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Clutch-size Dependent Asynchronous Hatching and Brood Reduction in *Junco hyemalis*

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Asynchronous hatching of eggs may allow a reduction in number of offspring through starvation (brood reduction) to match the amount of food supplied by adult birds to the nest (Lack and Lack 1951, Lack 1954). Experimental manipulations of hatching synchrony generally have not supported the brood-reduction hypothesis (reviewed by Amundsen and Stokland 1988), and other explanations have been proposed for asynchronous hatching that are independent of brood reduction (reviewed by Clark and Wilson 1981). In particular, Clark and Wilson (1981) offered a "nest failure" hypothesis, closely related to Hussell's (1972) "predation" hypothesis, that asynchronous hatching in small birds, especially passerines, reduces the probability of total nest failure (see also Richter 1982; Slagsvold et al. 1984; Clark and Wilson 1985; Hussell 1985a, b; Slagsvold 1985, 1986a, b). This polemic concerning asynchronous hatching and brood reduction in passerines has tended to focus on between-species comparisons, obscuring potentially important within-species variation that is known to occur (Clark and Wilson 1981). I present evidence that suggests the Dark-eyed Junco (*Junco hyemalis*), a ground-nesting montane emberizid, employs both asynchronous hatching and brood-reduction strategies that depend on the number of eggs laid.

A total of 103 nests of "Pink-sided" Dark-eyed Junco (*J. h. mearnsi*) was found during 5 breeding seasons in northern Utah (Smith and Andersen 1982, 1985). The fate from eggs to termination was known for 83 clutches. At least 1 egg hatched in 65 nests, and the day on which all eggs within a clutch hatched was known for 44 clutches. Masses of nestlings within 1-2 days of hatching were known for all nests included in the analysis.

To determine the rate of asynchronous hatching among clutch sizes, I made three assumptions. First, the last-hatched egg was laid last (e.g. Zach 1982). Second, differences in hatching times of 24 h or more between last and penultimate nestlings reflected incubation beginning before clutch completion (Clark and Wilson 1981). Finally, differences of more than 1.0 g between the two smallest nestlings during the first 3 days after hatching represented asynchronous hatching, whereas differences of less than 0.5 g between the two smallest nestlings represented nearly synchronous hatching. In all cases where hatching times and masses were known, last-hatched nestlings in asynchronously hatched clutches were <1.0 g lighter than nest mates. Juncos weigh approximately 1.75 g at hatching (Smith and Andersen 1982), and only females incubate eggs.

TABLE 1. Frequency of number of young fledged based on number of eggs that hatched in Dark-eyed Junco nests in which at least 1 young fledged. Instances of brood reduction are indicated with asterisks.

Initial clutch size	No. of eggs hatched	No. of young fledged	Observed frequency
3	3	3	5
3	2	2	3
3	2	1	1*
4	4	4	21
4	4	3	3*
4	3	3	3
4	2	2	3
4	1	1	1
5	5	5	4
5	5	4	2*
5	5	3	1*
5	5	2	2*
5	3	3	1

Fifty junco nests fledged at least 1 young during the study (Table 1). The most common clutch size was 4 ($n = 31$), with 3-egg clutches ($n = 9$) usually representing renesting or second nesting attempts (Smith and Andersen 1982). Five-egg clutches ($n = 10$) usually were associated with delayed breeding due to late-lying snowpack (Smith and Andersen 1985).

Significantly fewer 3-egg clutches exhibited asynchronous hatching than did 4- and 5-egg clutches (likelihood ratio $\chi^2 = 14.81$, $df = 2$, $P = 0.0006$). In clutches with known hatching dates, 0 of 8 (0%) 3-egg, 17 of 29 (59%) 4-egg, and 7 of 9 (78%) 5-egg clutches hatched asynchronously. No obviously smaller ("runt") nestlings were found in any 3-egg nests and only 1 4-egg nest with asynchronous hatching had a runt. However, in the 7 5-egg nests with asynchronous hatching, 5 had 1 runt and 2 had 2 runts, suggesting a positive relationship between hatching spread and increased clutch sizes (Slagsvold 1986b).

Significantly fewer 3- and 4-egg clutches experienced partial brood losses than did 5-egg clutches (likelihood ratio $\chi^2 = 7.29$, $df = 2$, $P = 0.03$). No nestlings died in the 5 3-egg nests in which all eggs hatched (Table 1). One nestling died in a clutch where 2 of 3 eggs hatched; although near fledging mass, it was found dead in the nest after a severe thunderstorm. Only 3 of 24 4-egg clutches in which all eggs hatched experienced death of a nestling (Table 1), one of which was not the last hatched. Five of 9 5-egg clutches in which all eggs hatched experienced brood reduction, the order of disappearance of nestlings always being the smallest followed by the next smallest, etc. (Adult juncos removed unhatched eggs and dead nestlings from the nest.) Thus, facultative brood reduction appeared to be common only in 5-egg clutches.

TABLE 2. Richter (1982) index (q) of relative survival of last-hatched nestling calculated for 3 clutch sizes in Dark-eyed Juncos.

Clutch size	Proportion of surviving nestlings		q
	Last-hatched	Not last-hatched	
3-egg	8/9	14/14	0.889
4-egg	29/31	80/81	0.947
5-egg	5/10	33/38	0.576
Overall	42/50	127/133	0.880

Proportionally more nestlings fledged from 3- and 4-egg clutches that fledged at least one young (22 of 23 [96%] and 109 of 112 [97%] nestlings, respectively) than from 5-egg clutches (38 of 48 [79%] nestlings; likelihood ratio $\chi^2 = 13.88$, $df = 2$, $P = 0.001$). Productivity was significantly different among clutch sizes (Kruskal-Wallis test adjusted for ties [Zar 1984], $H = 11.46$, $P < 0.005$); 5-egg clutches were most productive ($\bar{x} = 3.80$ fledglings) followed by 4-egg ($\bar{x} = 3.52$) and 3-egg ($\bar{x} = 2.44$) clutches (Table 1). Productivity of 3-egg clutches was significantly lower than that of 4- or 5-egg clutches (nonparametric multiple comparisons with unequal sample sizes [Zar 1984]; $Q = 3.05$ and 3.07 , respectively; both $P < 0.01$). The difference in productivity between 4- and 5-egg clutches was not statistically significant ($Q = 0.69$).

These results demonstrate significant intraspecific variation in asynchronous hatching and brood reduction (see also Howe 1976, 1977, 1978; Bancroft 1985). The conclusion that juncos exhibit a brood-reduction strategy based on clutch size is further strengthened by calculating Richter's (1982) index, q , a measure of survival of the last-hatched nestling relative to that of its nest mates, for different clutch sizes (see Clark and Wilson 1985 and Hussell 1985b for critical discussions of this index). For 4-egg clutches q approached 0.95 (Table 2), which is close to 1.00, the value predicted for total brood survival. The value 0.95 is much higher than any reported by Richter (1982) but comparable to values reported by Clark and Wilson (1985) for small passerines. On the other hand, q was only 0.58 for 5-egg clutches (Table 2), suggesting that a brood-reduction strategy is associated with that clutch size. These analyses also show that calculating indexes, such as the one proposed by Richter (1982), without regard to clutch size masks important intraspecific interbrood variation in brood reduction and asynchronous hatching.

Results presented here are similar to those reported for the Snow Bunting (*Plectrophenax nivalis*), another ground-nesting emberizid, by Hussell (1985a). He found a 1-day hatching asynchrony in 4-egg clutches with rare starvation, increased asynchrony in larger clutches, and increased brood reduction from star-

vation with increasing brood size. As Hussell (1985a) pointed out, the first two findings are predicted by the nest-failure model of Clark and Wilson (1981), as modified by Hussell (1985a). The third finding, however, would be predicted from the brood-reduction hypothesis, assuming that nonstarvation mortality of late-hatched chicks, e.g. trampling, is negligible. The most productive junco clutches were those with 5 eggs, in which brood reduction commonly occurred. The increase in brood reduction associated with 5-egg junco clutches may be explained by examining two relatively unrelated events: physiological state of females at egg laying and intrinsic ability of parents to feed young. Clutch size and laying date are related to feeding conditions at oogenesis (Drent and Daan 1980), but clutch size may not be related to feeding conditions at hatching or number of nestlings a pair is capable of raising (Robertson 1973, O'Connor and Morgan 1982). In many cases juncos could not raise all 5 nestlings to fledging (Table 1), suggesting that pairs differed in their ability to feed 5 young, because 5-egg clutches hatched during periods of peak insect abundance (Smith and Andersen 1982). In those cases asynchronous hatching allowed a brood-reduction strategy. Because 5-egg clutches fledged the most offspring on average, all females that can lay 5 eggs should do so, but allow a mechanism for reduction if the parents cannot provision the nestlings. Parents of 3- and 4-chick broods are able to fledge all chicks with negligible starvation, so the optional chick should be the fifth one. Lack's brood-reduction hypothesis commonly has been interpreted to mean that adults can trim brood size during periods of low food abundance (references in Bancroft 1985). Lack specifically referred to the amount of food brought back to the nest, so that the intrinsic ability of parents to feed nestlings may be an important component of brood reduction (see Högstedt 1980).

Addressing this apparent support for both the nest-failure and brood-reduction hypotheses, Hussell (1985a) stated "if nest failure is important in determining optimum asynchrony and brood reduction is adaptive, we are likely to find both conformity of observed asynchrony to the optimum predicted from the nest failure model and efficient brood reduction at this degree of asynchrony" (his emphasis). My results corroborate that conclusion.

Should ground-nesting passerines, which sustain high rates of predation (e.g. Ricklefs 1969), be expected to exhibit predominantly synchronous or asynchronous hatching? Clark and Wilson (1981) concluded that synchronous hatching should predominate in groups likely to experience heavy predation during the nestling period. Combining studies of birds that nest on the ground with those that nest in bushes and shrubs, they suggested that synchronous hatching was more common in that group. Reexamining table 1 in Clark and Wilson (1981), however, reveals that 85% (11/13) of the ground-nesting species ex-

hibited incubation before the last egg was laid. While the daily probability of survival of nestlings in ground nests is probably lower than that of eggs (e.g. Hussell 1985a), nestlings are at risk for relatively short periods of time because most ground-nesting passerine chicks leave the nest 6–10 days after hatching (Smith and Haggerty unpubl. data). Thus, in most cases the prediction from Clark and Wilson's model would be some degree of hatching asynchrony in ground-nesting passerines (see also Hussell 1985a).

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