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# The morphology, flight, and flocking behaviour of migrating raptors

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## ABSTRACT

**Question:** Is there a clear relationship between the morphology of raptors, their styles of flight, and flocking behaviour during autumn migration?

**Methods:** We documented the autumn migration and flocking behaviour of raptors at the Macbride Raptor Migration Research Station in Johnson County, Iowa between 1992 and 2003. We then compared the flocking behaviour of raptors of different species and flight styles. We also compared our results with the predictions of common hypotheses on the evolution of flocking behaviour in birds.

**Conclusions:** Raptors of different species and styles of flight exhibit both unique tendencies to flock and different flock sizes during autumn migration. Raptors that utilize primarily powered flight (falcons, harriers, and accipiters) are less likely to flock and exhibit a smaller flock size than do soaring raptors (buteos and eagles). The 'thermal location and utilization' hypothesis is the only hypothesis on the evolution of flocking behaviour that is generally applicable to the migration of raptors at this mid-western site.

*Keywords*: autumn migration, flight style, flocking behaviour, morphology, raptor.

## INTRODUCTION

The assemblage of raptors that passes almost any site in North America during autumn migration includes a diverse array of species (Heintzelman, 1986; Kerlinger, 1989) that exhibit distinct body types, styles of flight, and flocking behaviours (Kerlinger, 1989). Here we explore the relationship between raptor morphology, flight, and flocking behaviour at a mid-western study site and examine the relevance of common hypotheses on the evolution of flocking behaviour to migrating raptors.

The raptor species commonly observed during autumn migration in most regions of North America can be placed into five body types (Kerlinger, 1989): falcons, harriers, accipiters, buteos, and eagles (Fig. 1). Falcons have high-aspect (long, streamlined, and pointed) wings that provide very good thrust/drag ratios during powered (flapping) flight, and falcons are able to fly quickly over long distances. Harriers also have long wings, but their wings are

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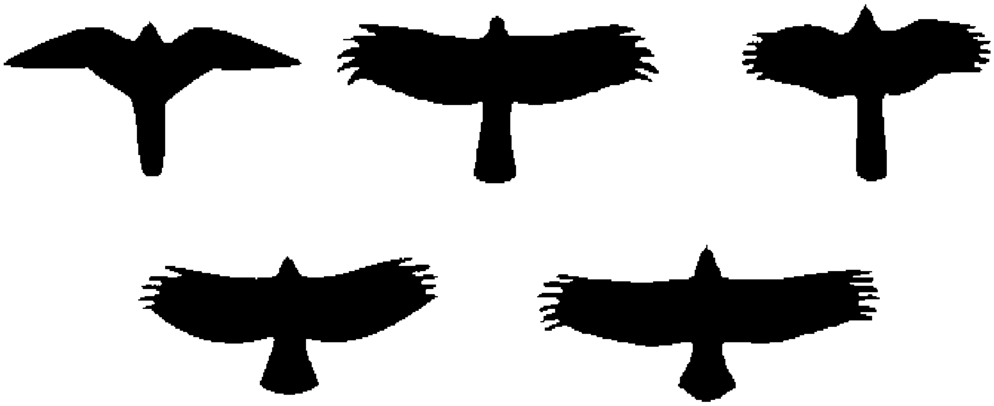

**Fig. 1.** Raptor body types: Top, from left to right: falcon, harrier, accipiter. Bottom, from left to right: buteo, eagle. (Silhouettes courtesy of nps.gov/acad/naturescience/hawkwatch-update-archive-2007.htm)

more intermediate in shape (Kerlinger, 1989) and they are not capable of the high-speed, powered flight of falcons. Accipiters have short, rounded, lower-aspect wings, and long tails that enable them to make sharp turns while pursuing avian prey in forested habitats. Buteos have relatively long, low-aspect, rounded wings, short tails, and intermediate body size. Eagles also have long, low-aspect, rounded wings and short tails, but have large body size. Neither buteos nor eagles are as manoeuvrable as accipiters.

The different body types of these groups of raptors often produce distinct types of flight (Kerlinger, 1989). Although falcons certainly are capable of gliding (including soaring) during migration (Cochran, 1975), they typically have been observed in powered (flapping) flight at our study site; the high-aspect wings of falcons are well suited for fast-powered flight over the open fields of eastern Iowa. Migrating harriers often erratically intersperse relatively long periods of gliding with powered flight; harriers seem to take advantage of both deflected winds and thermal updrafts to glide slowly while migrating and hunting, but utilize powered flight more than soaring. Accipiters are capable of effective powered flight as well as gliding during migration, and often combine regular bouts of flapping and gliding to produce undulating flight (Kerlinger, 1989, 1995). At our study site, falcons, harriers, and accipiters have been observed in powered flight most frequently and have not exhibited soaring flight regularly. Buteos and eagles are limited both in the speed of their powered flight (low-aspect wings) and in their manoeuvrability (short tails), but are effective when gliding, especially soaring in deflected winds and thermals. At our study site, buteos and eagles have been observed soaring most frequently, although they also regularly exhibit powered flight.

The morphology and performance of a bird during flight is a product of natural selection (Kerlinger, 1989). Raptors that can catch prey more effectively and migrate most efficiently will have greater fitness than birds that are less competent predators and migrators. Although individual raptors can change wing and tail shape during flight so that each is capable of all the types of flight that have been described here, the general morphology of a bird greatly affects its performance in flight, including the frequency with which it exhibits different types of flight. The general morphology of raptors also may influence or determine the tendency of individuals of a given species to flock and details of flocking behaviour.

If the morphology of raptors and their typical styles of flight were unrelated to flocking behaviour across species, then the tendency to flock and flock size would be the same for each species and for birds with unique styles of flight (powered vs. soaring). If, however, the morphology of raptors and their flight styles are related to flocking behaviour, then the tendency to flock and flock size should differ across species and flight styles. We expected raptors that utilize primarily powered flight during migration to be less likely to flock and to have smaller flock sizes than raptors that soar extensively while migrating.

Several hypotheses have been proposed that identify the advantages of flocking, and explain the function and evolution of flocking behaviour in birds (Kerlinger, 1989, 1995). These hypotheses include one that is relevant to some groups of birds but does not seem generally applicable to migrating raptors. Four other hypotheses may be appropriate for at least some raptors and are evaluated here. We have identified a single hypothesis that is generally applicable to the migrating raptors at our study site.

## SITE DESCRIPTION AND METHODS

The Macbride Raptor Migration Research Station (MRMRS) was established in 1992 in rural Johnson County, Iowa as a joint venture of Cornell College and the University of Iowa. Researchers observe and document migrating raptors and also trap and band migrants. For many years, MRMRS was one of the few full-time raptor research sites in featureless country; most raptor migration studies are done where geographic features (called leading-lines) – such as mountain ranges, coastlines, and major river systems – funnel migrants from a large area past a single observation point (Mueller and Berger, 1967a; Heintzelman, 1986; Kerlinger, 1989). The MRMRS is located in a gently rolling landscape far from mountains and coasts, and over 60 miles from the Mississippi River.

During most years (1992–1995; 1997–2003), raptor migration was observed from Labor Day until Thanksgiving. Typically, raptors were identified and recorded passing MRMRS from about 09.00 h until about 15.00 h daily. When a migrant was first observed, we determined and recorded the species, age, and sex of each individual when possible. We also recorded whether each migrant was alone or part of a single species flock; if multiple individuals were migrating together, we recorded their flock size. Our criteria for recognizing a flock included whether the individuals: (1) were in close proximity to one another; (2) utilized the same updrafts; (3) interacted during flight; (4) maintained the same direction during their migration past our site; and (5) changed direction or altitude together during the time they were observed. Sometimes individuals of the same species were visible simultaneously but not considered to be part of a flock because the flight of each individual appeared to be unrelated to that of other birds of that species. We did not record information on mixed-species flocks.

We considered the proportions of observations that we made of a species or birds that exhibited a unique flight style (powered vs. soaring) that were of single birds and flocks to reflect the tendency of individuals of each species or flight style respectively to flock. We compared the proportion of observations that were of single birds and flocks across species and flight styles using the Pearson chi-square test. We then compared flock size across species and birds that utilized different flight styles respectively using a Kruskal-Wallis test. In the comparison of flock size across species, we only analysed species in which we had observed flocks more than nine times.

## RESULTS

Raptor migration rates at MRMRS are lower than those documented at leading-line migration sites, but the general assemblage of migrants documented at MRMRS is quite similar to that observed at leading-line sites in the mid-western and eastern United States (R.W. Black *et al.*, in preparation). We observed individuals of about a dozen species each fall (Table 1), but most of these birds were members of just five species: sharp-shinned hawks (*Accipiter striatus*), Cooper's hawks (*Accipiter cooperii*), broad-winged hawks (*Buteo platypterus*), red-tailed hawks (*Buteo jamaicensus*), and bald eagles (*Haliaeetus leucocephalus*). The assemblage of migrants also included American kestrels (*Falco sparverius*), merlins (*Falco columbarius*), peregrine falcons (*Falco peregrinus*), northern harriers (*Circus cyaneus*), goshawks (*Accipiter gentilis*), red-shouldered hawks (*Buteo lineatus*), and rough-legged hawks (*Buteo lagopus*) most years, but in lower numbers.

Most observations of migrating raptors at MRMRS are of single individuals, although flocks of over 500 birds have been recorded. Both raptor species and raptors that utilized different flight styles varied significantly ($\chi^2 = 848.4$, d.f. = 12, $P < 0.001$; $\chi^2 = 271.5$, d.f. = 1, $P < 0.001$) in the frequency at which single birds and flocks were observed (Tables 2 and 3). Species that utilized primarily powered flight (falcons, harriers, and accipiters) generally migrated as single individuals and were rarely observed in flocks, but soaring raptors – buteos and eagles (especially *B. platypterus* and *H. leucocephalus*) – were frequently observed in flocks. Furthermore, flocks included as many as 90% of the individuals of certain species (especially *B. platypterus*) observed during some years, but less than 5% of the individuals of other species (including *F. columbarius*, *F. peregrinus*, *A. cooperii*, and *A. gentilis*). In general, flocking was not commonly observed in species that exhibited primarily powered flight during migration, but was more likely in species that relied upon gliding (especially soaring) during migration.

Raptor species and raptors that utilized different flight styles also varied significantly (Kruskal Wallis $H = 356.0$, d.f. = 5, $P < 0.001$; $H = 78.6$, d.f. = 1, $P < 0.001$ respectively) in flock size (Tables 4 and 5). Flock size was dramatically greater in *B. platypterus* than in

**Table 1.** Summary of fall migration at Macbride Raptor Migration Research Station

| Year | No. species observed | No. individuals observed | Most frequent species and (% of total assemblage) |
|---|---|---|---|
| 1992 | 8 | 1381 | Bp (25.4); Bj (24.6); Hl (6.1); As (4.1); Ac (3.5) |
| 1993 | 11 | 1083 | Bp (49.6); Bj (25.5); As (10.2); Hl (7.1); Ac (5.4) |
| 1994 | 12 | 1806 | Bj (37.5); Bp (29.5); As (18.5); Hl (8.1); Ac (3.7) |
| 1995 | 13 | 942 | Bj (46.7); As (21.2); Bp (13.2); Ac (11.7); Hl (4.9) |
| 1997 | 12 | 1100 | Bj (33.7); Bp (25.3); As (24.3); Hl (6.7); Ac (4.0) |
| 1998 | 10 | 4552 | Bp (86.4); Bj (7.7); As (3.0); Ac (1.1); Hl (0.9) |
| 1999 | 13 | 1029 | Bj (40.7); As (21.8); Bj (21.5); Ac (8.3); Hl (4.0) |
| 2000 | 13 | 1248 | Bj (38.5); As (24.7); Bp (17.1); Ac (7.8); Hl (5.0) |
| 2001 | 13 | 1568 | Bp (58.5); Bj (16.7); As (15.6); Ac (5.0); Hl (2.1) |
| 2002 | 13 | 1263 | Bp (36.0); As (23.5); Bj (21.8); Hl (9.2); Ac (5.8) |
| 2003 | 11 | 1974 | Bp (41.1); Bj (25.0); As (18.1); Hl (7.4); Ac (6.4) |

*Note*: Bp = *Buteo platypterus*; Bj = *Buteo jamaicensus*; Hl = *Haliaeetus leucocephalus*, As = *Accipiter striatus*; Ac = *Accipiter cooperii.*

**Table 2.** The tendency of raptors to be observed as single birds or in flocks

| Species | % observations that were single birds | % observations that were flocks | Total no. observations |
|---|---|---|---|
| *Accipiter cooperii* | 96.3 | 3.7 | 806 |
| *Accipiter gentilis* | 96.7 | 3.3 | 30 |
| *Accipiter striatus* | 91.4 | 8.6 | 2310 |
| *Aquila chrysaetos* | 93.8 | 6.2 | 16 |
| *Buteo jamaicensus* | 85.4 | 14.6 | 3672 |
| *Buteo lagopus* | 100.0 | 0.0 | 30 |
| *Buteo lineatus* | 100.0 | 0.0 | 23 |
| *Buteo platypterus* | 51.8 | 48.2 | 709 |
| *Circus cyaneus* | 98.6 | 1.4 | 141 |
| *Falco columbarius* | 97.1 | 2.9 | 68 |
| *Falco peregrinus* | 100.0 | 0.0 | 39 |
| *Falco sparverius* | 89.7 | 10.3 | 87 |
| *Haliaeetus leucocephalus* | 80.4 | 19.6 | 684 |
| All | 85.4 | 14.6 | 8615 |

**Table 3.** The tendency of raptors with different flight styles to migrate as single birds or in flocks

| Flight style | % observations that were single birds | % observations that were flocks | Total no. observations |
|---|---|---|---|
| Powered flight | 93.0 | 7.0 | 3481 |
| Soaring | 80.2 | 19.8 | 5134 |
| All | 85.4 | 14.6 | 8615 |

**Table 4.** Summary of flock size across raptor species

| Species | Range in flock size | Mean flock size | No. flocks observed |
|---|---|---|---|
| *Accipiter cooperii* | 2 | 2.0 | 30 |
| *Accipiter striatus* | 2–6 | 2.2 | 199 |
| *Buteo jamaicensus* | 2–10 | 2.4 | 537 |
| *Buteo platypterus* | 2–850 | 23.9 | 342 |
| *Falco sparverius* | 2–4 | 2.6 | 9 |
| *Haliaeetus leucocephalus* | 2–7 | 2.4 | 134 |

*Note*: This summary includes only those species in which more than nine flocks were observed.

**Table 5.** Summary of flock size across raptor flight styles

| Flight style | Range in flock size | Mean flock size | No. flocks observed |
|---|---|---|---|
| Powered flight | 2–6 | 2.2 | 243 |
| Soaring | 2–850 | 9.6 | 1014 |

*Note*: This summary includes only those species in which more than nine flocks were observed.

other raptor species, and flock size was greater in soaring raptors than in birds that utilized primarily powered flight.

## DISCUSSION

Autumn raptor migration past our study site involves the same general assemblage of species that has been documented in migration past other mid-western or eastern study sites. But the migration rates documented at MRMRS are lower than those observed at lead-line sites. Raptor migration in featureless country probably occurs as a broad, somewhat diffuse front, rather than as a concentration of individuals funnelled by observation points at leading lines.

We have determined that raptor body type, flight style, and flocking behaviour are related and vary across the species and related groups of raptors that migrate through eastern Iowa. Raptors with high- or intermediate-aspect wings, which relied primarily upon flapping flight during autumn migration, rarely flocked. When they did, they formed small flocks. In contrast, raptors with lower-aspect wings that utilized primarily gliding, especially soaring, during migration were much more likely to flock and some (especially *B. platypterus*) exhibited large flock sizes.

At least five hypotheses have been presented in the literature to explain the function and evolution of flocking in birds (Kerlinger, 1995). The 'aerodynamic efficiency' hypothesis claims that birds can fly more efficiently when arranged appropriately in flocks than when flying alone (Kerlinger, 1995). Individuals that migrate in flocks with fixed distances and angles between birds may have an aerodynamic advantage over individuals that migrate alone or in less structured flocks. Trailing birds in particular may experience reduced drag due to the wing-tip vortices created by the flapping flight of the bird ahead of it (Kerlinger, 1995). Many flocking raptors, however, utilize gliding and soaring flight, and neighbours in a flock of soaring birds are not as likely to receive this advantage. Furthermore, flocking raptors generally do not migrate with fixed distances and angles between neighbours. Indeed, *B. platypterus* individuals change their position within the flock frequently.

The 'detecting predators' hypothesis suggests that birds in a flock are more likely to be aware of and avoid predators than single individuals, simply because there are many more eyes scanning for predators in flocks (Kerlinger, 1989). Although some small hawks may be vulnerable to predation by other raptors (Klem *et al.*, 1985; Kerlinger, 1989), most mid-sized and large raptors seem to be relatively free of daytime predation after fledging. This hypothesis, then, is not generally applicable to the entire assemblage of migrating raptors at most sites.

The 'foraging' hypothesis suggests that individual birds may forage more efficiently when in flocks than when foraging alone (Kerlinger, 1989). If prey are patchily distributed and locally abundant, the individuals of a flock may be more likely to discover valuable food patches when flock mates locate food than if they were foraging alone. This hypothesis may apply to those raptor species that rely upon local patches of insect prey (Kerlinger, 1989), but this relatively small subset of migrating raptor species does not include any that are common in the mid-western United States. Furthermore, one of the most common raptors to migrate in flocks in the eastern and mid-western United States, *B. platypterus*, may fast during migration (Smith *et al.*, 1986) and thus cannot receive any foraging-related benefits from flocking.

The 'orientation/navigation' (or 'route-finding') hypothesis suggests that groups of migrants may be more likely to orient or navigate effectively than individuals. In species where lifespans can be long, many individuals in a large flock are likely to be experienced migrators and may serve as effective guides or leaders for the flock. It also may be that the migration pathways produced by averaging the navigational abilities of the individuals of the flock effectively reduce the significance of errors made by single birds (Kerlinger, 1989). The advantages of leaders within a flock probably are highest in mixed-age flocks and there is some evidence that older birds do lead flocks in migrating *B. platypterus* (Heintzelman, 2004). Other migrating raptor species, however, exhibit differential migration in which experienced and inexperienced birds migrate at different times (Mueller and Berger, 1967b; Haugh, 1972; Geller and Temple, 1983; Hoffman, 1985; Kerlinger, 1989). In such species, including at least two common migrants at our study site (*B. jamaicensus* and *A. striatus*), experienced individuals cannot show less experienced birds the migration route.

Powered flight is far more energetically expensive than soaring. The 'thermal location and utilization' hypothesis (Kerlinger, 1989, 1995) suggests that the individuals of a flock not only can locate thermal updrafts more efficiently than single birds, but that birds may conserve significant resources by soaring in thermals instead of utilizing powered flight. A member of a flock could easily monitor the behaviour of flock mates, and move to thermals that were discovered by other birds. Furthermore, an individual soaring in a thermal could easily monitor the ascent rates of neighbours and then adjust its position within the flock to take best advantage of the strongest thermals. These advantages accrue both to individuals in flocks as small as two and to birds in very large flocks.

Of these five hypotheses, only the 'thermal location and utilization' hypothesis offers a good, general explanation of the flocking behaviour exhibited by migrating raptors at our study site. The species that flock most frequently and with the greatest flock sizes at our site (*B. platypterus*, *B. jamaicensus*, *H. leucocephalus*) all utilize primarily soaring flight, the type predicted by this hypothesis. Furthermore, our observations of flock formation in updrafts (both thermals and deflected winds) coincide well with the predictions of this hypothesis. Once one or a few individuals discovered and began to utilize an updraft by circling within it and gaining altitude, other birds flew to that updraft and also began soaring within it. Soon the updraft was utilized by more individuals than the initial bird(s). Members of the flock continued to climb until they reached the top of the updraft, then they glided to the south. Individuals of one species, *B. platypterus*, were very active within the flock, changed positions frequently, and sometimes climbed very rapidly when they located the strongest updrafts; these birds demonstrated the very behaviour predicted by this hypothesis.

The relationships described here between raptor morphology and styles of flight are consistent with those described by some authors but differ somewhat from those documented by others (Cochran, 1972, 1975, 1985). It is important to remember that individuals of each raptor species are capable of all types of flight (powered, undulating, and gliding/soaring), but probably utilize the type that provides the greatest advantage under a given set of conditions. Observations of flight made in different locations that have distinct conditions may well be unique. Similarly, only one of the hypotheses of flocking behaviour in birds is generally applicable to the assemblage of migrant raptors at our study site, but other hypotheses may be appropriate under the different conditions present at other sites.

The results of this study add to a growing body of evidence that animals often benefit by being alert to the distribution and behaviour of conspecifics. Just as great blue herons (*Ardea herodias*) achieve higher feeding rates when they forage in areas that already contain foraging herons than in areas that lack herons (Krebs, 1974), soaring raptors are more likely to migrate efficiently when they soar in thermals that already are being used by other birds than when they fly alone. 'Public information' gleaned from conspecifics may benefit individual animals in many ways, including during feeding, foraging while at risk of predation (Valone and Templeton, 2002), during mate choice (Nordell and Valone, 1998), as well as in efficient migration.

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## REFERENCES

Cochran, W.W. 1972. A few days of fall migration of a sharp-shinned hawk. *Hawk Chalk*, **11**: 39–44.

Cochran, W.W. 1975. Following a migrating peregrine from Wisconsin to Mexico. *Hawk Chalk*, **14**: 28–37.

Cochran, W.W. 1985. Ocean migration of peregrine falcons: is the adult male pelagic? In *Proceedings of the Fourth Hawk Migration Conference* (M. Harwood, ed.), pp. 223–237. Rochester, NY: Hawk Migration Association of North America.

Geller, G.A. and Temple, S.A. 1983. Seasonal trends in body condition of juvenile red-tailed hawks during autumn migration. *Wilson Bulletin*, **91**: 625–626.

Haugh, J.R. 1972. A study of hawk migration in eastern North America. *Search*, **2**: 1–60.

Heintzelman, D.S. 1986. *The Migrations of Hawks*. Bloomington, IN: Indiana University Press.

Heintzelman, D.S. 2004. *Hawks and Owls of Eastern North America*. New Brunswick, NJ: Rutgers University Press.

Hoffman, S.W. 1985. Autumn Cooper's hawk migration through northern Utah and northeastern Nevada, 1977–1982. In *Proceedings of the Fourth Hawk Migration Conference* (M. Harwood, ed.), pp. 207–218. Rochester, NY: Hawk Migration Association of North America.

Kerlinger, P. 1989. *Flight Strategies of Migrating Hawks*. Chicago, IL: University of Chicago Press.

Kerlinger, P. 1995. *How Birds Migrate*. Mechanicsburg, PA: Stackpole Books.

Klem, D., Hillegass, B.S. and Peters, D.A. 1985. Raptors killing raptors. *Wilson Bull.*, **97**: 230–231.

Krebs, J.R. 1974. Colonial nesting and social feeding as strategies for exploiting food resources in the great blue heron (*Ardea herodias*). *Behaviour*, **51**: 99–134.

Mueller, H.C. and Berger, D.D. 1967a. Wind drift, leading lines, and diurnal migrations. *Wilson Bulletin*, **79**: 50–63.

Mueller, H.C. and Berger, D.D. 1967b. Fall migration of sharp-shinned hawks. *Wilson Bulletin*, **79**: 397–415.

Nordell, S.E. and Valone, T.J. Mate choice copying as public information. *Ecol. Lett.*, **2**: 74–76.

Smith, N.G., Goldstein, D.L. and Bartholomew, G.A. 1986. Is long-distance migration possible for soaring hawks using only stored fat? *Auk*, **103**: 607–611.

Valone, T.J. and Templeton, J.J. 2002. Public information for resource assessment: a widespread benefit of sociality. *Phil. Trans. R. Soc. Lond. B*, **357**: 1549–1557.