pian Terns (*Hydroprogne tschegrava;* Bergman 1953), Arctic Terns (*Sterna paradisaea;* Cullen 1956), Sandwich Terns (*Sterna sandvicensis;* Veen 1977), and Little Terns (*Sterna albifrons;* Nadler 1976) apparently resemble Least Terns in delaying the nocturnal occupation of their breeding colonies until after the onset of egg-laying and incubation. Tinbergen (1967) hypothesized that off-colony nocturnal roosting prior to egg-laying functioned to reduce predation on adult Common Black-headed Gulls "since the breeding habitat, with its cover, is more dangerous to gulls than are wide open spaces [used for roosting]." Least Terns, however, typically nest and roost in equally open habitats, suggesting that this behavior might also function to lower predation on eggs and juveniles by reducing the period of time that colony locations are subject to discovery by nocturnal predators.

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Development of Formation Flying in Juvenile White Ibises (*Eudocimus albus*)

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Nice (1943) described five stages in the development of altricial birds, beginning with hatching and ending with independence. The first three phases, which involve nestling growth and behavioral development, have been well studied (e.g. Ricklefs 1968, Kushlan 1977); the latter two phases, which encompass the fledgling period, have been relatively little studied. This situation is unfortunate as mortality in birds is high at this time (Lack 1968, Recher and Recher 1969). There are few studies of development

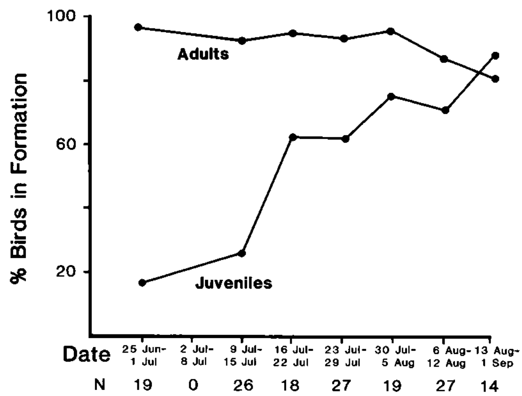

Fig. 1. Percentage of adult and juvenile White Ibises that flew in formation throughout the summer (25 June to 1 September 1984). N represents the number of flocks observed during each interval.

of flight in recently fledged birds, and these few have dealt only with nestlings exercising their wings or making short flights (e.g. Winterstein and Raitt 1983, Thomas 1984). Provine (1984), who studied the ontogeny of flight in domestic chicks, stressed that little is known about how young birds "fine tune" their flight skills. Here, we document the development of flying in tight formations by recently fledged White Ibises (*Eudocimus albus*).

Although it has been proposed that structured flight formations (skeins, V formations, etc.) have behavioral functions (e.g. advertising information centers; Williams et al. 1976, Ward 1978), one benefit of the close association with other birds may be reduced energy expenditure as a result of improved aerodynamics (Storer 1948). For example, Lissaman and Schollenberger (1970) suggested that by flying together rather than separately, 25 birds could increase their flight range by approximately 71%.

White Ibises usually fly in V-shaped formations or skeins, although there is some variation in the shape. Rudegeair (1975) and Heppner (1974) present detailed descriptions and diagrams of flock formations. We observed ibises flying over the North Inlet Marsh 4 km west of Georgetown, South Carolina from 25 June through 1 September 1984. Approximately 20,000 White Ibises breed on Pumpkinseed Island in Winyah Bay about 2 km south of the marsh. In 1984, most juveniles fledged between late June and early July after an approximate 7-week nestling period. Thus, the juveniles that we watched ranged in age from recently fledged individuals (≈7 weeks old) to 16–17-week-old birds. Although some adult and juvenile ibises foraged in the salt marshes at North Inlet, most flew 10–25 km north-northwest from Pumpkinseed Island to forage in freshwater marshes and swamps. All of the flocks we observed probably had been in flight for at least 2 km. Flocks flew at elevations of

TABLE 1. Size and composition of White Ibis flight formations at North Inlet Marsh, South Carolina, during the summer of 1984.

Week no.	Date	Mean flock size[a]	Percentage of adults	Percentage of juveniles
1	25 June–1 July	69.8 (19)	97.9	2.1
2	2–8 July	— (0)	—	—
3	9–15 July	43.0 (26)	88.6	11.4
4	16–22 July	21.7 (18)	86.4	13.6
5	23–29 July	27.6 (27)	91.3	8.7
6	30 July–5 Aug	18.6 (19)	90.9	9.1
7	6–12 Aug	13.5 (27)	85.7	14.3
8	13 Aug–1 Sept	8.8 (14)	59.4	40.6

[a] Number of flocks given in parentheses.

25–500 m, with most at approximately 100 m. For each observation, we counted the number of adult (white plumage with black wing tips) and juvenile (mostly brown plumage dorsally) ibises, and classified each bird as either (1) flying in formation (another ibis was ≤2 m in front and slightly to the side of it), or (2) flying out of formation (another ibis was not ≤2 m in front and slightly to the side of it). By this definition, the "lead" or "point" bird was out of formation. Even if these birds were classified as in formation, our results do not change. Most ibises flying out of formation were >15 m from their nearest neighbor. We counted only those flocks that contained at least one member of both age classes. In more than 64,000 observations of flying ibises, only one juvenile was seen in something other than a mixed-aged flock. We grouped data for analysis into weekly intervals (except for the last interval, which included 20 days) beginning 25 June. During each interval, we observed flocks on 3–6 days. Kendall's rank correlation coefficient (τ) was used to assess the relationship between time (week number) and percentage of adults and juveniles in formation. All tests were two-tailed.

Juvenile ibises increased their tendency to fly in formation during the course of our observations (17.8% of all juveniles in late June vs. 88.0% in late August; $\tau = 0.810$, $P = 0.011$; Fig. 1). The percentage of adults in formation remained relatively stable during the study (Fig. 1), with a slight, but significant, decrease in the mean percentage of adults flying in formation ($\tau = -0.714$, $P = 0.030$). As the number of adults in flocks declined steadily from late June ($\bar{x} = 68.4$) through the end of August ($\bar{x} = 5.2$; $\tau = -0.904$, $P = 0.0028$; Table 1), and as adults were the point birds in the majority of the flocks, at least part of this decline in the percentage of adults flying in formation can be attributed to the smaller number of adults flying in formation in late summer (percentage of adults in formation vs. mean number of adults in flock; $\tau = 0.619$, $P = 0.07$). Kendall's partial correlation coefficient (Siegel 1956) was used to clarify the relationship between the percentage of adults in formation and the flock size. This statistic measured the relationship between the percentage of adults in formation and week number when the other independent variable, mean number of adults in flock, was held constant. There was a significant decrease in the association between percentage of adults in formation and week number when the effect of flock size was partitioned out ($\tau = -0.460$), suggesting that the percentage of adults in formation was not independent of flock size.

The percentage of juveniles in formation was not influenced by their numbers in a flock. The mean number of juveniles in the flock was not related to either week number ($\tau = 0.238$, $P = 0.562$) or percentage of juveniles in formation ($\tau = 0.238$, $P = 0.562$). Therefore, the correlation coefficient for describing the relationship between the percentage of juveniles in formation and week number, when juvenile flock composition was held constant ($\tau = 0.799$), was not different from the original analysis ($\tau = 0.810$). Thus, although adult White Ibises did not vary their tendency to fly in formation, there was a shift in the tendency of juvenile White Ibises to fly in formation.

The high rate of mortality among juvenile birds (Lack 1954), including ciconiiforms (Recher and Recher 1969), indicates the selective pressure for young birds to develop behavioral patterns as rapidly as possible. Juvenile White Ibises developed the ability to fly in formation as frequently as adults within 2 months of their first flight. Because (1) a major portion of this ibis population migrates in the fall (Bildstein et al. 1982), (2) migration is energetically costly (Tucker 1971), and (3) overwintering is a stressful time for birds (Fretwell 1972), the ability to gain the possible aerodynamic advantages associated with flying in formation may be especially important in enabling juvenile ibises to reach adulthood.

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