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## PYRAMIDING BEHAVIOR IN THE INCA DOVE: ADAPTIVE ASPECTS OF DAY-NIGHT DIFFERENCES<sup>1</sup>

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*Key words:* Behavior; huddling; Texas; thermo-regulation; dove.

Huddling, primarily at night but occasionally during the day, is well documented as an energy-saving behavior during cold weather in a number of passerines

and nonpasserines, particularly in small and medium-size species (Dorst 1974, Welty 1978). Protected places such as tree holes, rock crevices, and ledges are common huddling sites. A significant increase in efficiency has been demonstrated. Brenner (1965) found an energy saving of 92% in food-stressed starlings huddled in groups of four and Le Maho (1977) noted reductions in fat loss up to 50% in huddled Emperor Penguins. Huddling in rows is common in some dove species (Bent 1932) and a rather exaggerated version, pyra-

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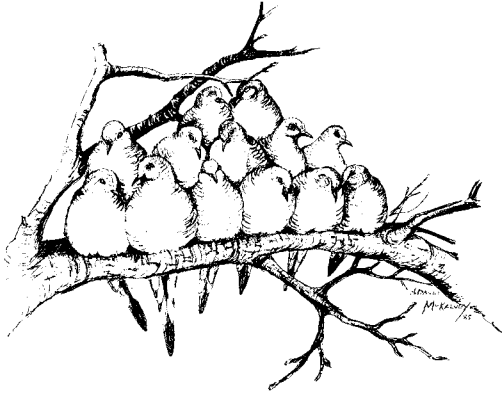


FIGURE 1. A typical pyramidal huddle formed by Inca doves. Drawing by David McKelvey from a photograph.

midging (huddling in tiers) has been noted, without detail, in the Inca Dove, *Columbina inca*, by Breninger (1887) and Johnston (1960). The former recorded a single instance in an Arizona population and the latter described it as occasional behavior in populations in New Mexico. In both cases, pyramiding was observed in roosting birds in the evening or night during cold weather. The potential for energy savings by pyramiding is substantially greater than for simple huddling because 50 to 100% more surface area is protected per individual in a pyramid compared with simple huddling.

Pyramiding was first observed in urban congregations of *C. inca* in San Antonio, Texas, during the senior author's first winter (1977) there and observations continued for seven consecutive winters. The pyramid depicted in Figure 1 is typical: the doves huddled in rows, facing downwind, with feathers fluffed, and positioned on a moderately wide flat perch. Two-row pyramids were formed with a minimum of five birds; three-row pyramids with at least nine doves were observed. The largest pyramid observed contained 12 doves in three rows. Pyramids were dynamic—the outside birds on the bottom row often flew to the top row and then the whole pyramid adjusted for several seconds to a new equilibrium which normally lasted only about 5 min before a new adjustment occurred. Pyramiding behavior lasted for about 1 hr, after which the birds dispersed as a flock to feed. Often, nonhuddling doves were seen within a few feet of the pyramid and there were no obvious differences noted between them and the pyramiding birds. Aggressive behavior was not observed among pyramiding individuals or between pyramiding individuals and nonpyramiding doves.

Birds used the same pyramiding perches over the winter and in subsequent years. Window sills, the roofs of small buildings in yards, and flat, wide branches not more than 3 m above the ground in deciduous trees were common pyramiding sites. On roofs, doves positioned themselves away from bushes that might conceal predators. When in use, these sites were in direct sunlight in wind-protected areas near bird feeders.

In contrast to Breninger (1887) and Johnston's (1960)

observations, we observed pyramids during the day, either in the morning or afternoon. The highest temperature at which a pyramid was seen was  $-6^{\circ}\text{C}$  and the frequency of pyramiding increased with declining temperatures. Doves often huddled in pairs or groups when daytime temperatures were higher than  $6^{\circ}\text{C}$  but below approximately  $15^{\circ}\text{C}$ . Night roosts were usually in small trees or bushes and consisted of individuals roosting singly, in huddled-pairs (the most commonly observed configuration), and/or in loosely knit larger groups (3 to 12) individuals. Pyramiding was never observed in night roosts.

*Columbina inca*, one of the world's smallest doves (approximately 50 g), is primarily a tropical and semi-tropical species (Bent 1932). On the northern edge of its range it lives as a nonmigratory, urban commensal (Quay 1982). First reported in Texas in 1904, it has dispersed as far north as the Dallas region, but is restricted to urban habitats in this state. The small size of this dove, its nonmigratory nature and semi-tropical affinity suggest that it may be particularly vulnerable to cold. During and immediately following unusually cold weather with overnight temperatures below  $-6^{\circ}\text{C}$ , we often found dead or weakened doves. This vulnerability may explain why a species that is so aggressive in the spring and summer (Johnston 1960) has adopted such a cooperative behavioral strategy in the winter. A dove of similar size, *C. passerina*, which is common in rural habitats locally, and two considerably larger doves, *Zenaida asiatica* and *Z. macroura*, which are common to urban and rural habitats in South Texas, are all migratory (Passmore 1981).

There appears to be a paradox in the timing of the pyramiding behavior: the doves pyramid during the warmest portion of the winter's daily temperature cycle and roost alone or loosely huddled when it is relatively colder, and when it would seem that they could conserve the most energy by pyramiding. This paradox may be resolved by considering MacMillen and Trost's (1967) demonstration that *C. inca* exhibits nocturnal hypothermia at low temperatures. Hypothermia as an energy-saving mechanism is incompatible with huddling (Vickery and Millar 1984). However, we suggest that, during particularly cold weather, Inca Doves use these two mechanisms, pyramiding during the day and hypothermia at night, alternately and in sequence on a daily cycle to maximize energy efficiency. A similar situation has been described for wintering *Peromyscus* by Vickery and Millar (1984).

Predation may accentuate the advantages of diurnal vs. nocturnal pyramiding (Weatherhead et al. 1985). Our observations indicate that *C. inca* is particularly vulnerable to diurnal depredations by domestic cats but is relatively secure on its fragile nighttime roosts. Nocturnal torpidity probably does not increase the Inca Dove's vulnerability. In contrast, preferred pyramiding sites are often vulnerable to predators, but this appears compensated for by the higher vigilance of groups. Even though they made numerous attempts, we never observed domestic cats successfully taking prey from pyramiding groups.

On the central plateau in southern Mexico, *C. inca* occurs at an elevation of at least 2,000 m (Robertson, pers. observ.), where they sometimes experience temperatures associated with pyramiding in San Antonio;

however, we do not know if these lower latitude populations respond to cold in the same manner.

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## PRAIRIE FALCON AERIE SITE CHARACTERISTICS AND AERIE USE IN NORTH DAKOTA<sup>1</sup>

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*Key words:* *Falco mexicanus*; *Prairie Falcon*; *North Dakota*; *aerie site characteristics*; *aerie use*; *nesting habitat*.

Stewart (1975) believed that in North Dakota, Prairie Falcons (*Falco mexicanus*) were uncommon and local in the badlands and on adjacent plains along the Little Missouri and Missouri rivers. However, there have been no comprehensive studies of the species in the state. Information about aerie sites will help to identify Prairie Falcon nesting habitat and aid comparison of aerie site characteristics to those in other places.

#### STUDY AREA

This study was conducted from 1982 to 1985 in an 11,250-km<sup>2</sup> area (Fig. 1). Dominant study area features are the Little Missouri River, easily eroded badlands, and large buttes. Mixed-grass prairie is the dominant vegetation. Small areas of short-grass prairie are found in the southwest and on the uplands of the Little Missouri River drainage. A xeric scrub grassland occurs in eroded areas in the extreme southwest (Stewart 1975). Forest covers less than 2% of the land (Jakes and Smith 1982). Ranching and dryland farming are traditional

land uses, but recently there has been increased oil development in the study area.

#### METHODS

An aerie is a cavity in which Prairie Falcons nest or attempt to nest. "Aerie site" or "site" means an aerie and its surroundings. There may be more than one aerie in an aerie site, though each site is occupied by only one pair of Prairie Falcons in a nesting season.

During the nesting season each year, my assistants and I searched for aeries reported to the North Dakota Game and Fish Department or the U.S. Fish and Wildlife Service since 1975. We located seven previously unreported aeries. We determined aerie site and aerie characteristics when banding nestlings or after each nesting season. At each site we measured the length and height of the cliff face, aerie height above the base of the cliff, and aerie dimensions. Five cliffs were estimated to be at least 500 m long. Most aerie shapes were very irregular, so volumes for the natural aeries were estimated to be 75% of the product of the maximum aerie height, width, and depth. Relief, the vertical distance from an aerie to the lowest elevation visible from the aerie cliff, was determined from U.S. Geological Survey 7½' topographic maps. The lowest visible elevation was usually less than 3 km from an aerie. Cliff aspects were assigned to the closest 45° compass bearing. We recorded cliff substrate, aerie placement (e.g., ledge, cavity, on stick nest, etc.), and land uses within approximately 2 km of each aerie. Char-

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