

MULTIPLE BROODING AS A REPRODUCTIVE STRATEGY: TIME-CONSERVING ADAPTATIONS IN MOURNING DOVES

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ABSTRACT.—The Mourning Dove (*Zenaida macroura*) has a suite of adaptations that promotes multiple brooding, a common characteristic among columbids. Mourning Doves are well adapted for multiple brooding because they produce food (crop milk) for young nestlings *in vivo* and feed older nestlings a diverse granivorous diet. This facilitates extended breeding seasons and, thus, multiple brooding. Other traits such as constant incubation, fast nestling growth, and fledging at low weight serve to shorten the nesting cycle and enhance the number of broods that can be produced. Constant incubation also allows columbids to have no incubation patch. The effect of small clutch size on the length of the nesting cycle is ambiguous. Predation as a selective force augments the advantage of short nesting cycles.

Mourning Doves also are adapted to renest quickly. By constructing small nests and reusing old nests, they can initiate nesting cycles quickly despite their ritualized building behavior. Small clutch size and a lesser role in crop-milk production allow females to initiate new clutches quickly, and sometimes to overlap nesting cycles. Received 7 January 1985, accepted 25 September 1985.

THE importance of multiple brooding (i.e. producing two or more clutches per breeding season) as a reproductive tactic has been noted (e.g. Spencer and Steinhoff 1968, Burley 1980), but the relation between multiple brooding and other life-history traits has received little attention (but see Tinkle 1969, Parmelee and Payne 1973). Among North American birds, the Mourning Dove (*Zenaida macroura*) is the champion of multiple brooding. Unlike most temperate bird species that attempt one or two clutches per breeding season (Lack 1968), Mourning Doves often attempt from three to six (Swank 1955, Hanson and Kossack 1963). The species is impressively successful—although the Mourning Dove is the most frequently harvested game bird in North America (Keeler 1977), both the wintering (Alison 1976) and breeding ranges (Morse 1975) have extended northward in the last few decades. Mourning Doves are common breeders in all the contiguous states and parts of Canada, Mexico, and the Caribbean (Goodwin 1983).

Many behavioral and physiological traits of Mourning Doves can be explained by strong selection for multiple brooding. After briefly reviewing the breeding behavior of Mourning Doves, we identify a suite of traits that apparently are adaptations for multiple brooding. We

focus on a single species for which there is extensive ecological and behavioral information, but the proposed "adaptive suite" (Bartholomew 1972) probably is applicable to pigeons and doves (family Columbidae) in general because members of the group are remarkably alike in breeding behavior (Kendeigh 1952).

BREEDING BEHAVIOR

Mourning Doves are monogamous, and pair bonds sometimes persist between nesting seasons (Mackey 1965). Pairs begin courtship in early spring, typically after the male has established a territory containing potential nest sites. During nest building, the male selects twigs and delivers them individually to the female, who arranges them into a small platform (Nice 1922). Pairs often reuse nests, including old nests of other pairs and other species (McClure 1950, Scanlon et al. 1981).

Egg-laying begins 2–3 days after nest initiation. Clutch size is constant at two eggs, and incubation begins after the first is laid (Cowan 1952). Larger clutches of three and four eggs occur about 1% of the time, but probably result from intraspecific nest parasitism (Weeks 1980). Mourning Doves incubate constantly, with males sitting from about 1000 to 1800 and fe-

males for the remaining hours (Harris et al. 1963, Blockstein 1982). Neither sex develops the vascularized incubation patch typical of other birds (Maridon and Holcomb 1971). The eggs hatch after 13–14 days.

Young Mourning Doves are fed crop milk, a cheesy conglomeration of epithelial cells sloughed from the crop mucosa of both parents (Levi 1963). Beginning about the third day after hatching, seeds are mixed with crop milk in gradually increasing proportions; at 6–8 days of age, the young are essentially granivorous (Taylor 1941, Mackey 1954, Laub 1956). The young fledge at about 14 days, but the male continues to feed them for about a week (Hitchcock and Mirarchi 1984).

Mourning Doves have one of the longest breeding seasons of all North American birds (Peters 1961); nesting pairs sometimes breed from April through September (McClure 1950, Hanson and Kossack 1963). A single nesting cycle (defined as the period from laying the first egg to fledging the last young) is 28–30 days; pairs usually attempt to raise multiple broods.

The breeding behavior of Mourning Doves is typical of columbids. Columbids are monogamous (Delacour 1980), and they build small platform nests (Goodwin 1983). Nest building takes 1–3 days; the interaction between sexes is as described above (Kendeigh 1952, Goodwin 1983). Clutch size usually is constant for a species, at either one or two small eggs. Rahn et al. (1975) found that columbids produce eggs that are on average less than half the size of those laid by birds of equal weight. Incubation is continuous, with the exchange between sexes occurring in the morning and late afternoon. Columbids have a bare ventral aperture year-round that does not become vascularized during the breeding season. The length of time that nestlings are fed crop milk varies among species, but young columbids usually assume the diet of their parents midway through the nestling period. The long breeding season typical of Mourning Doves has been documented for many columbid species (Frith 1982), and multiple brooding has been reported for many of the species that have been closely studied [e.g. Band-tailed Pigeons (*Columba fasciata*), MacGregor and Smith 1955, Gutierrez et al. 1975; Rock Doves (*C. livia*), Burley 1980; Wood Pigeons (*C. palumbus*), Saari 1979; *Columbina talpacoti*, Haverschmidt 1953; *Ducula*

spilorrhhoa, Crome 1975b; *Columbina inca*, Johnson 1960; White-winged Doves (*Zenaida asiatica*), Cottam and Trefethen 1968; *Z. galapagoensis*, Grant and Grant 1979]. Most columbids that have been bred in captivity produce multiple broods (Delacour 1980, Goodwin 1983).

The family Columbidae has colonized successfully an array of habitats that ranges from jungles to deserts. Of the 284 known columbid species, there are representatives on every continent except Antarctica and every major island in the world (Goodwin 1983). The Passenger Pigeon (*Ectopistes migratorius*) was perhaps the most numerous single avian land species of recent times (Schorger 1955).

REPRODUCTIVE STRATEGY

Most birds synchronize reproduction with a brief period of abundant, high-quality food for nestlings (Lack 1950, Skutch 1950, Thompson 1950). Columbids, however, produce food (crop milk) for young nestlings *in vivo* and feed older nestlings a diverse diet of seeds (Browning 1959). Thus, breeding need not be synchronized with availability of particular foods. The resultant protracted breeding season has led to a propensity for multiple brooding.

When multiple brooding strongly affects fitness, the time required to complete nestings is critical. The less time a single nesting takes, the more nestings are possible in a breeding season (see also Ricklefs 1984). Columbids could adapt for rapid production of multiple broods by (1) reducing the time interval between successive nesting attempts and (2) reducing the length of the nesting cycle. A complex of time-conserving traits allows Mourning Doves to accomplish both (Fig. 1).

The nesting interval.—Many studies have documented the short nesting interval of Mourning Doves. After a nesting failure, the period until a new clutch is begun ranges from 2 to 25 days, with the most frequent time interval being 6 days in one study (Hanson and Kossack 1963) and 3–5 days in another (Swank 1955). After a successful nesting, Mourning Doves usually begin a new clutch in 3–6 days (Harris et al. 1963, Caldwell 1964).

Accumulation of nesting material is a slow process for columbids because collecting and exchanging twigs is ritualized, at least partly to enhance gonadogenesis in females (Cheng and Balthazart 1982). Still, Mourning Doves

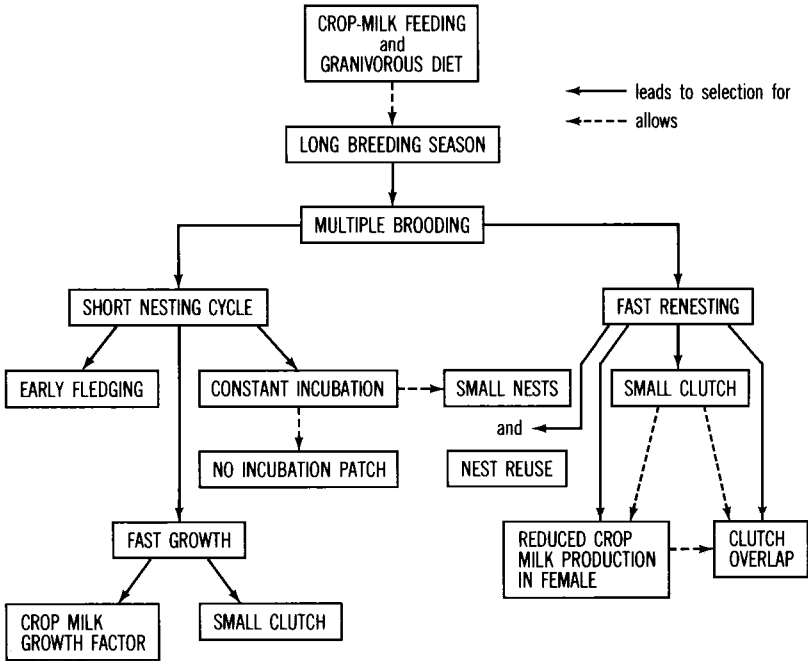


Fig. 1. Flow diagram outlining the proposed evolution of multiple brooding and associated traits in Mourning Doves.

shorten the process by building small, crudely structured nests. Mourning Doves also collect nesting material near the nest site (Cowan 1952, Sayre et al. 1980), which probably serves to ensure males of paternity (see Lumpkin et al. 1982) in addition to saving time and energy. Nests are completed in 2-3 days (Cowan 1952, Goforth and Baskett 1971). Under the constraint of ritualized building, collecting enough twigs to construct a nest comparable to those of other open-nesting birds probably would take Mourning Doves an additional 4-5 days. Poor nest construction evidently reduces nesting success for Mourning Doves (Coon et al. 1981), but this negative effect undoubtedly is ameliorated by constant incubation. Koepcke (1972) suggested that small nests are an adaptation for concealment, but this seems unlikely because parents much larger than the nest itself are always present.

By reusing old nests, columbids eliminate the time required for building. For Mourning Doves, nest reuse occurs in as many as 35-40% of nesting attempts (McClure 1950, Harris et al. 1963, Scanlon et al. 1981), but does not ensure better nesting success (Woolfenden and Roh-

wer 1969, Westmoreland and Best 1985). Thus, it seems plausible that it evolved to reduce time between nesting cycles.

Crop-milk production is stimulated by secretion of prolactin, which simultaneously suppresses gonadal activity (Bates et al. 1935, 1937). Female Mourning Doves play a lesser role than males in crop-milk feeding (Blockstein 1982) and reduce crop-milk production 4-6 days before males (Mirarchi and Scanlon 1980). This may allow the antigonadal effect of prolactin to wane, so egg production for the next clutch can begin (Hanson and Kossack 1963). By requiring less crop milk, small broods also may ameliorate the effect of prolactin in females, thus allowing quick "recycling" of the ovary after the crop-milk phase.

Individual columbids may eliminate nesting intervals altogether by overlapping nesting cycles, i.e. simultaneously caring for two sets of offspring at different stages of development. Small clutch size may facilitate nest overlap due to the comparatively low energetic cost of producing and feeding only two offspring (Burley 1980). Burley found that experienced captive pigeons care for two sets of offspring (one in

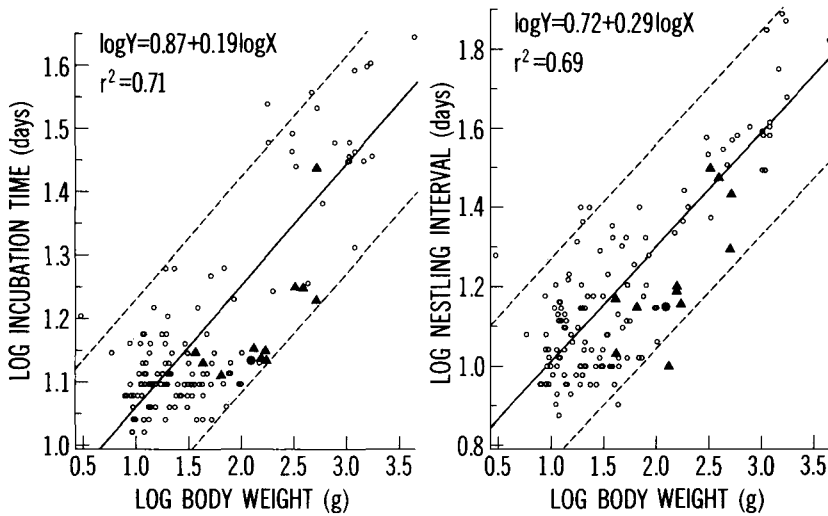


Fig. 2. Relationship between body weight and incubation or nestling interval for 140 species of altricial, open-nesting land birds. The regression line was calculated for noncolumbids (open circles). Triangles represent columbids, and the enlarged closed circle represents Mourning Doves. Incubation and nestling times from Harrison (1978); body weights from various sources (references available from senior author).

the egg stage and the other as nestlings) 70% of the time. Captive (Hanson and Kossack 1963) and wild (Mark Sayre pers. comm.) Mourning Doves sometimes overlap clutches by 14% or more by laying eggs when the young of the previous nest are 10 or 11 days old. There is also circumstantial evidence for overlap in wild Wood Pigeons and Stock Doves (*Columba oenas*) (Murton and Isaacson 1962).

The nesting cycle.—If columbids are strongly selected to have short nesting cycles (Fig. 1), the trend should be apparent when they are compared with other birds. To examine this, we compared the time required for incubation and nestling growth with body weight for 140 altricial species of open-nesting land birds (Fig. 2). The columbids save time in both the incubation and nestling stages. Overall, columbid nesting cycles are 22% shorter than those predicted by the regression line. Only one value for columbids lies outside the 95% confidence interval, but 11 of 12 of the incubation and 10 of 11 of the nestling intervals fall below the regression lines. The probability of this occurring by chance alone in either case is <0.01 (sign test, Gibbons 1976).

Several traits of Mourning Doves may serve to shorten incubation time. Small egg size undoubtedly has a large influence, as a positive correlation exists between incubation time and

egg weight (Rahn and Ar 1974). However, constant incubation probably also plays a role. Mourning Dove eggs and nestlings less than 6 days old essentially are ectothermic (Breitenbach and Baskett 1967). Bird eggs cool rapidly when parents are absent and rewarm slowly after their return (Drent 1972). Most birds take respites from incubation, usually to forage (Skutch 1962, Ricklefs 1974, Drent 1975). Columbids store large quantities of food in their crops, so incubation is not interrupted by a need for food. The constant source of heat supplied from laying until late nestling growth ensures continuous development. Through constant nest attentiveness, Mourning Doves, Ringed Turtle-Doves (*Streptopelia risoria*), and White-winged Doves can maintain their eggs at viable temperatures even during extreme heat (Russell 1969, Walsberg and Voss-Roberts 1983).

Constant incubation probably also eliminated the need for vascularized incubation patches in columbids. According to Ackerman and Seagrave (1984), incubation patches in birds exchange little heat with eggs during the steady-state conditions that occur when eggs are covered continuously. Thus, for columbids, development of incubation patches would be unnecessary. Constant incubation also may have led to the evolution of white (noncryptic) egg coloration in columbids. However, cryptic col-

TABLE 1. Fledgling weight:adult weight ratios for columbids.

Species	Weight (g)		Ratio
	Fledgling	Adult	
<i>Columba livia</i>	352 (8) ^a	313 (8)	1.13
<i>C. palumbus</i>	277 (3)	500 (9)	0.55
<i>Columbina talpacoti</i>	28 (2)	45 (2)	0.62
<i>Ducula spilorrhoa</i>	260 (5)	500 (5)	0.52
<i>Ptilinopus superbus</i>	30 (6)	120 (5)	0.25
<i>Streptopelia decaocto</i>	<70 (7)	145 (7)	<0.48
<i>Zenaida asiatica</i>	113 (4) ^b	170 (4)	0.66
<i>Z. macroura</i>	72 (1)	115 (1)	0.63

^a Sources: (1) McClure 1941, (2) Haverschmidt 1953, (3) Murton et al. 1963, (4) Cottam and Trefethen 1968, (5) Crome 1975a, (6) Crome 1975b, (7) Rana 1975, (8) Burley 1980, (9) R. A. Ackerman pers. comm.

^b Estimated from linear extrapolation of growth-rate curve.

oration may result in higher hatching success even when eggs are incubated continuously (Westmoreland and Best 1986).

Columbids are an exception to the general rule that nestlings of species with small clutches have slow growth rates (Ricklefs 1968). Growth rates of columbids are comparable to, if not faster than, those of raptors and passerines. Their method of feeding young may be the reason. Crop milk is high-quality food for nestlings, being composed of 65–81% water, 13–19% protein, 7–13% fat, and 1.5% ash (Needham 1942). It also contains an unidentified factor that promotes fast growth. Pace et al. (1952) compared growth rates of White-rock (*Gallus gallus*) chicks fed chick ration *ad libitum* with those of chicks whose diet was supplemented with small amounts (5 g/day) of Rock Dove crop milk. Although crop milk was fed for only 6 days after hatching, treatment chicks grew significantly (*t*-test for slopes, $P < 0.001$, analysis ours) faster than controls until the experiment ended when chicks were 42 days old. Evidently, crop milk stimulated chicks to eat more ration.

Some young columbids feather quickly and leave the nest at relatively low weight. Ricklefs (1968) found that the ratio of fledgling weight to adult weight for 94 noncolumbid species ranged from 0.62 to 1.42. For seven of eight columbid species the ratio ranges from 0.25 to 0.66 (Table 1). In concert with fast growth, early fledging must significantly shorten the nestling period. After leaving the nest, young Mourning Doves usually become independent in 4–7 days (Hitchcock and Mirarchi 1984). Ad-

mittedly, our comparison of nesting cycle lengths would be more reliable if we included this period, but there are few published data on the postfledging period of columbids or noncolumbids.

Small clutches also may be an adaptation for a short nesting cycle. Mourning Dove eggs usually are laid on alternate days (Hanson and Kossack 1963), so increasing clutch size to three would have a direct, although minor, effect on the duration of the nesting cycle. A larger clutch also may prolong the incubation period, as Zimmerman (1983) found with Dickcissels (*Spiza americana*). During the early nestling stage, parents with a given amount of crop milk may opt to raise a small brood quickly or a large brood slowly (Lack 1968). Some evidence suggests, however, that some individual columbids may simply increase crop-milk production for a larger brood. Murton et al. (1963) found that adding a third nestling to some Wood Pigeon nests had no effect on growth during the crop-milk stage. This is not true, however, for other Wood Pigeons (Murton et al. 1974), feral pigeons (Burley 1980), or Mourning Doves (Blockstein unpubl. data). After the crop-milk phase, nestling growth may be limited by the rate at which the parents gather seeds. Haas (1980) found that Mourning Dove nestlings attended by a single parent after the crop-milk phase take up to 3.8 days longer than normal to fledge. He did not, however, report fledging weights. Murton et al. (1974) studied the effects of brood size on growth rates of nestling Wood Pigeons, a species that normally lays two eggs. They found that nestlings in broods of three grew more slowly than those in broods of two, but parents of three-year broods nevertheless were often successful in fledging the young. Band recoveries within one month of fledging indicated that young from broods of three had lower survival, but the difference was not statistically significant. Further study is necessary to resolve whether or not small clutch size is an adaptation for short nesting cycles.

The importance of predation.—Adaptations that shorten the nesting cycle also are advantageous in reducing the probability of predation. When the nesting cycle is short (i.e. there are fewer days of nest exposure), there is less chance of a nest being discovered by a predator (see Mayfield 1975). Also, the loss of a small clutch represents less wasted parental investment. Predation-related advantages undoubtedly

contribute to the success of the columbid reproductive strategy, but clutch overlap and reuse of nests built by other individuals or other species cannot be explained as adaptations for predator avoidance. Also, this proposed suite of adaptations is relatively ineffective at reducing losses to predation. From Ricklefs's (1969: 12) data on daily nest failure, the mean rate for Mourning Doves is about the same as that for the 15 other open-nesting, altricial species listed (2.1% vs. 2.4%, respectively, Student's *t*-test, $P = 0.38$). Thus, we believe that predation probably is of secondary importance in the evolution of the columbid reproductive strategy.

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securing favorable action upon it. These investigations, now in progress under Government auspices, are thus the direct outgrowth of the work of the Union, and especially of that of its Committee on the Migration and Distribution of Birds. The vast amount of valuable material gathered by this Committee has now been turned over by the Union to the Depart-

ment of Agriculture, for elaboration and publication; and the returns of the A. O. U. observers are now directly sent to the Department of Agriculture, which defrays the considerable expense necessarily involved in the preparation, distribution, and collection of the schedules, as well as the preparation of the returns for publication."