailey 1959, Koenig 1980) or a χ^2 test of independence with Yates' correction (Siegel 1956); difference at the $P \leq 0.05$ level were considered significant.

RESULTS AND DISCUSSION

Frequency of occurrence of runt eggs in North American woodpeckers.— Table 3 lists the frequency of runt eggs and the frequency of sets with

TABLE 1

FREQUENCY OF OCCURRENCE OF RUNT EGGS REPORTED IN THE LITERATURE[a]

Species	Eggs examined	Runts	% runts	Source
Canada Goose (*Branta canadensis*)	500	3	0.60	Manning and Carter 1977
Domestic fowl (*Gallus domesticus*)	199,137	103	0.05	Warner and Kirkpatrick 1916
	151,736	131	0.09	Pearl and Curtis 1916
Gulls (*Larus*, 4 spp.)	4559	1	0.02	Barth 1967
Anis (*Crotophaga*, 2 spp.)	438	1	0.23	this study (museum)
Picidae (17 spp., not incl. *M. formicivorus*)	7979	38	0.48	this study (museum)
Acorn Woodpecker (*Melanerpes formicivorus*)	1157	50	4.32	this study (museum and field)
House Wren (*Troglodytes aedon*)	1347	2	0.15	Kendeigh et al. 1956
Starling (*Sturnus vulgaris*)	2000	2	0.10	Ricklefs 1975
Red-winged Blackbird (*Agelaius phoeniceus*)	1100	2	0.18	Rothstein 1973 (museum)
Common Grackle (*Quiscalus quiscula*)	1277	1	0.08	Rothstein 1973 (field)
	560	3	0.54	Rothstein 1973 (museum)

[a] Field data except where noted; studies based on fewer than 250 eggs are excluded.

runts for 18 species of North American picids. The results of statistical comparisons between species are the same using either of these measures. None of the 136 two-way comparisons between species other than the Acorn Woodpecker is significant. Compared to the Acorn Woodpecker, however,

TABLE 2

FREQUENCY OF OCCURRENCE OF RUNT EGGS IN FIELD AND MUSEUM SETS OF ACORN WOODPECKER EGGS

	Eggs examined	Sets examined	Runts	Sets with runts	% runts[a]	% sets with runts[a]
Museum (examined)	767	147	37	36	4.82	24.5
Museum (solicited data)	193	37	7	7	3.63	18.9
Field	203	43	6	5	2.96	11.6

[a] All 2- and 3-way comparisons non-significant.

TABLE 3
FREQUENCY OF OCCURRENCE OF RUNT EGGS IN NORTH AMERICAN WOODPECKERS

Species	Eggs examined	Sets examined	Runts	Sets with runts	% runt eggs	% sets with runts	Comparison with *M. formicivorus*[a]
Colaptes auratus (Common Flicker)	2574	422	15	13	0.583	3.08	***
Dryocopus pileatus (Pileated Woodpecker)	236	63	0	0	0.000	0.00	***
Melanerpes carolinus (Red-bellied Woodpecker	239	57	1	1	0.418	1.75	**
M. aurifrons (Golden-fronted Woodpecker)	416	86	1	1	0.240	1.16	***
M. uropygialis (Gila Woodpecker)	175	48	0	0	0.000	0.00	**
M. erythrocephalus (Red-headed Woodpecker)	731	155	5	5	0.684	3.23	***
M. formicivorus	1157	227	50	48	4.322	21.15	—
M. lewis	619	110	3	3	0.485	2.73	***
Sphyrapicus varius (Yellow-bellied Sapsucker)	417	87	1	1	0.240	1.15	***
S. thyroideus (Williamson's Sapsucker)	235	44	1	1	0.426	2.27	**
Picoides villosus (Hairy Woodpecker)	502	129	4	4	0.797	3.10	***
P. pubescens (Downy Woodpecker)	743	154	1	1	0.135	0.65	***
P. scalaris (Hadder-backed Woodpecker)	203	51	0	0	0.000	0.00	***
P. nuttallii (Nuttall's Woodpecker)	271	64	1	1	0.369	1.56	***
P. borealis	75	20	1	1	1.333	5.00	
P. albolarvatus (White-headed Woodpecker)	449	104	3	3	0.668	2.89	***
P. arcticus	64	17	1	1	1.563	5.88	
P. tridactylus	30	7	0	0	0.000	0.00	

[a] All other 2-way comparisons non-significant.
* $P < 0.01$.
*** $P < 0.001$.

the frequency of runts is significantly different in 14 of the 17 species (82%). The 3 species not significantly different are those with such small sample sizes (Arctic Three-toed [*Picoides arcticus*], Northern Three-toed [*P. tridactylus*] and Red-cockaded [*P. borealis*] woodpeckers), that they are statistically indistinguishable from any of the other species examined.

TABLE 4
FREQUENCY OF OCCURRENCE OF RUNT EGGS IN SMALL AND LARGE SETS OF ACORN WOODPECKER EGGS

	All sets		Incubated sets only	
	2–5	6–13	2–5	6–13
Number of runts	26	24	4	12
Normal eggs	676	431	237	175
Total	702	455	241	187
% runts	3.70	5.27	1.66	6.42
χ^2 (df = 1)	1.29^{NS}		5.37*	

* $P < 0.05$.

Combining data, the frequency of runt eggs in Acorn Woodpeckers is highly significantly greater ($P < 0.001$) than in the other picids (Table 1). No other departures from the low incidence of runt eggs emerge for any of the species or genera examined.

Why do Acorn Woodpeckers lay so many runt eggs?—Pearl and Curtis (1916), in a comprehensive study of egg dwarfism in the domestic fowl (*Gallus domesticus*), concluded that runts are laid by hens in active laying condition, that they are not associated with sexual immaturity, that they are an isolated event in the life of a hen, and that there is no obvious genetic basis underlying their production. These conclusions suggest no factor which might differ significantly from 1 species to another, thereby resulting in a higher or lower than normal frequency of runt eggs.

In the Acorn Woodpecker, a high frequency of runt eggs is present in samples from both California (4.2%, N = 927) and the southwest (5.0%, N = 84). What unique aspect of the biology of this species might be conducive to the production of runt eggs? One clearly unusual feature is the group living habit of this woodpecker—birds live in bisexual groups of up to 15 individuals of all ages (MacRoberts and MacRoberts 1976, Koenig 1978). Within these groups the precise mating system is not known, but I have recently found that under some circumstances more than 1 female may lay eggs in a nest (Koenig 1978). These communal nests are usually distinguishable because they contain more eggs than nests of single females. If runt egg production in Acorn Woodpeckers is related to communal nesting, larger clutches should contain disproportionately more runts. This is tested in Table 4 for (1) all sets and (2) those known to have been incubated (i.e., complete). In both cases the proportion of runt eggs is higher in the larger sets; this difference is not significant for the complete sample but is for those sets known to be complete.

TABLE 5
FREQUENCY OF SETS OF ACORN WOODPECKER EGGS WITH RUNTS ACCORDING TO INCUBATION STATUS

	Incubated	Incubation uncertain
Number of sets with runts	14	34
Number of sets with no runt	67	112
Total sets	81	146
% sets with runts	17.3	23.3
χ^2 (df = 1)	0.79^{NS}	

Data from groups of woodpeckers of known composition at Hastings Reservation provide more direct support for a relation between runt eggs and communal nesting. Four of the 5 sets with at least 1 runt egg occurred in sets of 7 eggs produced by groups in which 2 females are believed to have been nesting. A fifth set contained only 3 eggs when discovered and the nest subsequently failed. However, the group associated with the failed nest also contained 2 females who nested together the following year. A final runt, the sole egg of its "clutch," was discovered in an abandoned nest used by a group also with 2 probable breeding females. However, 7 other sets to which 2 females were suspected, or known to have contributed, did not contain runt eggs.

The actual time during the laying cycle when Acorn Woodpeckers lay runt eggs may be critical in explaining their occurrence. Table 5 compares the proportion of sets with runts among those known to have been incubated vs those whose incubation status is uncertain. If runts are usually laid last, sets collected prior to their completion should not contain runts, and a higher fraction of incubated sets should contain runts than sets whose status is unknown. If runts are laid first, or at any time in the clutch sequence, incubated and uncertain sets should contain about the same proportion of runt eggs. The result (Table 5), is that the proportion of sets with runts is slightly, but insignificantly, lower among incubated sets. This supports the hypothesis that runt eggs are laid either early, or at no particular time in a clutch. There is no satisfactory way to decide between these hypotheses with the available data.

I suspect that, as in the domestic fowl (Pearl and Curtis 1916), Acorn Woodpeckers lay runt eggs at any time during the laying cycle. If this is true, it is likely that these eggs are accidental (and, since they do not hatch, maladaptive), regardless of how common they may be. Why, however, should accidents resulting in runt eggs be especially common in

Acorn Woodpeckers? One possibility is that there is greater inter-individual contact within the social groups of this species than between the pairs of other species, especially between females nesting together. An increased number of interactions, particularly those involving maneuvers within the limited space provided by nest holes, might result in collisions or other physical accidents which would throw off the normal sequence of events during egg production and result in a runt egg.

Two predictions of this hypothesis are: (1) there should be a higher incidence of runt eggs among hole nesters in general than open-nesting birds, and (2) there should be a higher incidence of runt eggs among communal nesting species than those with other breeding systems. The first of these predictions is only marginally supported by data comparing the rate of runt egg production in all species of woodpeckers combined except the Acorn Woodpecker with that of the other species in Table 1. The frequency in woodpeckers is significantly higher than that reported for gulls (*Larus* spp.), the field sample of the Common Grackle (*Quiscalus quiscula*), and the 2 domestic fowl samples. However, the incidence in woodpeckers is also greater than in Starlings (*Sturnus vulgaris*) ($P < 0.05$) and the House Wren (*Troglodytes aedon*) ($P < 0.12$), both hole nesting species.

The second of the above predictions can be tested with data from the Groove-billed (*Crotophaga sulcirostris*) and Smooth-billed (*C. ani*) anis, both communal nesters. However, the frequency of runt eggs in these 2 species is significantly less than in the Acorn Woodpecker (Table 1), contrary to the prediction. Thus, neither the effects of hole nesting nor communal nesting alone can explain a high frequency of runt eggs. Possibly both must be combined in order to produce this anomaly.

If runt eggs are maladaptive in the Acorn Woodpecker, then to the extent that their incidence is a function of communal nesting they may be considered a disadvantage of group living (Alexander 1974). Nearly 5% of the energy put into egg production by females is wasted in producing unviable runt eggs. However, my data do not preclude an adaptive basis for runt eggs. They might, for example, be consistently laid first, or even several days before the rest of the clutch, and serve as a synchronizing "signal" indicating when and where the other female(s) in the group should lay her (their) eggs. The occurrence of a runt in only 4 of the 11 nests in which 2 females are believed to have been nesting at Hastings Reservation, however, suggests that other less energetically wasteful, behavioral cues are adequate for reproductive synchronization in most instances. Alternatively, runt eggs could be a result not of reproductive cooperation but rather of reproductive competition between communally nesting females. Fights between such females for dominance, access to nests, males, or other

resources during the breeding season might result in a high frequency of abnormal eggs, especially by subordinate individuals.

Though the function of runt eggs, if any, is unclear, their incidence appears to be related to communal nesting and possibly hole nesting, at least in the Acorn Woodpecker. Other factors influencing runt egg production clearly exist—perhaps any feature of the ecology of a species affecting the probability of physical contact and temporary injury during the laying cycle affects the incidence of runt eggs.

SUMMARY

The incidence of runt eggs among most North American woodpeckers and all other species for which data are available is uniformly low (average 0.54%). In the Acorn Woodpecker, however, over 4% of all eggs are runts, and over 20% of all sets contain at least 1 runt. Both museum and field data support the hypothesis that this high frequency is related to communal nesting. I suggest that an unusual amount of inter-individual contact as a result of females nesting together within the confined space of a nest hole may be responsible for this high frequency of runt eggs. However, predictions from this hypothesis that hole nesters and other communal nesters should by themselves have high frequencies of runt eggs are not supported by the data presently available. Other data will be necessary before meaningful interpretations of the significance of interspecific variation in the frequency of runt eggs can be made.

ACKNOWLEDGMENTS

I would like to thank the curators who compiled data on the frequency of runt eggs in collections under their care and permitted me to measure eggs: J. C. Barber (National Museum of Natural History), L. C. Binford (California Academy of Sciences), R. A. Bradley (Florida State Museum), E. Cardiff (San Bernardino County Museum), J. A. Hamber (Santa Barbara Museum of Natural History), N. K. Johnson and V. Dziadosz (Museum of Vertebrate Zoology), L. F. Kiff (Western Foundation of Vertebrate Zoology), D. Maurer (Field Museum of Natural History), D. M. Niles (Delaware Museum of Natural History), H. W. Pelzl (American Museum of Natural History) and R. W. Schreiber (Los Angeles County Museum). Florence Amamoto and Pam Williams helped to measure eggs. C. R. Grau, F. W. Lorenz and F. A. Pitelka contributed their knowledge of egg physiology and ecology. The latter suggested reasons for the high incidence of runt eggs in the Acorn Woodpecker and has been a continuing source of assistance and information during my work. The study was supported by an NSF pre-doctoral grant, an NSF fellowship, the Museum of Vertebrate Zoology and the Department of Zoology, University of California, Berkeley. The manuscript was helped by the comments of John Davis, Pam Williams and Jon C. Barlow.

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MUSEUM OF VERTEBRATE ZOOLOGY AND HASTINGS RESERVATION, UNIV. CALIFORNIA, BERKELEY, CALIFORNIA 94720. (MAILING ADDRESS: STAR ROUTE BOX 80, CARMEL VALLEY, CALIFORNIA 93924.) ACCEPTED 15 FEB. 1979.