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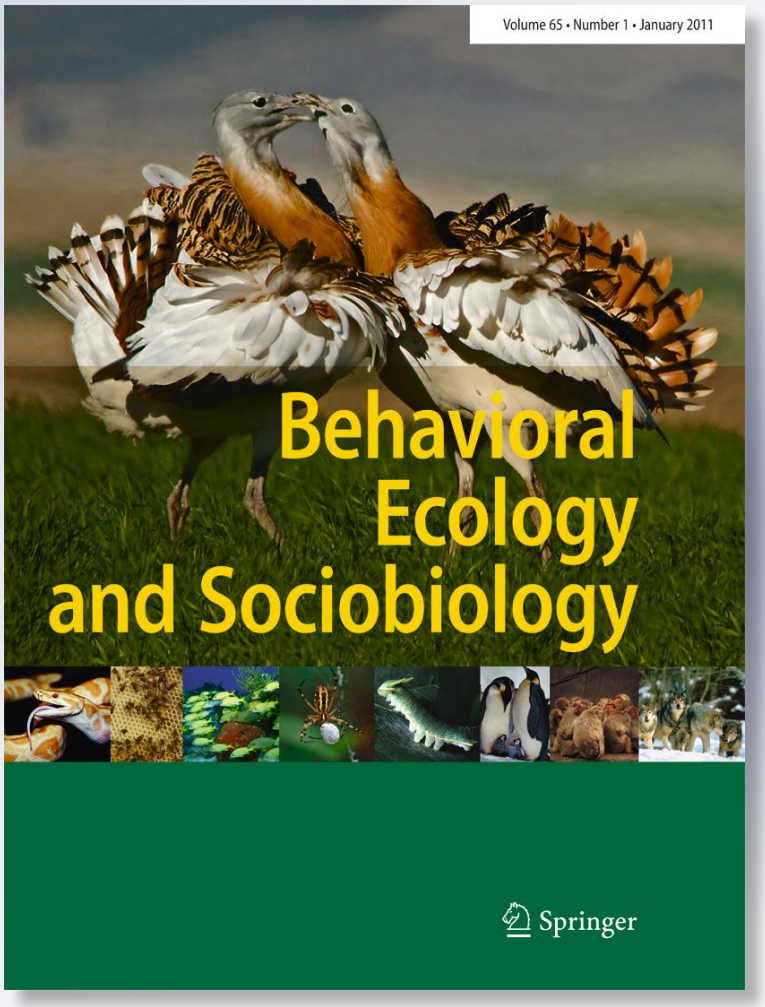

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ORIGINAL PAPER

The fly-and-social foraging hypothesis for diurnal migration: why American crows migrate during the day

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Abstract Most migratory species migrate at night, and the benefits associated with nocturnal migration have been well reviewed; however, less attention has been paid to the benefits associated with diurnal migration. There are two theories for diurnal migration: (1) diurnal migration allows for the use of thermals and therefore reduces energy loss, and (2) the fly-and-forage hypothesis, which suggests that diurnal migrants can search for prey and forage as they migrate. We investigated whether American crows (*Corvus brachyrhynchos*) engage in the fly-and-forage strategy of diurnal migration as they migrated north in the spring. We tracked eight radio-tagged crows as they migrated hundreds of kilometers in the spring to determine if they were diurnal migrants, whether they migrated with conspecifics, whether they stopped to forage, and if they did stop, whether they forage with conspecifics. All crows migrated during the day, and while on several occasions crows were seen migrating in close association with conspecifics, all crows were also observed migrating alone. On average, crows migrated approximately 300 km the day they left their wintering grounds, and over the course of this day, they stopped twice and foraged at these locations for 35 min. On all but one occasion, the stops made during migration were to forage with groups of conspecifics. While the fly-and-forage hypothesis for diurnal migration has primary been applied to raptors, many diurnal migrants forage socially, and the presence of foraging conspecifics and/or heterospecifics may be a significant benefit in locating food resources and ultimately migrating during the day.

Keywords American crow · Communal roost · Conspecifics · Diurnal migration · Social foraging

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Introduction

Avian migration has fascinated humans for centuries, and hundreds of studies have been conducted to understand why, when, and how birds engage in these amazing feats. While many of these studies have been directed at species that migrate at night, the reason certain species migrate during the day has received less attention (Alerstam 2009). Generally, there are two hypotheses for diurnal migration: (1) diurnal migrants, such as raptors that soar, use thermals in order to reduce the energetic cost of migration (Kerlinger 1989), and (2) species exhibit fly-and-forage migration in order to take advantage of foraging opportunities while migrating (Strandberg and Alerstam 2007; Alerstam 2009). In addition, there are species that migrate day and night, and these migrations are often associated with migration over inhospitable landscapes (e.g., oceans, deserts; Gill et al. 2009).

One of the difficulties in understanding migration is the logistical challenge of documenting behaviors during migration. To date, most studies documenting the behavior of individuals as they migrate from one location to another have used Global Positioning System (GPS) satellite telemetry units (Strandberg and Alerstam 2007) or geolocators

(Stutchbury et al. 2009). These tools provide data on where an individual is at a particular point in time during the migration process. These data can illustrate how, for example, an osprey (*Pandion haliaetus*) may alter its migration to migrate over a lake in search of fish (see Strandberg and Alerstam 2007) or marsh harriers (*Circus aeruginosus*) alter their routes to take advantage of rich foraging areas (Strandberg et al. 2008). From these studies, the fly-and-forage hypothesis for diurnal migration has been proposed (Standberg and Alerstam 2008; Klaassen et al. 2008; Alerstam 2009). This hypothesis has both quantitative support from satellite tracking of raptors and qualitative support from field observation of swallows and raptors foraging as they migrate. However, there is another suite of diurnally migrating species that do not forage while flying, like swallows, or actively hunt prey when flying, like raptors, but may benefit from diurnal migration by being able to use social cues (i.e., conspecifics foraging at a location) to locate resources.

There are several species of diurnal migrants that are known to forage socially, for example turkey vultures (*Cathartes aura*; Prior and Weatherhead 1991), American white Pelicans (*Pelecanus erythrorhynchos*; Mcmahon and Evans 1992), rooks (*Corvus frugilegus*; Henderson and Hart 1991), mallards (*Anas platyrhynchos*; Pöysä et al. 1998), sandhill cranes (*Grus canadensis*; Sparling and Krapu 1994), American crows (*Corvus brachyrhynchos*; Verbeek and Caffery 2002), and barn swallows (*Hirundo rustica*; Fujita and Higucki 2005). Many of these species may also be taking advantage of thermals while migrating during the day (e.g., vultures), but the presence of conspecifics or heterospecifics in an area may indicate foraging opportunities (Thomson et al. 2003). Many of these diurnal migrants are feeding on spatially and/or temporally variable resources. For example, vultures and corvids are taking advantage of carrion, while waterfowl have specific habitat requirements that may be rare across the landscape. Therefore, we are proposing that these species use a fly-and-forage strategy during diurnal migration in order to take advantage of the presence of conspecifics to locate foraging opportunities. Migration during the day may be beneficial for many species, as an individual can both migrate toward their destination and use social cues from conspecifics and/or heterospecifics to find foraging opportunities.

While it is interesting that some diurnal migrants such as waterfowl, wading birds, and corvids are known to forage socially, direct observations of behaviors during migration are needed. Satellite telemetry is a great tool for tracking individuals over large geographic areas, but direct observations are needed to investigate whether these species are foraging socially during migration. In order to address this question, we manually tracked radio-tagged American crows during spring migration to determine how often these individuals engaged in social foraging while migrating, as well as how often they roosted communally. American crows are by all accounts diurnal migrants (Good 1952; Graber et al. 1987), although it does not soar or engage in tradition fly-and-forage strategies (i.e., hunting for prey or capturing aerial insects). While the species is a partial migrant, in the northern, interior portion of its range, where this study was conducted, most crows are migratory. In the winter, American crows are very social, engaging in foraging flocks and communal roosts (Graber et al. 1987). The primary food sources in winter and early spring are waste agricultural products, human garbage, and carrion. This study investigated the behavior of migrating American crows, but more specifically: (1) What time of day do they migrate?, (2) Do they migrate with conspecifics?, and (3) Do they engage in sustained long-term flights or stop periodically and forage with conspecifics? Finally, we discuss our observations of migrating crows in the context of how social foraging may influence the migration strategies of not only crows but also other diurnal migrants.

Methods

In the first 3 weeks of February between 2004 and 2009, we captured American crows in Champaign and Vermilion Counties in east-central Illinois. Crows were captured using Australian crow traps (Kalmbach and Aldous 1940), primarily while feeding in agricultural areas. Upon capture, crows were aged, weighed using a Pesola spring scale, banded with the US Geological Survey leg bands, and fitted with 2-g radio-transmitters (JDJC Corp. Fisher, IL). Because of the limited number of transmitters and the need to distinguish migrant from resident crows, we attached transmitters to relatively heavy (>500 g) individuals. We also only used adult crows in the study. Transmitters were mounted to the rachis of the central tail feather using sutures and epoxy. The average battery life of a radio-transmitter was 3 months. We tracked radio-tagged crows using vehicles with mounted antennas, and in order to assist in tracking the crows, we used an Automated Radio Telemetry System (ARTS; Cochran and Lord 1963). The use of ARTS and tracking vehicles allowed us to stay in nearly constant contact with radio-tagged crows. We continuously tracked crows from the last week of February through the third week of March from 2004 to 2009. Because of the enormous amount of time associated with tracking crows, we only attempted to track one or two crows each year. The location of a crow's roost was determined every day, and at dawn, the crow was tracked manually to determine if it migrated from or simply foraged in the local area. For crows in and around Champaign–Urbana (~10 km radius area), the ARTS system could not

detect the bird when it was on the ground foraging, although it could detect the bird once it flew and was a few meters above the ground; therefore, we could remotely monitor the crows to determine when an individual was engaged in flights that were longer than necessary to move to a new foraging area. If the bird was flying, we could use ARTS to provide a bearing and, thus, help us determine where to begin searching for the crow with the tracking vehicle. Migrating crows can be detected from a tracking vehicle at a distance of approximately 20 km (A. Raim, unpublished data). Once the crow engaged in sustained flight or in a direction not consistent with known foraging locations, the driver of the tracking vehicle would attempt to stay within visual contact of the crow and at least within the range the transmitter could be detected. The migrating crow's track was recorded using a vehicle-mounted GPS unit. When the crow could be seen, the error rate (difference between the GPS location and the actual location of the crow) was less than 2 km, and when the crow was out of sight, the driver of the vehicle would move the antenna in order to localize the direction of the transmitter. The amplitude of the radio signal can vary based on the height of the bird and topography, and the estimated location of migrating crows was at least within 5 km of the actual location. Crows were tracked until either the transmitter signal could not be detected or behavioral observations suggested that the individual was on its breeding grounds (e.g., seen building a nest or remained in the area for at least a week).

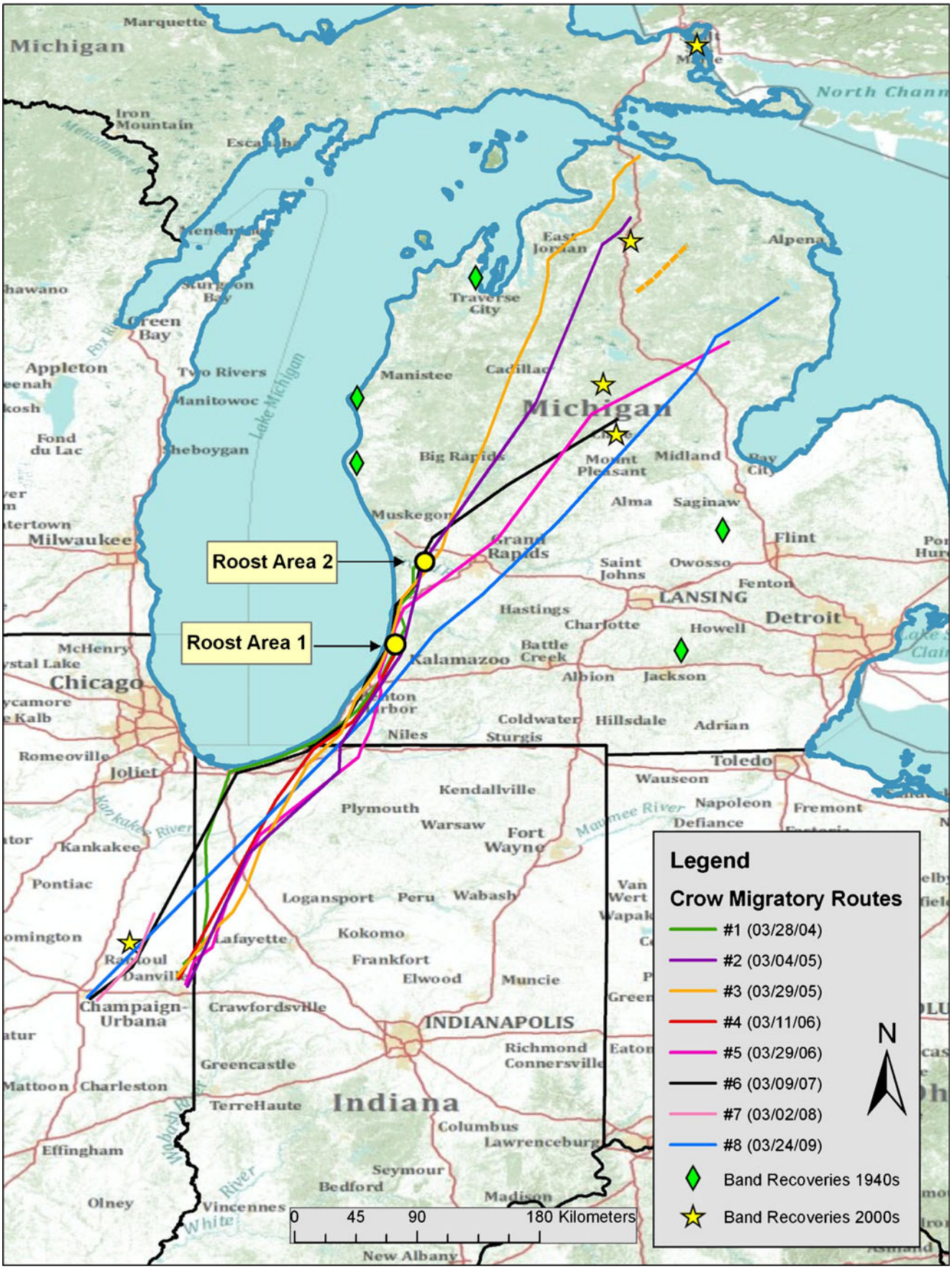
We recorded behavioral observations while the crow was migrating or when it landed. When crows were migrating, we recorded the number of conspecifics migrating with them; we considered birds to be migrating together if they were flying in the same direction and within approximately 100 m of each other. When the crows landed, we noted whether or not they were foraging and if so, with how many conspecifics or heterospecifics. In the evenings, the location of the crow's roost was determined, and at sunrise, the roost was identified as a communal or solitary roost. We considered communal roosts to have at least ten conspecifics in the same tree or adjacent trees to the radio-tagged crow.

On several occasions, we were able to determine crows' flight speeds. This was done by tracking the crow from one known location to another location while recording the time. We assumed a straight line of flight which is likely not the case; thus, this is a conservative flight speed estimate. We only used flight speeds that were determined over a distance of at least 30 km. Because migratory behavior can evolve quickly (Berthold et al. 1992), we used band recoveries from a study in east-central Illinois in the 1930s and 1940s (Black 1941) to investigate if 60 years prior, crows wintering in east-central Illinois were migrating through or nesting in the same locations they are today.

Results

We captured 19 crows and put ten transmitters on crows that weighed more that 500 g; average crow mass in late February and early March is 494.5 g (SE=10.7 g), and the average mass of radio-tagged crows was 529.4 g (SE=10.8 g). Of these ten crows, nine migrated, and one bred in the area. Of the nine crows that migrated from the area, we were able to track eight as they migrated north in the spring; one crow departed, and we were not able to relocate or track it. Two of the eight crows were lost before they reached their breeding grounds (Fig. 1). All of the nine crows departed from a communal roost and migrated during the day; there was no indication that these crows migrated in flocks. We observed all migrating crows at least once and often several times migrating by themselves, although other crows were also seen flying with them at various times (Table 1). All crows left in the morning; however, three of the eight left the communal roost and fed with conspecifics in agricultural field or landfills before migrating later in the morning (Fig. 2, Table 1). All eight crows migrated to the north at a bearing of approximately 25°. The crows migrated on average 6 h 19 min on their first day of migration. All eight crows migrated either along Lake Michigan or within sight of the Lake (<5 km) without flying over it. Six of the eight crows were tracked to what was presumed to be their breeding grounds; two were seen building nests, and the other four were observed in courtship displays and did not move from the area for at least a week to 10 days. Of the two crows that were lost while tracking, we lost one after tracking it for 4 h, while we tracked the other for 3 days and lost it as it crossed Lake Huron, presumably continuing north to breed in the Upper Peninsula of Michigan or Canada. Of the seven individuals, we tracked for at least a full day their distance from roost location to roost location that ranged from 178 to 490 km (Fig. 1). All crows roosted at communal roosts while migrating, and crow numbers 1, 4, and 8 all roosted in communal roosts within 8 km of each other in 2004, 2005, and 2009, respectively (Fig. 1; roost area 1). Crow numbers 2, 3, and 6 all roosted in another location within 10 km of each other in early March 2005, late March 2005, and 2007, respectively (Fig. 1; roost area 2). When crows reached their presumed breeding grounds, they roosted by themselves or with one or two conspecifics.

On average, crows stopped to forage twice per day while migrating; these foraging stops ranged from 5 to 82 min, but were on average 35.4 min long. Of the 17 times that a crow was observed shortly after landing until it departed, in all but one situation, they were in the company of other foraging crows. The number of other crows ranged from 1 to >60. On seven occasions, crows



◀ **Fig. 1** Migratory routes of American crows wintering in east-central Illinois and the location of recoveries of crows banded in winter in east-central Illinois

were observed foraging with common ravens at carcasses. This was only observed in Michigan, as the raven's range does not extend south of central Michigan. It is likely that a few short foraging stops were missed, as on nine occasions a crow's radio signal was lost for 8 to 19 min. When a signal is lost, it is usually due to a bird landing in a valley or near buildings, which attenuates the signal. It is possible that these crows landed and quickly departed before we were able to locate them and record their behavior.

On ten occasions, we were able to estimate flight speeds of three different crows; their flight speed ranged from 29.3 to 60.4 km/h, with an average speed of 43.9 km/h. Given recoveries of crows banded during this study and previous studies (Fig. 1), most breeding areas are more than 500 km from crows' wintering sites. None of the crows we tracked in the current study migrated 500 km in a single day, and most migrated the farthest on the first day they left their wintering grounds (Fig. 3).

Discussion

Our study supports the hypothesis that American crows employ a fly-and-forage strategy when migrating and that when foraging during migration they forage socially. This diurnal migration strategy allows crows to take advantage of social foraging opportunities along their migratory route. While migrating individuals did not initiate migration with a large number of conspecifics, on every occasion but one, the migrating crow was observed foraging with conspecifics and on some occasions with congeners. These observations coupled with the fact that crows roosted communally every night during migration highlight the sociality of the species; however, the decision on whether or not to migrate and where to migrate appears to be an individual decision. For species, such as crows, the traditional benefits of nocturnal migration—better migratory conditions at night, more time during the day to forage, avoidance of predators, and use of orientation cues such as sunset and stars (Kerlinger and Moore 1989; Lank 1989)—may not outweigh the benefits of using the presence of conspecifics to locate food and roosting sites while migrating during the day.

While currently crows are commonly observed to be feeding in agricultural fields and urban areas, historically, their primary food source was probably carrion. In areas not dominated by agriculture and urban development, carrion remains an important food source (Knight and Anderson 1990). It is likely that when migratory behavior evolved in crows, an extremely important food source was carrion. Given that carrion is spatially and temporally variable, diurnal migration would allow individuals to make progress toward reaching their destination while searching for food resources. There is likely an extensive expenditure of energy associated with searching for carrion or foraging conspecifics; thus, migrating during the day may allow the opportunistic discovery of carrion or foraging conspecifics while making progress toward their breeding grounds. Additionally, we know that species that feed on spatially and temporally variable food items engage in complex behavior to gather information from conspecifics and heterospecifics about the location of food (Marzluff et al. 1996). Many species that forage on spatially and temporally variable food items also roost communally, and information is often "shared/derived" from conspecifics at communal roost sites (Ward and Zahavi 1973). Therefore, if migrating crows do not locate sufficient food resources while migrating, communal roosting may provide an additional opportunity to locate food. Communal roosts may also offer additional protection against predation (McGowan et al. 2006). Diurnal migration may not only facilitate the ability to locate food resources by cueing in on conspecifics but also the presence of heterospecifics. For example, Prior and

Table 1 The date and time at which crows migrated from east-central Illinois, the number of conspecifics they migrated with, the number of times crows stopped to forage as they migrated, number of days migrating, and distances migrated per day

Crow number	Date and time when migration began	Range of the number of migrating conspecifics	Average no. of feeding events per day (no. of days tracked while migrating)	Distance migrated per day (km)
1	March 28, 2004; 05:38	0–3	1.00 (2)	280, 102
2	March 4, 2005; 07:45	0–2	2.25 (4)	178, 214, 68, 265
3	March 29, 2005; 05:22	0–53	2.67 (3)	371, 219, 125
4	March 11, 2006; 06:00	0–14	2.00 (1)	287
5	March 29, 2006; 08:21	0–2	1.33 (3)	490, 56, 75
6	March 9, 2007; 06:03	0–6	N/A	243, 141, 154
7	March 12, 2008; 08:45	0–2	1.00 (0.5)	54
8	March 17, 2009; 05:59	0–32	2.33 (3)	297, 80, 55

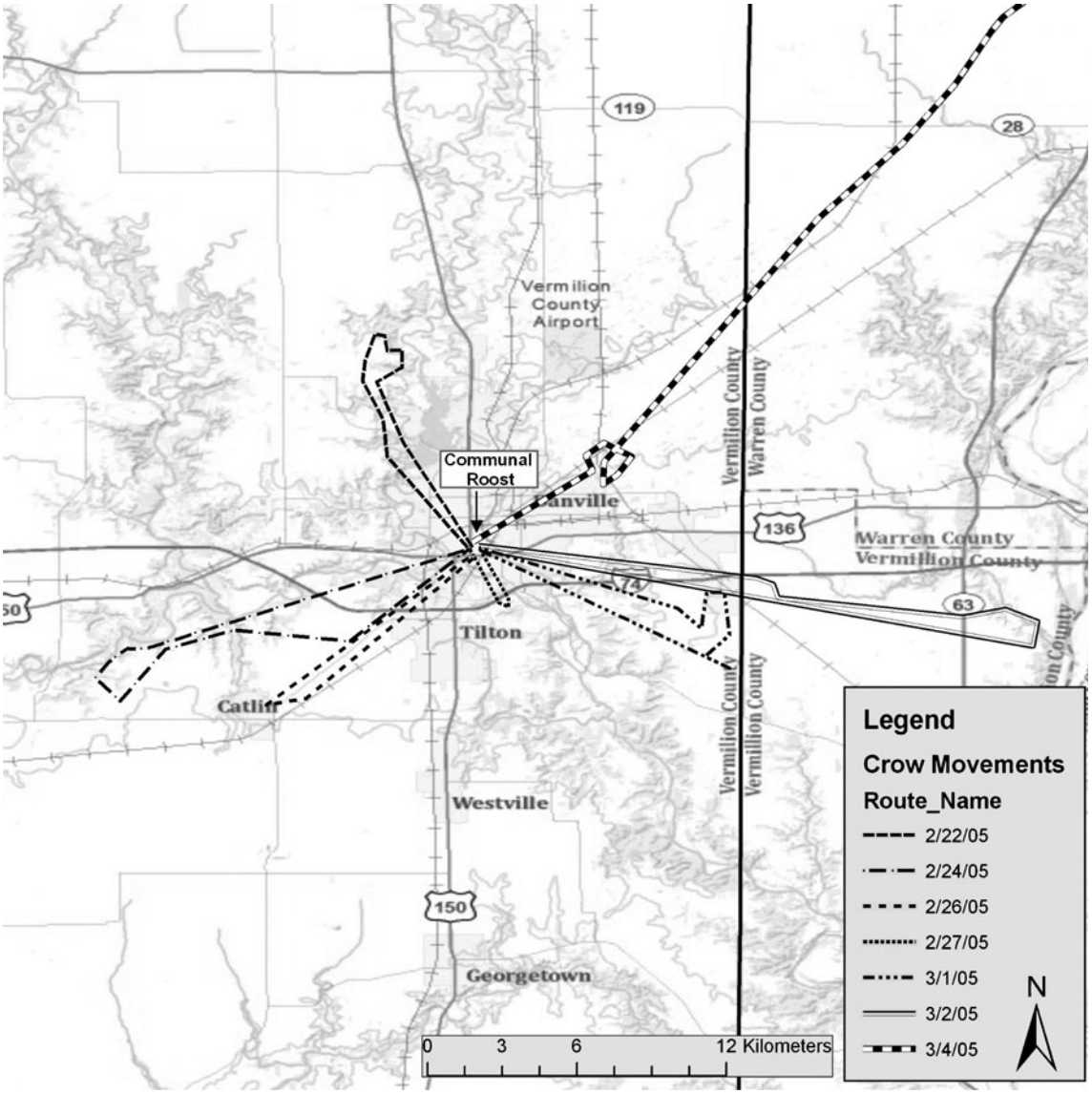


Fig. 2 This crow (number 2) engaged in many movements several kilometers from its roost site; however, on March 4, after foraging for about 1 h in a nearby field, it migrated 178 km to the northeast

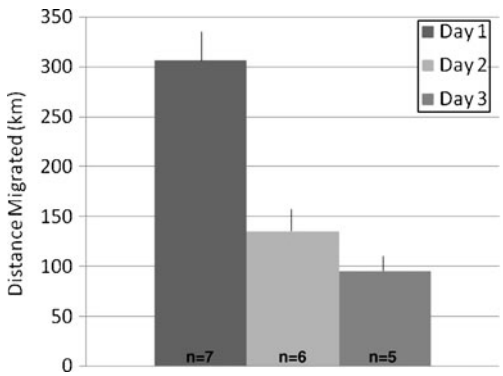


Fig. 3 Average distances migrated by American crows on the first, second, and third day after they left their wintering grounds in east-central Illinois

Weatherhead (1991) found that turkey vultures use the presence of American crows to locate carrion. In North America, common ravens, turkey vultures, American crows, and blue jays have all been observed foraging simultaneously on carrion (Boarman and Heinrich 1999; Heinrich 1988). The use of heterospecifics to find food may be more important to species other than American crows. Because crows are a partial, short-distance (~500 km) migrant, most migratory individuals likely migrate through areas with conspecifics at least in the first few hundred kilometers. However, other species (e.g., turkey vultures) that migrate longer distances and through areas with few or no conspecifics may rely to a greater extent on the presence of heterospecifics to locate carrion.

Importance of communal roosts in American crow migration

The migratory route taken by the American crows in our study suggests that in some instances, migrating individuals abruptly changed trajectory in the afternoons to go to a communal roost location. Though it is difficult to see in Fig. 1, crow numbers 3 and 4 were migrating consistently in a north or northeastern direction until they reached the area (within ~15 km) of a communal roost, at which time they abruptly changed direction. Our observations suggest that they may have followed "local" crows to nearby large communal roosts. Of the eight crows we tracked, three roosted in a same large communal roost in three different years, and three other crows roosted in a different roost in two different years. Communal roosts may be an easy source of food for migrating crows. If migrants can follow experienced individuals to rich foraging locations, then they may be able to quickly deposit fat before continuing their migration. Two migrating individuals left a communal roost the day after they began migration only to forage with conspecifics in nearby areas. One of the individuals stayed in the area and remained at the roost for 3 days before continuing its migration. The other individual foraged for about 1 h before continuing its northward migration. Many large crow roosts have been in existence for decades (>40 years; Emlen 1938; Black 1941; Graber et al. 1987). From band recoveries of crows, we know birds wintering in Illinois migrated through or bred in central Michigan in the 1940s. Therefore, these roosts used by migratory crows along Lake Michigan may have been in existence for decades. These consistent roosts may provide the ideal stopover location for migrating diurnal species. In the case of American crows wintering in east-central Illinois, following the shore of Lake Michigan to these communal roosts, as it appears that all eight birds did, may be an ideal strategy to take advantage of these communal roosts as they migrate to their breeding grounds.

Fly-and-forage hypothesis in relation to other highly social species

We are proposing that American crows, and likely many other highly social species, use a fly-and-forage strategy during diurnal migration. Many species that forage on spatially and/or temporally variable food sources will likely benefit from migrating toward their destination during the day while simultaneously taking advantage of any foraging opportunities that may be present. The hypothesis that species engage in a fly-and-forage strategy during the day to take advantage of social foraging opportunities is not mutually exclusive. Diurnal migrants may take advantage of both, thermals, which increases the benefit of diurnal migration, and opportunities to forage socially. While this hypothesis does not explain why all species migrate during the day, it does provide a broader framework for understanding why many species migrate diurnally. The focus of this study was not to evaluate the behaviors of all birds known to migrate diurnally, although a quick overview suggests that many species that migrate diurnally forage on spatially and/or temporally variable food sources, including waterfowl, wading birds, corvids, blackbirds, American robins, and vultures. In the case of American crows, social behavior does not appear to control when and where to migrate to, as the individuals in the study made individual decisions of when and where to migrate, but during migration took advantage of social foraging opportunities.

Many species that are social foragers and migrate during the day are generally short-distance migrants. One interesting aspect of crow migration is that all but one crow migrated much greater distances the first day of migration than in subsequent days. There are at least two possible reasons why they would migrate less in subsequent days. First, they used most of their fat reserves and, therefore, are not fit enough to migrate farther. Second, we assume that these adult birds were exhibiting some degree of breeding site fidelity; however, to what extent they were evaluating other potential breeding locations is unknown. It is possible that they move less distance as they approached their ultimate breeding location because they were taking more time to evaluate potential breeding locations.

In summary, more information is needed on the behavior of species as they actively migrate from one location to another; these data can help elucidate why certain species use certain migration strategies. In the case of American crows, all evidence suggests that diurnal migration is a strategy associated with their social behaviors.

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