

response. Although this possibility has not been disproven, there is no evidence to date that one Swamp Sparrow syllable is more powerful than another.

It is always easier to fail to reject the null hypothesis of no discrimination than to support the alternative that discrimination occurs. Using the same experimental design and with smaller sample sizes, however, Peters et al. (1980) were able to show discrimination by male Swamp Sparrows on the basis of syllable type (i.e. Swamp Sparrow syllables versus Song Sparrow syllables). Furthermore, they were able to show discrimination by Song Sparrows on the basis of temporal pattern, again with smaller sample sizes than used here. Thus, we are probably safe in concluding that (a) male Swamp Sparrows are much less sensitive to temporal pattern than they are to syllable type, and (b) male Swamp Sparrows are less sensitive than are male Song Sparrows to temporal pattern.

Our results also contrast to those of Searcy et al. (in press, *Anim. Behav.*) on song discrimination in adult, female Swamp Sparrows. These authors examined the response of captive, female Swamp Sparrows to the same test songs used here. The number and intensity of copulation solicitation displays were used to measure response. Female Swamp Sparrows showed significantly weaker response to the Complex song than to the Swamp Synthetic song. We have shown here that male Swamp Sparrows do not respond differentially towards these two songs. Thus, we can also conclude that male Swamp Sparrows are less sensitive to temporal pattern than are female Swamp Sparrows.

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The Development of Effective Endothermy and Homeothermy by Nestling Piñon Jays

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Hatchling altricial birds begin life as obligate ectotherms but develop into endotherms within a few days. The literature characterizing the development of endothermy by individual chicks has grown considerably over the past two decades, yet the relevance of such characterizations to broods in nature has been questioned (Dunn 1975).

Individual endothermy is the ability of an isolated chick to maintain its metabolism within its thermoneutral zone (TNZ) and to raise its metabolism in response to ambient temperatures (T_a) outside its TNZ. This may not coincide with the development of effective endothermy, i.e. the ability of an individual within a brood and nest to maintain its metabolism within its TNZ and to raise its metabolism at T_a 's beyond its TNZ. Furthermore, the degree to which chicks are able to maintain a constant body temperature (T_b), i.e. homeothermy, may differ between isolated individuals and broods. This study was designed to determine the degree of these discrepancies. The reasons such discrepancies exist and the potential ecological importance of effective endothermy and homeothermy will be addressed elsewhere (Clark in prep.).

The Piñon Jay (*Gymnorhinus cyanocephalus*) nests early in the year (as early as February in the Flagstaff, Arizona area), when T_a is characteristically low (Balda and Bateman 1972). Diurnal T_a during incubation and the nestling period is often at or below 0°C. Female jays incubate the eggs and brood the young continuously. During this time the female and the young are fed entirely by the male. When chicks are capable of thermoregulation, the females leave the nest to forage with the males, leaving the young jays unattended for a period of 60–70 min (Bateman and Balda 1973). Thus, young jays exist under conditions that can be considered harsh for a passerine bird.

Piñon Jays commonly raise broods of 4 and 5. The modal clutch size in 1976 and 1977 was four. Chicks were removed from their natural nests and taken to the lab for metabolic tests. In all cases one

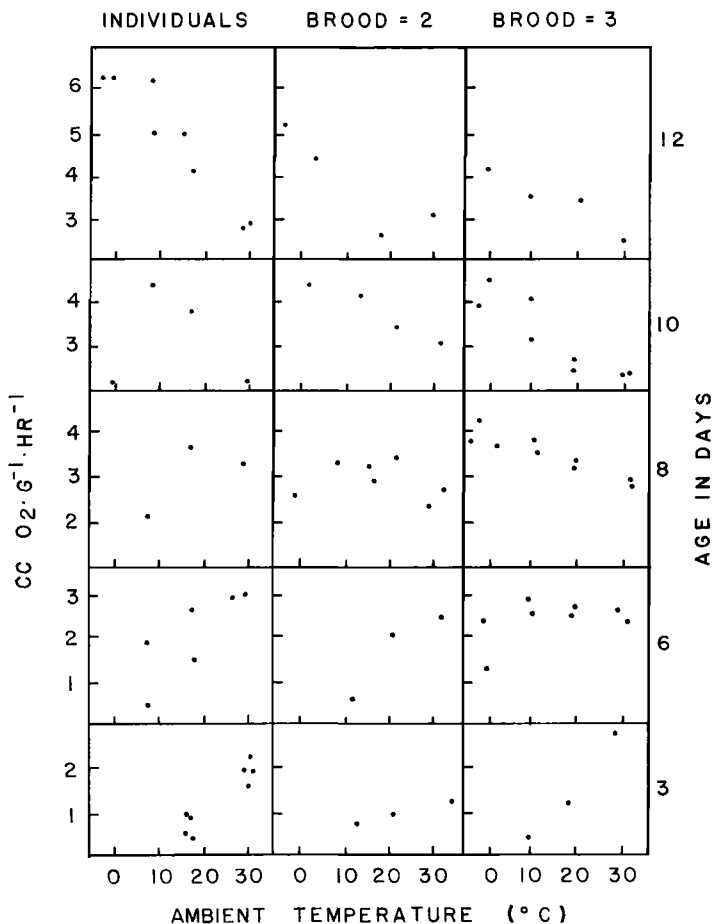


Fig. 1. Metabolic rates of nestling Piñon Jays as a function of T_a . Each point represents the O_2 consumption per gram of chick after 1 h. In the case of broods of 2 and 3, each point represents the O_2 consumption of the entire brood divided by the brood weight.

chick was left in the nest to prevent the parent from deserting. Due to severe predation by the Common Raven (*Corax corax*) and the asynchrony of hatching, it was not possible to construct larger broods artificially. Thus, broods of three were the largest brood size tested.

Chicks were removed from the nest between 0830 and 0900 and transported to the laboratory, a trip lasting 20 min, in a wool cap enclosed within a cardboard box to prevent excessive cooling. Three-day-old chicks were kept in the breast pocket of a flannel shirt during transport.

The metabolic apparatus consisted of a clear acrylic metabolic chamber constructed with angled baffles at each end to ensure complete mixing of the air. The metabolic chambers were placed in constant temperature cabinets, and air was drawn through each chamber at a flow rate of 0.9–1.0 l/min by a vacuum pump. The outlet air was passed through a desiccant (drierite), a CO_2 absorbant (ascarite), and a flowmeter before an aliquot of air was passed through a Beckman E-2 paramagnetic oxygen analyzer. Oxygen consumption, corrected to STP, was calculated using the equation for a flow-through system of Depocas and Hart (1957).

Once in the laboratory, chicks were weighed and warmed at a T_a of 34°C and fed until replete. Initial T_b was measured by inserting a YSI telethermometer probe approximately 0.75–1.0 cm into the cloaca. Chicks tested as isolated individuals were set upon an elevated screen placed in the metabolic chamber. Broods were tested in natural Piñon Jay nests. Trials were conducted at T_a 's of 30°, 20°, 10°, and 0°C for 1–1.2 h duration. If the O_2 fraction in the sample fell close to zero, the trial was discontinued,

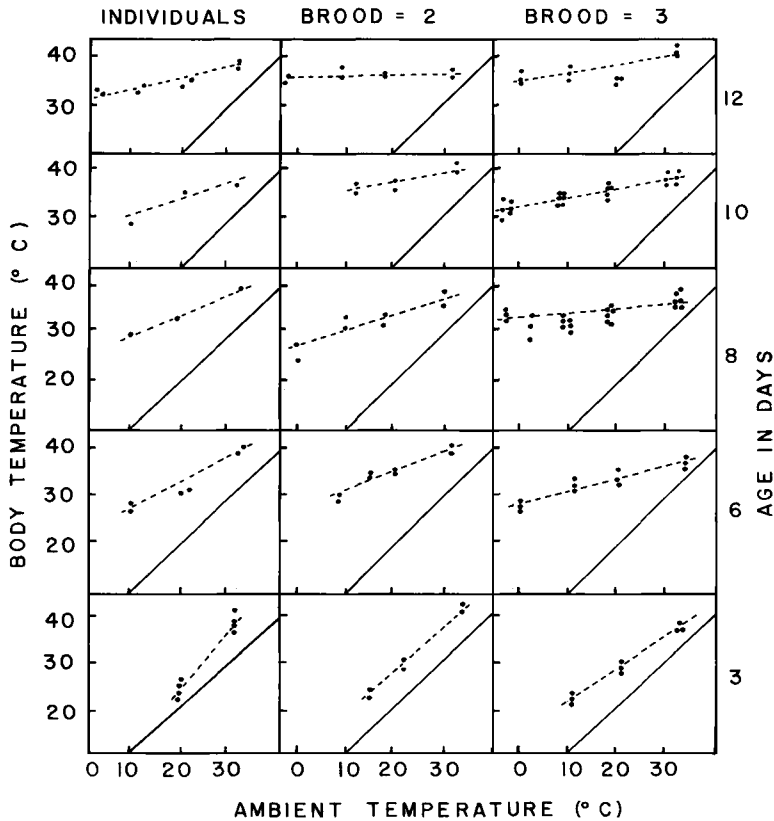


Fig. 2. Nestling Tb as a function of Ta. Each point represents the Tb of a chick at the end of a metabolic trial. Each trial lasted 1 h for a given Ta. The solid diagonal line represents the theoretical relationship between Tb and Ta for a nonregulating object. The dashed regression lines were fitted to the data using the SAS general linear model program.

resulting in missing trials at low Ta's for young chicks. Because the objective was to look for an endothermic response rather than to kill the chicks, we feel these missing trials are acceptable. Oxygen consumption in acceptable trials remained constant after approximately 40 min, but values reported here are based on the last reading obtained before chicks were removed from the chamber. Final Tb and weight were recorded after each trial. Chicks were then fed until replete. When Tb was below the initial Tb, the chicks were warmed before being tested at the next lowest Ta. Up to four metabolic trials per chick per day were performed. Chicks were not used again at older ages.

Within a nest, elevated metabolic responses to low Ta (0°C for at least 1 h) were first seen at 8 days of age for broods of 3, and 10 days for broods of 2. Isolated individuals showed an endothermic response at 12 days (Fig. 1). In general, the larger brood exhibited an endothermic response to a given Ta earlier than did the smaller brood, while isolated individuals showed an even more delayed onset of an endothermic response. As individuals within nests were not tested, it is not possible to determine the relative contribution of a nest or sibling.

Tb is plotted against Ta for brood size and age in Fig. 2. Analysis of covariance shows that larger clutches effectively regulate Tb at earlier ages (Table 1). At 3 days of age, no endothermic response is seen in isolated chicks or in chicks from broods of 2 or 3. Broods of 2 are better able to keep Tb above Ta than are isolated individuals, and broods of 2 and 3 do not differ in their ability to maintain Tb above Ta. Similar trends are seen for chicks at 6 days of age. At 8 days broods of 3 are better able to maintain Tb above Ta than are broods of 2. This is concurrent with the ability of broods of three to exhibit an endothermic response of 0°C for at least 1 h. At this age broods of two are no better at maintaining Tb above Ta than are isolated individuals. When chicks are 10 days of age, broods of 2 and 3 do not differ

TABLE 1. Analysis of covariance for a test of significance between slopes of Tb vs. Ta for isolated individuals (1), broods of 2 within a nest (2), and broods of 3 within a nest (3). *F* values contained in the table are based on the SAS general linear model for analysis of covariance. Significance levels are indicated by **0.01 and ***0.001.

Age	1 vs. 2	2 vs. 3
3	11.56**	0.62
6	56.09***	0.15
8	3.99	19.77***
10	79.77***	0.45
12	463.14***	152.60***

in their ability to keep Tb above Ta. This occurs when both brood sizes can maintain an endothermic response at 0°C for a least 1 h. Isolated individuals do not yet demonstrate this capability and are not able to maintain Tb above Ta as well as a brood of two.

Table 1 indicates that broods of 2 maintain Tb above Ta better than a brood of 3 at 12 days. This is principally due, however, to unusually high Tb's recorded for chicks within broods of 3 at the end of the metabolic tests at 30°C. If these Tb's are omitted, the slopes between broods of 2 and 3 are not significantly different. Although isolated individuals demonstrate an endothermic response to 0°C at 12 days, broods of two still maintain Tb above Ta more effectively.

Piñon Jays begin to shiver visibly at 5 days of age, thus demonstrating an early endothermic response. The reason this response was not observed in broods of two or isolated individuals is most likely due to the time when the O₂ fraction was recorded. Young jays may not be able to maintain an endothermic response for an hour during testing at a low Ta, i.e. 0°C. Reduction in heat loss relative to the chick's capacity to produce heat is the most likely reason for the observed differences in the ontogeny of the endothermic response between brood sizes at a given Ta. Marsh (1979) has shown that an increased thermal inertia is important in reducing heat flow by individual nestling Bank Swallows (*Riparia riparia*) prior to the maturation of muscle tissue for shivering thermogenesis. Our data confirm those of earlier studies (O'Connor 1975, Dunn 1976), which showed that the weight of individual chicks at the age of effective homeothermy is lower with increasing brood size. This suggests that a lower surface-volume ratio compensates to some degree for a lack of maturation of heat-producing tissues.

This study should serve as a cautionary notice in extrapolating data on the timing of individual homeothermy and endothermy to ecological problems involving entire broods. Our criterion of an endothermic response maintained for an hour at 0°C for complete endothermy in Piñon Jays is ecologically relevant, as given parents are often absent from the nest for similar lengths of time at similar low Ta's. Because Piñon Jay broods of 3 and 2 differ by 2 days in their ability to withstand 0°C Ta for an hour, female jays may have to attend smaller broods longer. This possibility was suggested by Dunn (1976), but no data have been published to date. There is some evidence, however, to show that this is the case in Starlings (*Sturnus vulgaris*) (Clark unpubl.). Further study should be aimed at examining the implications for adult birds of varying age of effective homeothermy and endothermy according to brood size.

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Geographic Variation in the Juvenal Plumage of the Lesser Nighthawk (*Chordeiles acutipennis*)

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In attempting to identify a series of Lesser Nighthawks (*Chordeiles acutipennis*) collected on the Pacific lowlands of Guatemala, and to ascertain the applicable trinomial to use, I encountered a striking degree of variation among juveniles in the collection of the American Museum of Natural History (AMNH). To evaluate the taxonomic usefulness of the juvenal plumage in the species, additional juveniles were borrowed from the University of Michigan Museum of Zoology (UMMZ), the U.S. National Museum of Natural History (USNM), the Carnegie Museum of Natural History (CM), the Field Museum of Natural History (FMNH), and the Moore Laboratory of Zoology (MLZ). A total of 32 juveniles was available for study. Seven plumage groupings arranged north to south can be recognized among these juveniles (Fig. 1).

C. a. texensis (including *inferior*).—The juvenal plumage of *texensis* is the palest gray with pale, more cinnamon, less ochraceous tippings on the feathers of the crown, interscapulars, and wing coverts. Dorsal feathers have extremely fine vermiculations, i.e. they are much less “blotchy” than in other races. Two juveniles from Lower California (“*inferior*”) are inseparable from 10 of comparable age from Texas, New Mexico, and Arizona. Color phases are not evident in this series of juveniles. *Specimens examined* (13): Baja California, AMNH 87446, 43850; Arizona, AMNH 51993, USNM 268828, 235064, 130577; New Mexico, USNM 365443, 204515; Texas, AMNH 81618–81620, USNM 14013, 18491.

C. a. micromeris.—The dorsal dark markings of the single juvenile specimen seen from the Yucatán Peninsula are coarser than those of the juvenal plumage of *texensis*, contrast more with the paler feather edges than in *littoralis*, and thus differ from both. Dorsally, including the tail, it is grayer, less buffy than *littoralis* but darker than *texensis*. The feather edgings are slightly more buffy, less cinnamon than in *texensis* but less deeply colored than in *littoralis*. *Specimen examined* (1): Yucatán, USNM 130206.

C. a. littoralis.—The four specimens available are uniform and differ from *texensis* in being a darker gray with a generally browner overall cast. The darker barring of dorsal feathers is heavier, more “blotchy,” and edgings of dorsal feathers and coverts are darker, more ochraceous. *Specimens examined* (4): Michoacan, La Placita, UMMZ 130530; Guerrero, Ajuchitlan, MLZ 43446; Oaxaca, Tehuantepec, UMMZ 137450; Chiapas, Arriaga, UMMZ 102227.

C. a. acutipennis.—The nine juveniles from within the range currently assigned to *C. a. acutipennis*, but also including Panamá, include two distinctively different forms:

A. These young are most similar to the young of *littoralis* but are yet darker, having a near sooty appearance, with more extensive and darker, richer, ochraceous-cinnamon feather edgings and tippings, thus giving the appearance of having a deep ochraceous-cinnamon wash over the dorsum. The black blotching is more pronounced, especially on the crown. The crown, mantle, and lesser coverts contrast rather sharply with the paler terials (Fig. 1). *Specimens examined* (4): Panamá, San Carlos, USNM 448729; Colombia, Turbaco, Choco (north coast near Cartegena), AMNH 123261; Venezuela, San Antonio del Golfo, Sucre, AMNH 706096, San Felix, Bolivar, CM 34356.

B. Five juveniles from Colombia, Guyana, and Brazil are much grayer. The ochraceous tipping of dorsal feathers and coverts is reduced, being restricted to the feather tips; it is most pronounced on the crown. The tail barring is dark and light, clear gray lacking a warm cast. The ventral coloration is paler. These specimens differ from juvenile *littoralis* in being darker gray dorsally with far less brown overcast. *Specimens examined* (5): Colombia, Riohacha (base of Guajira Peninsula), CM 78710, 78711; Guyana (British Guiana), La Penetiance (near Georgetown), FMNH 97795; Brazil, Santarém, CM 78612, 78644.

It is not unexpected for specimens from Choco and Panamá to be similar, but the similarity of those