Short Communications

Predicting Clutch Size of the House Wren with the Murray-Nolan Equation

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Although there have been many hypotheses and much research concerning factors that influence clutch size, there have been few attempts to predict clutch size. Murray (1979) suggested that females in a population should lay as few eggs per clutch as required to replace themselves and therefore maximize their survivorship and lifetime reproduction. Murray and Nolan (1989) used this idea to develop an equation that predicts clutch size for birds based on female survivorship and other demographic data. When such data for Prairie Warblers (*Dendroica discolor*) and Florida Scrub Jays (*Aphelocoma c. coerulescens*) were used in this equation, close agreement was found between predicted and observed clutch sizes (Murray and Nolan 1989, Murray et al. 1989).

To test the Murray-Nolan equation as a predictor of clutch size in House Wrens (*Troglodytes aedon*), I used demographic data extracted from the field notes of the Baldwin Bird Research Laboratory. Female House Wrens, unlike female Prairie Warblers and Florida Scrub Jays, often rear >1 brood during a season, so this paper represents an extension of earlier tests of the Murray-Nolan equation to a predominantly double-brooded species.

Between 1919 and 1940, S. P. Baldwin, S. C. Kendeigh, and others at the Baldwin Bird Research Laboratory, Gates Mills, Ohio, studied breeding and survivorship of House Wrens. Field notes of this research were made available to me from the library of the Bird Division, Museum of Zoology, University of Michigan. I compiled and analyzed the records from the notebooks for 1926-1937, the 12 yr of most active research. For each nest I recorded the band numbers of both male and female adults, the number of eggs laid, the number of eggs that hatched, the number of hatchlings that successfully left the nest (fledged), and the band numbers of those hatchlings that fledged. Each year, almost all breeding birds were captured at the box and banded or, if previously banded, had their band numbers recorded. Breeding birds not captured were usually those whose clutches failed shortly after laying began.

Breeding females were assigned an age of 1 yr if they had not been caught previously at the study sites (see Kendeigh and Baldwin 1937) or if they had been banded as nestlings during the previous year. Only 69 of 4,188 (1.7%) females banded as nestlings returned to breed on the study site; 64 of the 69 (93%)

laid clutches as 1-yr-olds, and the other 5 may have had nests as 1-yr-olds that failed before adult capture (Kendeigh unpubl. field notes). Most breeding females were 1-yr-old birds, although some females continued to breed through year 6 (Table 1).

I calculated survivorship schedules of females from egg laying through fledging for all nests and for successful nests (i.e. those nests that had at least one chick leave the nest) (Table 1). To determine survivorship to hatching, I used the mean hatching rate for all eggs for which hatching information was known; to determine survivorship during the nestling period, I used the mean fledging rate for all eggs for which fledging information was known. Because few wrens banded as nestlings return to breed in their natal habitats (Kendeigh 1934, Kuerzi 1941, Drilling and Thompson 1988), I estimated female survivorship from fledging to first-year adult by dividing the number of first-year females by the number of female fledglings from the previous year, assuming a fledgling sex ratio of one (i.e. that half the total number of fledglings are females). This survivorship value varied from year to year (range: 0.1833-0.4479; overall mean: 0.2862). Age-specific survivorship from year 1 to year 6 was based on recapture data of birds banded as yearlings or nestlings.

For each female age class, I calculated fecundity as half the average number of eggs laid per season (again assuming that the sex ratio of eggs is one). Generally, fecundity increased with age (Table 1), because of an increase in the proportion of double-brooded females in the older age classes. In calculating fecundity, I assumed that there was no conspecific egg dumping. Several investigators, including Kendeigh, found either no evidence of egg dumping (Rohwer and Freeman 1989, Kennedy and Power 1990) or low levels (<5% of nests) of egg dumping (Picman and Belles-Isles 1988) in House Wren populations (but see Price et al. 1989).

I used survivorship and fecundity values to calculate R_0, the net reproductive rate. The value of R_0 obtained for the Kendeigh population was 1.0009 (Table 1).

Application of the Murray-Nolan Equation.—The Murray-Nolan equation for predicting clutch size (CS) is

$$CS = \frac{\mu_s}{P_1 + P_2 + P_3},$$

where μ_s is the "total number of eggs that a female should lay in all clutches that produce one or more young to independence during a breeding season," and P_1, P_2 and P_3 are the probabilities of a female's rearing at least one, two, or three broods through

TABLE 1. Survivorship and fecundity schedules for female House Wrens studied at Baldwin Bird Research Laboratory (1926–1937). Survivorship (λ_x) and fecundity values (μ_x) are given for individuals from all nests, and survivorship values for individuals from nests that produced at least one fledgling.

| Female age (x) | All nests | | | Nests with ≥1 fledgling |
	λ_x	μ_x	$\lambda_x\mu_x$	λ_x
Day 0[a]	1.0000	0.0000	0.0000	1.0000
Egg hatching	0.7985	—	—	0.8935
Chick fledged	0.6878	—	—	0.8237
Year 1[b]	0.1967	3.7414	0.7359	0.2356
Year 2	0.0408	4.3870	0.1790	0.0489
Year 3	0.0144	4.1385	0.0596	0.0173
Year 4	0.0037	4.9048	0.0181	0.0045
Year 5	0.0012	5.0000	0.0060	0.0014
Year 6	0.0007	3.3333	0.0023	0.0008
Net reproductive rate (R_0)			1.0009	
Total survivorship of females from year 1 to year 6	0.2575			0.3085
Total no. of eggs predicted for successful clutches (μ_s)				6.48

[a] Egg being laid (by definition).
[b] Bird returning as yearling (first breeding age).

independence during a breeding season, respectively (Murray and Nolan 1989). According to this equation, if a female came from a population in which only one clutch was laid per season and all females were successful in producing young to independence (i.e. P_1 = 1.0), then the predicted clutch size would equal μ_s. In populations with an overall success rate (i.e. the sum of P values) of <1, the predicted clutch size would be higher than μ_s; in populations with an overall success rate of >1, which could occur if the success rates of first and later clutches were relatively high, the predicted clutch size would be lower than μ_s.

The determination of μ_s is given by the equation,

$$\mu_s = \frac{(a + 1)}{\sum\limits_{\alpha}^{\omega} \lambda_x},$$

where a is the primary sex ratio (the sex ratio of the eggs at laying), α is the average age of first breeding, ω is the age of last breeding, and $\sum\limits_{\alpha}^{\omega} \lambda_x$ is the sum of the survivorship values of females from successful nests (nests that produce at least one fledgling) from the onset of breeding to age ω. In House Wrens, a is assumed to be one, α is age one, ω is age six, and $\sum\limits_{\alpha}^{\omega} \lambda_x$ is 0.3085 (Table 1).

Because the survival of young wrens to independence was not known, I used survival to fledging to determine P_1, P_2 and P_3. Murray and Nolan (1989) likewise used survival to fledging to determine P_1 and P_2 for their prediction of Prairie Warbler clutch size. Murray et al. (1989) showed that, in calculating the clutch size of the Florida Scrub Jay, survival to independence and survival to fledging gave similar predictions.

When the values in Table 1 were used, μ_s = 6.48. The probabilities of rearing successful clutches were determined from data in Table 2. The probability of success in rearing one brood (P_1) is the number of first-brood successes per female (1,237/1,387 = 0.892). The probability of rearing a second brood (P_2) is the number of second-brood successes per female (262/ 1,387 = 0.189). The probability of rearing a third brood

TABLE 2. Probability of success (≥1 fledgling) of a clutch, according to its number in the sequence of all clutches started by an individual female in a season (n = 1,387 females).

| Clutch number | No. of first-brood clutches | | No. of second-brood clutches | | No. of third-brood clutches | | Total no. of clutches started | % successful |
	Started	Success-ful	Started	Success-ful	Started	Success-ful		
1	1,387	1,181	—	—	—	—	1,387	85.1
2	68	55	372	259	—	—	440	71.4
3	1	1	6	3	2	2	9	66.7
Total	1,456	1,237	378	262	2	2	1,837	81.8

(P_3) is the number of third-brood successes per female (2/1,387 = 0.001). The sum of the P values is 1.082. Predators, especially cats and snakes, were controlled in Kendeigh's population (Kendeigh 1942). Lower survivorship and P values might be expected had predators not been controlled.

Therefore, the Murray-Nolan equation predicts that the average clutch size of the House Wren in Ohio should be,

$$CS = \frac{\mu_s}{P_1 + P_2 + P_3} = \frac{6.48}{1.082} = 5.99.$$

The observed range of clutch size in this population was 2–9 eggs, and the overall average clutch size was 5.83 ± 1.02 eggs ($\bar{x}$ ± SD; n = 1,976 clutches). The predicted average clutch size is within 3% of the actual value. In House Wrens, however, there is seasonal variation in clutch size. Early clutches (laying began on or before 15 June) had an average of 6.29 ± 0.84 eggs (n = 1,108 nests), and late clutches (laying began after 15 June) had an average of 5.25 ± 0.92 eggs (n = 868 nests).

The equation provides a predicted value that is a fairly good estimate of the overall average clutch size in wrens, and represents the modal clutch size (6 eggs) for early nests (477 of 1,108 early nests, or 43%). The Murray-Nolan equation predicted mean clutch size to within 0.4 egg of observed clutch size in Prairie Warblers (3.49 vs. 3.89 eggs; Murray and Nolan 1989) and to within 0.1 egg of observed clutch size in Florida Scrub Jays (3.43 vs. 3.33 eggs; Murray et al. 1989).

In House Wrens, early clutches are generally at least one egg larger than late clutches. The average clutch size predicted by the Murray-Nolan equation is within 0.3 egg from the observed average early clutch size (5.99 vs. 6.29 eggs) but is almost 0.75 egg more than the observed late clutch size (5.99 vs. 5.25 eggs). Almost half of the birds that nested early laid seven or more eggs (477 of 1,108 clutches, 43%).

Birds may produce the replacement number of offspring in two ways, either by having one large early clutch or two or more smaller clutches. In House Wrens, single-broodedness would require that females lay clutches of at least 7.26 eggs (μ_s/P_1 = 6.48/0.892), approximately one egg larger than the average early clutch size. Only 40 of 1,108 birds (4%) that bred early laid eight or nine eggs.

The testing of the Murray-Nolan equation will be limited to populations in which demographic data are well-known. Factors such as study-site size may affect the collection of demographic data.

Female House Wrens that are unsuccessful in their last breeding attempt in a season are not less likely to return the following year than females that were successful, but the unsuccessful females that return move farther from their previous breeding sites than do successful females that return (Drilling and Thompson 1988). These findings suggest that suc-

cessful females would be more likely to be recaptured in a small study area than would unsuccessful birds.

Survivorship from fledging to year 1 could only be estimated in House Wrens because few nestlings returned to their natal areas for breeding. Only 1.7% of females banded as nestlings (and 2.7% of all nestlings) in Ohio returned to their natal areas to breed. Similar levels of overall nestling return were recorded in populations of House Wrens in Illinois (2.8%; Drilling and Thompson 1988) and Connecticut (3.1%; Kuerzi 1941). A 5% error in the estimation of survival to breeding would change the predicted clutch size from 6 eggs to either 5.7 or 6.3 eggs. The method used to estimate survivorship involved three assumptions: (1) that breeding females not previously banded were first-year birds (Kendeigh and Baldwin 1937), (2) that the sex ratio at fledging was one, and (3) that no differences in first-year survival occurred between the habitats from which immigrants came and the habitats in which reproduction was measured. Estimates of first-year survival, determined by dividing the number of "first-year females" by one-half the number of fledglings from the previous year, would be lower than actual values if fledgling productivity or first-year survival was lower in surrounding habitats than in the study sites. The study population nested in boxes while birds in surrounding areas presumably nested in natural cavities. However, there is no a priori reason to expect postfledging survival to differ in the two areas, and no consistent differences have been demonstrated in nest-predation rates between artificial and natural cavities (Nilsson 1984).

The Murray-Nolan equation has generated a predicted average clutch size that is close to the observed value in each of the three species to which it has been applied.

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The Taxonomic Status of *Myrmeciza stictothorax* (Todd)

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Despite the large increase in recent years in our knowledge of the distributions of South American birds, there remain an intriguing few species still known only from the holotype or the type series. Among the large family Formicariidae (*sensu* AOU 1983), there are several such species, including *Thamnophilus praecox*, *Pithys castanea*, *Phlegopsis barringeri* (all known only from the holotype), and *Myrmeciza stictothorax*. It has been suggested that *Phlegopsis barringeri* is based on an interspecific hybrid (Willis 1979), and we suspect that *Thamnophilus praecox* and *Pithys castanea* may have a similar basis. We now propose that the fourth taxon, *Myrmeciza stictothorax*, is neither a valid biological species nor an interspecific hybrid, but is a name based on a plumage abnormality of a male of the widespread species *Myrmeciza atrothorax*. We suggest it is possible, however, that *stictothorax* may be a valid subspecies of *atrothorax*.

Todd (1927) described a new genus, *Myrmophylax*, in which he placed what was then known as *Myrmoderus atrothorax*, and also a species described in the same publication, *stictothorax*. Peters (1951) retained the genus *Myrmophylax*, but Zimmer (1932) and Meyer de Schauensee (1966) placed both *atrothorax* and *stictothorax* in *Myrmeciza*. We follow the latter treatment, but do so more because it is a familiar format than because we are convinced that it is correct. As Zimmer (1932) noted, the genus *Myrmeciza* is very

heterogeneous, and we suspect that it is not monophyletic; the relationships of the species assigned to *Myrmeciza* are outside the scope of this paper.

Todd (1927) described *stictothorax* on the basis of a male and a female from the same locality, Apacy, on the west bank of the lower Rio Tapajós, Brazil. *Stictothorax* does not differ appreciably in size from *atrothorax* (Table 1), and Todd recognized the similarity of the two specimens of *stictothorax* to the respective sexes of *atrothorax*. The male of *stictothorax* differs from the male of *atrothorax* solely by the pattern of the breast, where approximately 20 of the black breast feathers contain white central regions. These white chest spots are variable in size, but all are small. The spots vary from 1.4 × 0.5 mm to 2.8 × 1.5 mm, approximately.

In examining the series of *Myrmeciza atrothorax* at several institutions (Carnegie Museum of Natural History [CM], American Museum of Natural History [AMNH], Field Museum of Natural History, and Museu de Zoologia, Universidade de São Paulo), we have seen 126 specimens of adult male *atrothorax*. Among these, we found two specimens, both of the nominate subspecies, that have white markings on the breast feathers (Fig. 1). Specimen CM 56178, from French Guiana, has several feathers on the breast that have extensive pale (white or pale gray) subterminal patches. Such markings are not comparable to the pattern of the markings on the chest of the holotype of *stictothorax*. Two or three feathers, however, in the center of the breast of this specimen have white shafts and are similar to the white-marked breast feathers of *stictothorax*. AMNH 309869, from northern Brazil (Ma-