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REPEATABILITY OF CLUTCH SIZE IN HOUSE WRENS

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ABSTRACT.—Theories of clutch-size determination have focused primarily on first broods or on seasonal trends in clutch size. High repeatability between the sizes of first and second clutches could be expected because of individual genetic, vigor, and environmental differences. We examined the repeatability of clutch size in individual House Wrens (*Troglodytes aedon*) both within and across years using data collected between 1926–1937 by Kendeigh, Baldwin, and others. Contrary to expectation, repeatability of clutch size in first and second clutches within a year was low ($r_I = 0.10$) and only about one-third that of first or second clutches among different years ($r_I = 0.27$ or 0.30, respectively). Despite modest repeatability in clutch size, no significant correlation existed between number of fledglings in successful first broods and clutch size of second broods ($r = 0.006$). Clutch-size repeatability was associated with female identity and not nest box site, suggesting that differences in individual clutch size did not result from occupation of differentially suitable breeding territories. Estimates of heritability of clutch size were limited due to small numbers of fledglings that returned to natal study sites to breed; however, the estimate of heritability of clutch size was greater for mother-son combinations ($h^2 = 0.48$) than for mother-daughter combinations ($h^2 = 0.21$). *Received 11 Oct. 1990, accepted 18 June 1991.*

Clutch size in birds is controlled by a combination of genetic, ontological, and environmental factors. Theories of clutch-size determination have focused on first broods or on seasonal trends in clutch size. For birds that rear more than one brood in a season, the question of what is the most productive clutch size for an individual (sensu Lack 1947, 1966) may become complicated if clutch size (or fledging success) varies independently or inversely between one brood and the next (see Murphy and Haukioja 1986 for a review).

Repeatability (r_I) is the correlation between repeated measurements, separated in space or time, of a character from the same individual (Falconer 1981:127). Both environmental and genetic factors may contribute to repeatability, according to the formula:

$$r_i = (V_G + V_{Eg})/V_P,$$

where V_G represents genetic variance, V_{Eg} represents general environmental variance, and V_P represents total phenotypic variance (Falconer 1981:127). Repeatability sets an upper limit to heritability (h^2; Falconer 1981:127), the proportion of total phenotypic variance that is attributable to additive genetic variance ($h^2 = V_A/V_P$; Falconer 1981:148).

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Repeatability of clutch size is a measure of individual consistency in reproductive effort (Boag and van Noordwijk 1987, Lessells and Boag 1987). Given the potential heritability of clutch size and the potential for intraseasonal continuity in breeding circumstances, we would expect high repeatability in first- and second-clutch sizes within a breeding season, at least in comparison with repeatability in different years.

Alternatively, if strong trade-offs existed between first and second reproductive efforts (McGillivray 1983, Slagsvold 1984, Lindén 1988), intraseasonal repeatability could be low or negative because of energetic or time constraints.

Here we examine repeatability of clutch size in individual female House Wrens (*Troglodytes aedon*) both within a breeding season and across years. House Wrens are cavity nesters that are often double-brooded, generally laying first clutches of 4–8 eggs and second clutches of 3–7 eggs.

METHODS

Breeding biology of House Wrens was studied by S. P. Baldwin, S. C. Kendeigh, and their coworkers at the Baldwin Bird Research Laboratory in Gates Mill, Ohio, between 1919 and 1940. The study area and field methods were detailed by Baldwin and Bowen (1928) and Kendeigh (1941a).

Field notes of the Baldwin Bird Research Laboratory are in the library of the Bird Division, Museum of Zoology, Univ. of Michigan. Volumes for the years 1926–1937, the 12 years of most active research, were lent to EDK, who recorded for each nest the band numbers of adults, the number of eggs laid, and the numbers and band numbers of fledglings.

Breeding females that had been banded as nestlings during the previous year or that had not been caught previously on the study sites were assigned an age of one year (see Kendeigh and Baldwin 1937; Kennedy 1991). For determining repeatability of clutch size, identifiable replacement clutches were omitted, as were double broods in which first or second clutch size data were lacking.

For each comparison listed in Table 2, repeatability was calculated as the intraclass correlation coefficient from a one-way analysis of variance (ANOVA; Lessells and Boag 1987). To preserve environmental and ontological sources of variation, no adjustments in clutch size were made for differences in female age, nest site, or study year (see Hailman 1986). In the determination of intraseasonal clutch-size repeatability, however, a misleading bias towards low values existed because modal clutch size declined progressively during the breeding season from seven eggs in May to four eggs in August (Kendeigh 1941b). To control for this temporal trend, second-clutch sizes were adjusted by adding the difference between the sample means for first- and second-clutch size, usually about one egg. Using this approach, intraseasonal repeatability values were similar to those found by simple correlation of first- and second-clutch sizes.

Heritability of first-clutch size was estimated for both mother-daughter and mother-son data. Heritability (h^2) was calculated as two times the slope of the regression of offspring clutch size on mother clutch size (Hailman 1986).

To determine whether a bird's cost of rearing a large first brood affected the size of her second clutch, we calculated a product-moment correlation coefficient for the number of fledglings in successful first broods and the number of eggs in second clutches.

RESULTS

In 412 cases, the number of eggs laid in consecutive first and second clutches of banded House Wrens was recorded between 1926 and 1937 near Cleveland, Ohio (Table 1). Observed double clutches were laid by 376 individual females (some females bred in several years). In 660 additional cases, first clutch size was recorded, but no second breeding attempt was observed.

Among double clutches, first clutches contained three to eight eggs (mean ± SD: 6.4 ± 0.8 eggs), and second clutches contained two to nine eggs (5.3 ± 0.9 eggs). Egg sets from females that laid single clutches within a year (6.2 ± 0.9 eggs) were fractionally smaller than first-egg sets from females that laid two clutches within a year ($t = -3.37$, df = 1,070, $P < 0.001$; some females were represented more than once in one or both categories). Second clutches occurred at a higher rate among females that laid the most common first-clutch sizes of six or seven eggs than among females that laid first clutches that were smaller or larger than usual (41% vs 28%, respectively). Overall, second clutches were observed for about 39% of female House Wrens.

Second-clutch size did not differ significantly among first-clutch sizes (Table 1; ANOVA, $F_{5, 406} = 2.22$, $P > 0.05$); thus, seasonal egg output (total eggs laid in the first plus second clutch) of double-clutched females increased from 10.4 to 13.8 eggs as first clutches increased from five to eight eggs.

Repeatability of clutch size in House Wrens in first and second clutches within years was low and only about one-third that of first or second clutches among different years (Table 2). The ANOVAs from which the repeatability values were derived were significant for intraseasonal clutch size for experienced females but not for females in their first breeding season (Table 2). Intraseasonal repeatability of clutch size was associated with female identity and not nest box site or male identity, suggesting that differences in individual clutch size did not result from continued occupation of differentially suitable breeding territories (Table 2).

We found no relationship between the number of nestlings that fledged from successful first broods and the number of eggs laid in second clutches ($r = 0.006$, df = 305, $P > 0.5$).

To test if poor correlation between sizes of first and second clutches resulted from offsetting trends among years, we examined each year separately. Significant correlation existed between first and second clutch size in only one of eleven years with adequate data (1928: $r = 0.50$, $P < 0.005$, N = 33; ten other years: $r = -0.09$ to 0.204, $P > 0.20$, N = 14 to 60).

Patterns of interseasonal repeatability suggested an upper limit on the heritability of clutch size of about 0.3. Based on mother and daughter

TABLE 1
FREQUENCY OF CLUTCH-SIZE COMBINATIONS IN HOUSE WRENS

Eggs in first clutch	Eggs in second clutch									
	0[a]	2	3	4	5	6	7	8	9	Mean[b] ± SD
3	5			1	1					4.5 ± 0.7
4	18				2	2				5.5 ± 0.6
5	88			6	13	11	3			5.3 ± 0.9
6	285		4	24	95	41	7	1	1	5.2 ± 0.9
7	237	1	6	16	81	68	12	3		5.4 ± 1.0
8	26			1	4	5	2	1		5.8 ± 1.1
9	1									

[a] No second clutch recorded.
[b] Mean second clutch size for each first clutch size (excluding 0).

first clutches, clutch size heritability (h^2) was 0.211 (N = 42). For mother and son first clutches, clutch size heritability was 0.48 (N = 61).

DISCUSSION

Both genetic and non-genetic factors may increase repeatability of clutch size within a breeding season. There is evidence for a genetic component to clutch size. Mother-daughter heritability of size of first clutches has been found for Great Tits (*Parus major*; Perrins and Jones 1974, van Noordwijk et al. 1980), Song Sparrows (*Melospiza melodia*), Mallards (*Anas platyrhynchos*), European Starlings (*Sturnus vulgaris*), Lesser Snow Geese (*Anser c. caerulescens*), and Red (Willow) Grouse (*Lagopus lagopus*;

TABLE 2
REPEATABILITY OF CLUTCH SIZE IN HOUSE WRENS

Comparison	*F* ratio (df)[a]	Repeatability
First and second clutches in one year[b]	1.232 (411, 412)*	0.104
Females one year old[b]	1.139 (293, 294)^{ns}	0.065
Females more than one year old[b]	1.396 (117, 118)*	0.165
Any-age female at same nest box[b]	1.358 (145, 146)*	0.152
Any-age female, same box, same male[b]	1.493 (39, 40)^{ns}	0.198
Same box, different female[b]	0.840 (96, 97)^{ns}	−0.087
First clutches in different years	1.819 (157, 187)***	0.273
Second clutches in different years	1.917 (77, 90)**	0.299
Total eggs in first plus second clutches in different years	3.062 (36, 39)***	0.501

[a] * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, ns = $P > 0.05$.
[b] Corrected for between-brood differences in mean clutch size, see Methods.

see reviews by Hailman [1986] and Boag and van Noordwijk [1987], but see Lessells and Boag [1987] for correction on heritability value of Lesser Snow Geese). Non-genetic differences that might increase repeatability of clutch size include (1) differences in vigor among females, (2) differences in breeding habitat, and (3) differences in breeding phenology. Some females are likely to be in better breeding condition, i.e., health or nutritional state, than others for non-genetic reasons and therefore should lay and rear larger numbers of offspring (see Price and Liou 1989 and included references). Females that nest and breed in "good" habitat should be able to lay and rear more offspring than those in "poor" habitat (Perrins and Jones 1974, Högstedt 1980). Females that begin breeding early in the season may have large first and second clutches relative to birds with later initiation dates. For this pattern to occur, clutch size must decline seasonally, and dates of first clutch initiation must be highly asynchronous; House Wrens display both traits (Kendeigh 1941a, b; 1963). Moreover, female vigor, habitat quality, and early breeding may be positively interrelated.

Intraseasonal repeatability in the number of eggs laid in first and second clutches of House Wrens was low, with $r_I < 0.17$ even when only sedentary or experienced females were examined (Table 2). Murphy (1978) found similar low intraseasonal repeatability in clutch size in House Sparrows (*Passer domesticus*; $r_I = 0.08–0.12$). Most House Wrens had second clutches of five or six eggs, regardless of the size of their first clutches. This result contradicts Kendeigh's suggestion (unpubl. field notes) that compensating variation in the sizes of first and second clutches produced a fixed seasonal total of ca 12 eggs. Expectations of high repeatability arising from female-to-female differences in genetics, vigor, habitat quality, or breeding phenology were also apparently contradicted by observed low intraseasonal repeatability.

In House Wrens, second clutch size was apparently independent of earlier brood-rearing effort because no significant correlation existed between second clutch size and the number of first-brood fledglings. Finke et al. (1987) found no differences in the frequencies of House Wrens that attempted second clutches or in average second clutch size among females rearing control, experimentally enlarged, or experimentally decreased first broods. In contrast, female Great Tits that laid second clutches were generally those that produced relatively few fledglings in first broods (van Noordwijk 1987, Lindén 1988), suggesting a trade-off.

In stark contrast to the within-year results, moderate repeatability ($r_I = 0.27–0.50$) existed in first clutch, second clutch, and season-total egg number for House Wrens in different years (Table 2). Moderate repeatability of first clutch size or seasonal egg total in different years has also been found in Great Tits, Song Sparrows, Lesser Snow Geese (see review in Boag and van Noordwijk 1987), and Willow Grouse (Myrberget 1989; all $r_I = 0.23–0.51$) but not in Canada Geese (*Branta canadensis*; $r_I = 0.05$; see review in Boag and van Noordwijk 1987). Furthermore, heritability analyses suggested a significant genetic component to clutch size in House Wrens. However, the value for mother-son heritability of first clutches is likely an overestimate because it exceeds the value for repeatability of first clutches.

One potential interpretation for these seemingly conflicting results of low intraseasonal and high interseasonal repeatability is that first and second clutch sizes are influenced by separate genes. Such a genetic system seems unlikely in House Wrens, given the broad temporal overlap in breeding and the observation that repeatability of total eggs per season was greater than that for either first or second clutch size.

A second interpretation is that a tendency towards high intraseasonal correlation in clutch size may have been largely counterbalanced by a reproductive trade-off between early and late breeding periods. Under this scenario, two important biological phenomena (individual tendencies in clutch size and stress from reproduction) might go undetected because of their opposite impacts on the relationship between fledgling number in brood one and clutch size in brood two. The high repeatability observed for total eggs in first plus second clutches may have occurred because differences in reproductive stress were counterbalanced within this sum. In House Sparrows, high productivity in first broods suggested a high cost because it delayed the initiation of subsequent clutches and reduced subsequent fledgling success (McGillivray 1983). However, as in House Wrens, first-brood size in House Sparrows appeared unrelated to subsequent clutch size (McGillivray 1983), and intraseasonal repeatability in clutch size was low (Murphy 1978).

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