

on the Z and W chromosome (Gelter et al. MS). No hybrids between the two *Parus* species have been reported.

The similarity of the highly repetitive sequences in *Ficedula* and the observed differentiation of repetitive sequences in *Parus* suggest divergence of highly repetitive sequences by differentiation after speciation and correlation to overall differentiation between each species pair.

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Terminal-Egg Chilling and Hatching Intervals in the American White Pelican

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With the onset of pipping, incubation behavior of many bird species alters rapidly as parents adjust their behavior to the changing nest contents. Typically, parents settle less tightly over pipped eggs and apply their brood patch(es) less closely (Drent 1973). In species where the young hatch asynchronously, further disruptions to incubation arise when parents begin to tend their first hatched young (Beer 1962, Nelson 1978). In extreme cases, parents may permanently neglect late-hatching eggs, which die (Gullion 1954, Beer 1962, Spellerberg 1971).

The adaptive significance of terminal-egg neglect has not been determined, but it is noteworthy that it has been reported mainly for ground-nesting non-passerine species that commonly exhibit brood reduction after hatching. Graves et al. (1984) have suggested that neglect of the terminal egg would be an easy way for parents in one such species (the Herring Gull, *Larus argentatus*) to achieve brood reduction. Less extreme forms of terminal-egg neglect may also be relevant to brood reduction. It has been suggested, although not as yet directly proven under natural

conditions, that chilling of terminal eggs can cause their hatching to be delayed relative to older siblings (Nice 1954, Greenlaw and Miller 1983) with a corresponding increase in within-brood hatching asynchrony (Forbes and Ankney 1988). Any such increase in hatching asynchrony could have negative effects on the competitive ability of the youngest offspring (Knopf 1980, Mock 1984).

It is well established that chilling during most of the incubation period will cause mortality or retardation of development in many bird species (Lundy 1969, Webb 1987), but empirical evidence for these effects when chilling occurs only after the onset of pipping of the oldest egg in a clutch is evidently available for only a single nondomesticated species (the Ring-billed Gull, *L. delawarensis*) (Evans 1990). In this species, I found a significant extension of *hatching time* (time from first manifestations of external pipping until hatching) and greater within-brood hatching asynchrony in clutches that were experimentally chilled to 33°C from pipping of the oldest, or a-egg, onwards. I found similar increases in hatching time for Domestic Chicken (*Gallus gallus*) eggs intermittently cooled to 30°C or lower from pipping onwards. To determine whether a similar effect is present in species prone to brood reduction, I examined the American White Pelican (*Pelecanus erythrorhynchos*).

The American White Pelican normally lays two eggs but rarely fledges more than one young. The second, or b-egg, represents mainly an insurance egg that survives at ca. 20% of nests in which the a-offspring fails to survive (Cash and Evans 1986). Selective desertion of the b-egg has not been reported in pelicans, but less extreme manifestations of terminal-egg neglect occur in the form of a lower and more variable incubation temperature commencing after the a-egg pips (Evans 1989). Pelicans lack a brood patch and normally incubate eggs under their foot webs. Changes in thermal conditions at the onset of pipping result when parents remove their foot webs from the eggs and incubate them between their legs. This behavior is probably an adaptation to prevent the parent from crushing the pipped egg (Evans 1988a). After the a-chick hatches, core temperatures of (artificial) b-eggs can temporarily drop as low as 29°C, well below the mean core temperature of ca. 35°C (Evans 1989) and below temperatures reported for other Pelecaniformes (Webb 1987).

Pelican eggs were collected from an island colony of >2,500 nests (1989) at East Shoal Lake in south-central Manitoba, Canada. From observations of courtship activities made from a distance in early spring (April), it was possible to predict the breeding chronology of selected subcolonies (Evans and Cash 1985), which were then entered on the expected day of pipping onset. This procedure reduced the number of colony visits and kept disruptions to a minimum. Eggs were incubated in two identical darkened in-

cubators, each equipped with a low-noise fan and held at $60 \pm 10\%$ relative humidity. Incubators were located in a temporary plywood shed erected on the mainland adjacent to the colony. Power was supplied by a portable generator.

I initially collected 42 unpipped b-eggs from two-egg clutches in which the a-egg was pipped. Twenty-one b-eggs were immediately assigned at random to each of two incubation temperatures: $37.8 \pm 0.1^\circ\text{C}$ (control) and $33.0 \pm 0.1^\circ\text{C}$. When these had hatched, I set an additional 21 b-eggs at an intermediate temperature of $36.0 \pm 0.1^\circ\text{C}$. Only 5 nests with pipped a-eggs were readily available in the colony at the time the final collections were made, so 16 additional complete clutches of unpipped eggs were taken and placed in the vacant control incubator. When complete clutches were taken, single eggs from other two-egg clutches were left in each nest to minimize effects on productivity. B-eggs from the two-egg clutches were transferred to the experimental incubator as soon as their sibling a-egg pipped. It required only 1–4 days for all of the a-eggs to pip, hence the effect of the initial incubation of b-eggs at the control temperature was minimal. The a-eggs were maintained at the control temperature until they hatched. These eggs provided data from which to calculate the duration of within-clutch hatching asynchrony for this group. I examined all artificially incubated eggs every 3–5 (usually 4) hours, and noted their status as unpipped, pipped, or hatched. I calculated hatching times from this. When eggs were beginning to ring, hatch time was taken as midway between that visit and the next. Except where inclement weather intervened, young were returned to the colony within a day of hatching.

Ten of the 63 b-eggs (16%) were either infertile or contained embryos that had died earlier in incubation. Of the remaining 53 eggs, all hatched but one in the 33°C group. Hatching time varied significantly among the three incubation temperatures (ANOVA: $F = 30.77, P < 0.001$). This effect was due exclusively to a 14.4 h (52%) extension in mean hatching time at the lowest temperature, 33°C (Table 1). There was no retarding effect from chilling embryos to 36°C. The interval between setting the eggs in the incubators and the onset of pipping averaged 28.5 h for the 37.8°C controls and 39.0 h for the eggs chilled to 33°C ($t = 1.94, P < 0.05$, one-tailed test). Assuming the pre-pipping stages of eggs in these two groups were the same (the a-egg at each nest was pipped when the b-eggs were collected for these two treatments), I recognize a further mean delay of ca. 10.5 h for the 33.0°C treatment group. The amount of hatching asynchrony between the a- and b-eggs was obtained for 12 two-egg clutches (a-egg held at control temperature, b-egg at 36.0°C where no effect of chilling was present, see above). Hatching asynchrony for these eggs ranged from 24 to 55.5 h, with a mode of 48 h and mean of 43.7 h.

Developmental delay incurred by chilling piped eggs was not linear. An optimal plateau exists over a range from 36° to ca. 38°C, but further tests at 34° and 35°C would be required to determine more exactly the critical temperature at which a significant delay in hatching can be detected. The presence of a developmental temperature plateau suggests that there would be no particular advantage accruing to parents that compensated for egg cooling by subsequently maintaining unnecessarily warm temperatures to increase mean incubation temperature (cf. Webb 1987). The frequency of occurrence of incubation temperatures below some critical developmental value (e.g. Morton and Pereyra 1985) may be a more important parameter than the mean temperatures commonly reported. In American White Pelicans, further analysis of previously reported egg temperature data (Evans 1989: fig. 1) indicates that after the onset of pipping of a-eggs, the occurrence of (artificial) b-egg temperatures $\leq 33^\circ\text{C}$ more than doubled—from 9% to 22%. If one assumes that temperature readings taken one hour apart are independent events, this increase in the frequency of low readings after the onset of pipping is statistically significant ($\chi^2 = 19.26$, $P < 0.001$).

In the laboratory, the mean within-brood hatch asynchrony for the East Shoal Lake pelican population was 43.7 h, at least where terminal eggs were not subject to hatch retardation due to chilling. Most readings were bunched around 48 h, which presumably reflects a two-day laying interval (Knopf 1979). Using 43.7 h as a standard of comparison, the extension of the mean b-egg incubation period by 10.5 h before pipping and by another 14.4 h after pipping in eggs incubated at 33°C would increase within-brood asynchrony by ca. 57%. In Ring-billed Gulls, experimentally chilling clutches to 33°C after the onset of pipping in a-eggs increased hatching asynchrony by ca. 62% (Evans 1990). Because chilling during natural incubation is unlikely to involve a simple lowering of temperature to some constant suboptimal level (Evans 1989), these calculations probably do not represent the effects of terminal-egg neglect during natural incubation, but indicate that selective cooling of terminal eggs constitutes a potential mechanism for parents to significantly increase hatching asynchrony (Forbes and Ankney 1988), should it be in their best interests to do so.

Within-brood hatching asynchrony for naturally incubated pelican eggs at East Shoal Lake is ca. 2.5 days (Cash and Evans 1986), marginally longer than the 43.7 h I obtained for artificially incubated eggs not subjected to chilling-induced hatching delays. Unfortunately, it is not known whether this difference reflects the effects of terminal-egg neglect in the field data, or merely a greater frequency of longer laying intervals in the egg sample upon which the field data were based. Detailed measurements of hatching times for naturally incubated American

TABLE 1. Hatching time ($\bar{x} \pm \text{SE}$) in American White Pelican eggs in relation to incubation temperature during the final stages of incubation.

Treatment (°C)	n	Hatching time (h)	Delay ^a (%)	t ^b	P
37.8	19	27.6 \pm 4.6	—	—	—
36.0	17	28.2 \pm 4.5	2.2	0.40	>0.5
33.0	16 ^c	42.0 \pm 8.4	52.2	6.43	<0.001

^a Delay was calculated as the difference between mean hatching times of chilled and control (37.8°C) eggs, expressed as a percent of controls.

^b Comparison of chilled with control means after significant ANOVA.

^c Excludes 1 egg that piped but failed to hatch.

White Pelican eggs are also lacking, but daily observations from a blind (Evans 1989) suggested that the hatching time is approximately 24 h, similar to the means of 27.6 to 28.5 h I obtained for eggs artificially incubated at 37.8 and 36°C, respectively. The increase of mean hatching time to 42 h for piped eggs chilled to 33°C appears to be well beyond the natural range of hatching times and lies entirely outside of the range of values obtained in the laboratory at the warmer temperatures (range at 37.8°C is 21–35.5 h; at 36°C, it is 19.5–36 h). The results of this study, along with previous measurements of egg temperatures (Evans 1989), suggest that American White Pelicans do not normally employ terminal-egg neglect as a means of significantly increasing within-brood hatching asynchrony.

The possibility (Evans 1988b, 1989) that vocalizations from chilled embryos at the piped-egg stage enhance parental incubation behavior implies that parents may actively cooperate with the terminal egg to reduce neglect. Embryonic enhancement of parental incubation has been demonstrated experimentally in Common Murres (*Uria aalge*) (Tschanz 1968), and if verified in pelicans would also argue against the hypothesis that terminal-egg neglect is part of an adaptive parental brood reduction strategy in this species.

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Habitat Choice in Captive Arctic Warblers

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Many closely related species of birds occupy distinct habitats, and reasons for such habitat choice are an active field of research (Cody 1985a). Still, there have been few studies on the development of habitat preferences in captive birds, and little assessment of the extent to which habitat choice is innate. Partridge (1974) simultaneously introduced several hand-reared individuals of two species of tits (*Parus*) into an aviary, and found that individuals of each species foraged in their naturally preferred habitat. Greenberg (1987) demonstrated that young Worm-eating Warblers (*Helmitheros vermivorus*) had innate preferences for foraging in a specific microhabitat (dead leaves), but

did not investigate broad-scale habitat choice. Several authors have shown that early experience can affect habitat preferences, although they did not always compare naturally available habitats (Klopfer 1963; Greenberg 1983, 1984; Gluck 1984).

Different species, and even subspecies, in the genus *Phylloscopus* (Old World leaf warblers) occupy distinct habitats (Gaston 1974, Cody 1985b, Price MS). For example, along an altitudinal gradient in Kashmir, India, some species are restricted to broad-leaved forest, some to coniferous forest, while others are more generalized (Price MS). In this study, we brought chicks of the Arctic Warbler, *Phylloscopus borealis*, into