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Follow Your Elders: Age-related Differences in the Migration Behavior of Broad-winged Hawks at Hawk Mountain Sanctuary, Pennsylvania

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ABSTRACT.—We studied the flocking behavior of adult and juvenile Broad-winged Hawks (*Buteo platypterus*) migrating past Hawk Mountain Sanctuary in eastern Pennsylvania during September 1996 and 1997. Adults were more likely than juveniles to fly in flocks (78% versus 62%). All-juvenile flocks had a mean of 2.0 (±0.0) birds, all-adult flocks a mean of 4.5 (±0.4) birds, and mixed-age flocks had a mean of 4.7 (±0.4) birds. Adults, which made up 68% of all individuals in mixed-age flocks, were the first or "lead" birds in 80% of these flocks. Most (58%) adults migrated in the first, or leading, half of such flocks, and most (68%) juveniles migrated in the trailing half. Overall, our results suggest that migrating juvenile Broad-winged Hawks are more likely to follow adults than vice versa. Following experienced adults may help juveniles in two ways, first by allowing them to find thermals more quickly, and second by enabling them to better navigate to appropriate

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Risks associated with autumn migration differ between juvenile and adult birds, in part because juveniles have far less flight experience, no familiarity with migratory pathways or destinations, and (presumably) less flight ability than do adults. In some species, migrants minimize such differences by traveling in family groups, with adults leading juveniles to important stopover sites and wintering areas (e.g., Sandhill Cranes, *Grus canadensis*; Lovvorn and Kirkpatrick 1982). In other species, at least some juveniles migrate "largely independent" of adults, without the opportunity for following behavior (e.g., White Storks, *Ciconia ciconia*; Berthold 1996). In still other species, individuals migrate south together in large mixed-age flocks, but not necessarily in family groups (e.g., Broad-winged Hawks, *Buteo platypterus*; Goodrich et al. 1996). The extent to which juveniles in the last category of migrants take advantage of the flight and navigational skills of adults is little studied (Kerlinger 1985; Alerstam 1990; Berthold 1993, 1996).

Broad-winged Hawks are relatively small, Western Hemisphere buteos that breed mainly in eastern North America, and winter mainly in southern Central America and central South America (Goodrich et al. 1996). The species' concentrated movements frequently comprise the bulk of visible raptor migration along migration corridors in eastern North America (Kerlinger 1985, Zalles and Bildstein 2000). Broad-winged Hawks use slope and especially thermal updrafts for soaring on their southbound movements. Indeed, most individuals time their departure from North America each autumn to coincide with the occurrence of strong late summer and early autumn thermals (Bildstein 1999).

Unlike most of North America's migratory birds of prey, Broad-winged Hawks typically travel in relatively organized flocks of a few individuals to tens of thousands of birds (Kerlinger 1985, Kerlinger and Gauthreaux 1985, Kerlinger et al. 1985, Goodrich et al. 1996). Flocking in soaring migrants is thought to enhance each individual's ability to find and use thermals quickly and efficiently, and to help in orientation and navigation (Thake 1980; Kerlinger 1985, 1989). Because many—perhaps most—juvenile Broad-winged Hawks have been flying for fewer than 10 weeks before starting their first migration south (Bildstein 1999) and may not be as efficient in soaring flight as adult Broad-winged Hawks (Kerlinger 1989; Agostini 1997; Tabb 1973, 1979), we hypothesized that juveniles would follow adults into and out of thermals. To test this hypothesis, we recorded the behavior of adult and juvenile migrating Broad-winged Hawks flying in relatively linear, head-to-tail flocks while traveling between thermals and updrafts at Hawk Mountain Sanctuary in eastern Pennsylvania, near the beginning of the species' 6000- to 10,000-km southbound migration (Bildstein 1999).

METHODS

We recorded the behavior of adult and juvenile hawks flying past the North Lookout of Hawk Mountain Sanctuary, Kempton, Pennsylvania (40° 58′ N, 75° 59′ W; 464 m ASL) during five days (15–19 September) in 1996 and during 13 days (6–22 September) in 1997, at the time of peak autumn passage for the species (Bildstein 1999). All observations began at 7:30 EST and ended at 17:00 EST, weather permitting, and were restricted to birds that passed close enough to the lookout to allow us to age them by plumage, which represented approximately 20–70% of each day's flight. For birds traveling in flocks (i.e., groups of two or more birds flying in coincidental flight paths ≤75 m of their nearest neighbors, the distance within which birds seemed to coordinate their flight movements and beyond which they did not) the position of each individual was noted in linear sequence within the flock from the "leading" to "trailing" bird. We used chi-square tests for goodness-of-fit or chi-square tests for heterogeneity as appropriate (Sokal and Rohlf 1969), to test for age-related differences in likelihood of flocking and positions within flocks, and for differences in flock size based on the age composition of birds within flocks. All tests were considered significant at alpha level $P = 0.05$.

RESULTS

We observed 1355 adult and 325 juvenile Broad-winged Hawks on 18 days of observations during 1996 and 1997 (Table 1). Adults were more likely to migrate in flocks than were juveniles [78% versus 62%; χ^2 (for heterogeneity) = 34.4, df = 1, $P < 0.01$]. Flock size was 2–26 birds (mean = 4.5 ± 0.2 SE). Mean flock size for all-adult flocks was 4.5 ± 0.4 SE birds; for all-juve-

TABLE 1. Age composition of flocks and single birds and sizes of flocks of Broad-winged Hawks migrating past Hawk Mountain Sanctuary, Pennsylvania, 15–19 September 1996 and 6–22 September 1997.

Flock size	Number of flocks	% Adults	Percent flock type		
			All-adult (n)	All-juvenile (n)	Mixed-age (n)
1	421	71%	71% (299)	29% (122)	—
2	117	72%	54% (63)	9% (11)	37% (43)
3	63	82%	56% (35)	0% (0)	44% (28)
4	21	70%	43% (9)	0% (0)	57% (12)
5	20	83%	60% (12)	0% (0)	40% (8)
6–10	37	86%	41% (15)	0% (0)	59% (22)
11–26	23	94%	61% (14)	0% (0)	39% (9)

nile flocks, 2.0 ± 0.0 SE birds; and for mixed-age flocks 4.7 ± 0.4 SE birds, including 3.2 ± 0.3 SE adults. Although the size distributions of all-adult and mixed-age flocks did not differ significantly [χ^2 (for heterogeneity) = 5.7, df = 5, $P > 0.50$], more than half of these types of flocks consisted of three of more individuals, whereas all-juvenile flocks never exceeded two birds (Table 1). Adults, which comprised 68% of the birds in mixed-age flocks, were the first or "lead" birds in such flocks 80% of the time [χ^2 (for goodness-of-fit) = 6.8, df = 1, $P = 0.01$]. When traveling in mixed-age flocks, most (58%) adults migrated in the leading half of the flock, and most (68%) juveniles migrated in the trailing half of the flock [χ^2 (for heterogeneity) = 30.7, df = 1, $P < 0.01$; Table 2].

DISCUSSION

Our results suggest that juvenile Broad-winged Hawks are slower fliers than adult Broad-winged Hawks, and that juveniles tend to follow adults south on their first autumn migration. Furthermore, our observations indicate that juvenile Broad-winged Hawks are less likely to fly in flocks than are adult Broad-winged Hawks. Several authors have suggested that for soaring migrants, flocking enhances an individual's ability to locate and take advantage of thermals and updrafts (Thake 1980, Kerlinger 1989). In addition, all-juvenile flocks were less than half the size of all-adult flocks and mixed-age flocks, possibly because both juvenile and adult Broad-winged Hawks were more likely to join and flock with adults than with juveniles. Within mixed-age flocks, adults were more likely than expected to be the leading bird in the flock, and adults were more likely to be found in the leading half of the flock, whereas juveniles were more likely to be found in the trailing half of the flock.

Given that long distance raptor migration is energetically costly (Kerlinger 1989), that overwintering can be a stressful time for many raptors (Newton 1979), and that reproductive success in at least some species of raptors is closely tied to physical condition during early spring (Dijkstra et al. 1982), an ability to fly effectively in flocks may be especially important for Broad-winged Hawks. Indeed, there is evidence that such ability does develop rapidly, at least in some species of migrants (Petit and Bildstein 1986). Most of the juvenile Broad-winged Hawks we watched had been capable of flight for fewer than 10 weeks (Bildstein 1999). Whether or not juveniles develop "adult" flocking abilities prior to completing their autumn journey, on their return

TABLE 2. Distributions of adult and juvenile Broad-winged Hawks in mixed-age flocks migrating past Hawk Mountain Sanctuary, Pennsylvania, 15–19 September 1996 and 6–22 September 1997.

Flock size	Number of flocks	Percent adults		Flocks with ≥50%	
		In flocks	Leading flocks	Adults in leading half	Juveniles in leading half
2	43	50%	74%	32	11
3	28	60%	61%	17	11
4	12	48%	83%	10	8
5	8	58%	100%	8	4
6–10	22	77%	100%	21	1
11–26	9	84%	100%	9	1
All flocks	122	68%	80%	97	36

migration north the following spring, or later still, remains an unanswered question. Additional observations at autumn watchsites closer to and within the tropics, and at tropical and temperate locations along spring migration corridors, could help resolve this issue.

Although the extent to which juvenile Broad-winged Hawks depend upon and benefit from following behavior remains unknown, observations of large numbers of juveniles overwintering in Florida, far north of the species main wintering areas in Central and South America, and southeast of the species typical North American migration route (Tabb 1973, 1979; Kerlinger 1989), support the suggestion that juvenile raptors, including broadwings, are more prone to fly off course than are adults (Mueller and Berger 1967a, 1967b; Kerlinger 1989; Agostini 1997). If this is true, the following behavior that we observed may benefit juveniles in two ways, first by helping them locate appropriate atmospheric conditions (i.e., thermal and deflective updrafts) for soaring flight (Kerlinger 1989), and second by leading them to appropriate wintering areas (Alerstam 1990).

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