

Current Biology

Hidden Long-Distance Movements by a Migratory Bird

Highlights

- Some Kirtland's warblers move unexpectedly long distances during the breeding season
- The timing of movements indicate that individuals likely move to inform dispersal
- Distances moved are longer than described in a diverse group of birds and mammals
- Similar long-distance movements probably exist in other species but remain undetected

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In Brief

By tracking individual Kirtland's warblers across the annual cycle, Cooper and Marra discover that breeders and non-breeders prospect over longer distances than previously described in other taxa. Similar movements are likely common in other species but remain hidden due to technological limitations and research biases.

Report

Hidden Long-Distance Movements by a Migratory Bird

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SUMMARY

Technology has revolutionized our ability to track animals across the globe, significantly advancing our understanding of animal movement [1, 2]. Technological and logistical challenges, however, have led to non-migratory movements that fall outside of the territory/home range paradigm, receiving less attention. This may have resulted in a widespread underestimation of the frequency and spatial scale at which animals either move outside of their territories and home ranges or adopt altogether different space-use strategies. We used a breeding-range-wide automated radio-telemetry system to track movements in a migratory songbird, the Kirtland's warbler (*Setophaga kirtlandii*). By attaching radio tags on the wintering grounds and relocating the same individuals on the breeding grounds, we were able to sample the population without regard to their eventual breeding status or space-use strategy. We found that a surprising proportion of breeders and most non-breeders made long-distance (5–77 km) movements during the breeding season while conspecifics remained within their small territories. Movement frequency peaked during the nestling and fledgling periods, indicating that both breeders and non-breeders were likely prospecting to inform dispersal. A literature review revealed that Kirtland's warblers moved farther than most species in absolute distances and farther than all other species relative to normal daily movements. We argue that similarly long-distance movements likely exist in many other species but have gone undetected because of technological limitations, research biases, and logistical challenges. Underestimation of the scale of these poorly understood life history behaviors has important implications for the ecology, evolution, and conservation of animals.

RESULTS

Non-breeders More Likely to Move Long Distances

Of the 63 individuals that remained alive during the 2018 and 2019 breeding seasons, 20 (32%; 20♂, 0♀) did not breed and 43 (68%) bred. Non-breeders (12 of 20 [60%]; 12♂, 0♀) were significantly more likely to make long-distance movements than breeders (4 of 37 [11%]; 2♂, 2♀; $p \leq 0.001$). Three individuals (2♂ non-breeders and 1♂ breeder) made long-distance movements in 2017 but were not included in the above calculations because we do not have accurate estimates of breeding status in 2017 (STAR Methods).

Long-Distance Movements by Breeders and Non-breeders

Radio-tagged breeders were found 0–200 m from their nests while breeding, and most remained within 0–500 m of their nests after breeding. However, 6–23 days ($\bar{x} = 11 \pm 3.1$ days) after their nests fledged young ($n = 2$) or were depredated ($n = 3$), five breeders (3♂, 2♀), moved 6–46 km to spatially disjunct breeding areas (Video S1; Table 1). All 20 (20♂, 0♀) non-breeders exhibited territorial behaviors at multiple successive locations 200–1,000 m apart rather than at a single location. After 11–58 days

($\bar{x} = 33 \pm 3.7$ days), 14 non-breeders moved 5–77 km to spatially disjunct breeding areas (Video S1; Table 1).

Only one individual bred after making long-distance movements. He moved 25 km 3 days after his nest failed and then returned to his territory to nest with his original mate. Of the remaining 18 individuals, we re-sighted 15 (83%) after they ceased long-distance movements, and none paired or bred. The breeding status of the three remaining individuals was not definitively confirmed, but they ceased movements on July 10, 18, and 20, all after the species' latest known breeding attempt in Michigan (July 2) [3].

Movements Peaked during the Nestling and Fledgling Periods

From 2017 to 2019, the mean dates for the incubation, nestling, and fledgling periods were June 5 ± 0.4 days, June 20 ± 0.4 days, and June 28 ± 0.4 days ($n = 308$ nests). On average, non-breeders began long-distance movements on June 28 ± 3.6 days, and breeders began movements 1 week later (July 5 ± 5.4 days). Regardless of breeding status, 93% and 85% of long-distance movements occurred after the beginning of the nestling and fledgling periods, respectively (Figure 1). On

Table 1. Summary of Long-Distance Movements by Breeders and Non-breeders

Status	No. Movements	Individual Distances (km)	Total Distances (km)
Breeder	3 ± 1.1 (1–7)	20 ± 2.6 (6–46)	59 ± 31.7 (10–183)
Non-breeder	3 ± 0.9 (1–13)	19 ± 2.1 (5–77)	65 ± 15.6 (5–166)
Combined	3 ± 0.7	19 ± 1.7	63 ± 13.7

Mean (±SE) number of long-distance (≥ 5 km) movements, distances of individual movements, and total distance moved by Kirtland's warblers during the breeding season. Data shown are for breeders (n = 5), non-breeders (n = 14), and breeders and non-breeders combined (n = 19). Ranges are in parentheses.

average, non-breeders ceased long-distance movements on July 6 ± 2.1 days, and breeders ceased movements 5 days later.

Most Movements Occurred at Night

Of the 20 movements for which we could definitely determine time of day, 13 (65%) occurred at night, beginning 112 ± 21.6 min after sunset and 28 ± 21.4 min after nautical dusk, and 7 (35%) began during the day (\bar{x} = 92 ± 41.8 min after sunrise). Assuming a straight flight, flight durations indicated a flight speed of 17 ± 3.3 km/h (range: 0.6–47 km/h). An additional 23 movements most likely either began or ended between sunset and sunrise, suggesting that at least 36 of 62 (58%) movements took place at night.

Kirtland's Warblers Moved Farther Than Other Species

We found that the average and maximum distances moved by Kirtland's warblers were larger than the median values moved by other groups. Relative to their normal daily movements, Kirtland's warblers moved farther than all other species reviewed (Figure 2; Tables S1 and S2).

DISCUSSION

We discovered a long-distance alternative space-use strategy that was previously undescribed in Kirtland's warblers and occurred at a large spatial scale compared to a diverse group of birds and mammals. Discovery of these movements was only possible because of our ability to radio-tag birds on the wintering grounds and relocate the same individuals on the breeding grounds, which allowed us to track individuals regardless of their eventual breeding status or space-use strategy. All radio-tagged birds initially adopted a space-use strategy typical of most songbirds. However, 11% of breeders and 60% of non-breeders abandoned these common space-use strategies and began moving long distances (5–77 km), often at night, between spatially disjunct breeding areas. Our evidence suggests that Kirtland's warblers made these long-distance movements to inform future dispersal decisions, but we first explore several alternative hypotheses.

Why Move Long Distances during the Breeding Season?

Regardless of breeding status, individuals may have moved long distances to find areas with more food or fewer predators to

enhance survival during the breeding season or subsequent molting period (late July–September) [3]. Several lines of evidence make this unlikely. First, starvation of nestlings has never been observed in Kirtland's warblers [4], suggesting that breeding areas contain enough food to sustain adults and young. Second, monthly survival probability during the breeding season is high (0.96 ± 0.005 SE) [5], suggesting that predation on adults is not a major source of mortality. Finally, many individuals moved back and forth from the area they originally settled, suggesting it was adequate in terms of food availability and predation risk.

If movements were not motivated by enhancing survival, individuals may have moved long distances to pursue immediate breeding opportunities and/or prospect for information about habitat quality. Previous work has documented that some birds disperse long distances after a breeding attempt to reneest elsewhere within the same season [6]. Additionally, non-breeders have frequently been shown to breed when openings are experimentally or naturally created [7, 8]. Thus, pursuit of immediate breeding opportunities is a plausible motivation for both breeders and non-breeders. However, many of the movements did not take place until after the latest recorded date of reneesting, and only one individual nested after moving long distances. The fact that both breeders and non-breeders did not nest after moving long distances does not preclude seeking immediate breeding opportunities as a motivation but instead probably only indicates that opportunities to find mates outside of the settlement period are rare.

Although individuals were not successful in finding new nesting opportunities after moving long distances, we cannot rule out the possibility that males were seeking extra-pair copulations. Extra-pair paternity is widespread in songbirds [9] but has not been examined in Kirtland's warblers. However, floaters in most other species rarely sire offspring [10, 11], and if the primary motivation of these movements was to pursue extra-pair copulations, movement frequency should have peaked just prior to egg laying, when most females would have been fertile [12].

The fact that long-distance movements peaked during the nestling and fledgling periods and ceased prior to the end of the fledgling period suggests that individuals were prospecting for public information about conspecific reproductive success to inform dispersal the following season. Studies documenting the use of public information have shown that prospecting peaks during the nestling and fledgling periods because the feeding and presence of dependent young is an obvious signal of reproductive success [13, 14]. Although breeders and non-breeders often initiated long-distance movements at night, afterward they occupied breeding habitat during the day and therefore had the opportunity to gather public information through observation of these conspicuous behaviors. However, they may also have gathered personal or social information. Kirtland's warblers have been shown to use social information to inform habitat selection at the edge of their range in Wisconsin [15]. Future experimental manipulations could disentangle the types of information used [16–18].

Ultimately, our tracking devices did not last long enough to allow us to determine whether individuals dispersed to areas visited the previous year. This makes it impossible to be certain that individuals used information gathered during prospecting trips to inform later dispersal decisions. Nonetheless, after ruling out plausible alternatives and documenting a tight temporal

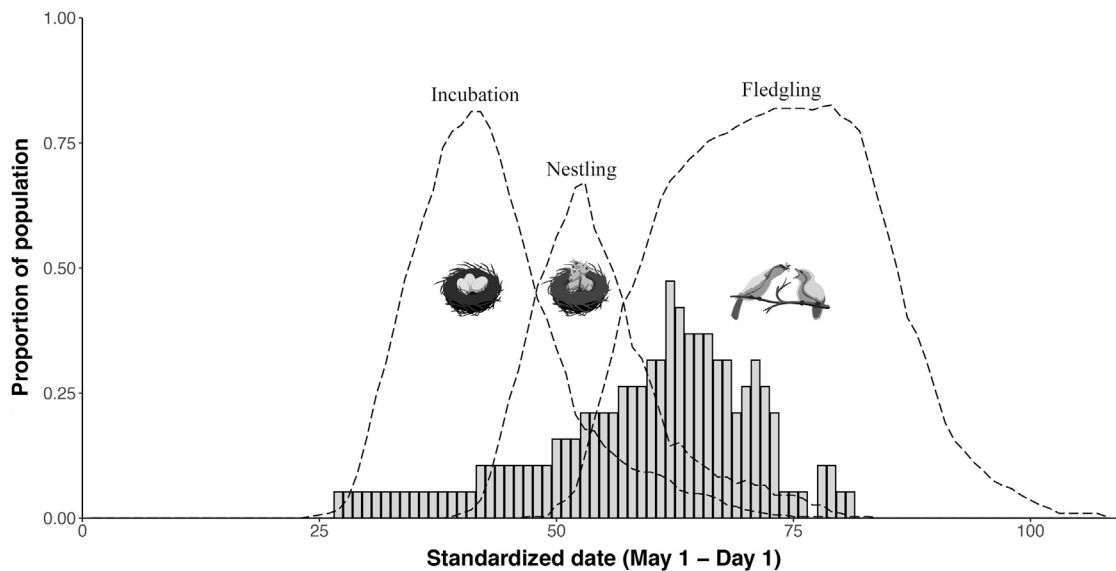


Figure 1. Seasonal Timing of Long-Distance Movements

Proportion of Kirtland's warblers (*Setophaga kirtlandii*) making long-distance movements in relation to when the rest of the population ($n = 308$) was in the incubation, nestling, or fledgling periods of the nesting cycle. [Video S1](#) shows movements by individual birds.

correlation between movement frequency and the availability of public information, we conclude that these long-distance movements were most likely prospecting trips.

Finding and Navigating to Distant Breeding Areas

The flight durations of some individuals implied direct flights, although in other cases indicated either implausibly slow flights (<1 km/h) or that individuals had to search for breeding areas. We do not know what cues individuals used to find breeding areas, but movements often took place at night when auditory and visual location cues would have been limited. Some individuals may have known where breeding areas were from previous visitation, but most individuals that made long-distance movements were in their first potential breeding season and therefore had few opportunities for previous exploration. Regardless of previous knowledge, individuals needed a method to orient and navigate. Most long-distance movements began shortly after nautical dusk, similar to both the onset of non-migratory landscape-scale movements by birds during stopover [19, 20] and migratory flights in Kirtland's warblers (N.W.C. and P.P.M., unpublished data) and other songbirds [21, 22]. Birds are known to use celestial cues to navigate [23, 24], and many stars are visible after nautical dusk, suggesting that Kirtland's warblers may have used a star compass. In addition to the availability of navigational cues, nocturnal migration reduces energetic costs, risk of dehydration, and risk of predation [21]. At distances observed in this study, however, lowered predation risk is the most plausible factor in determining the timing of movement [19].

Are Long-Distance Movements Unique to Kirtland's Warblers?

Movement distances in our literature review varied by nearly five orders of magnitude, with maximum alternate movement distances ranging from 70 m to more than 2,800 km (Table S2).

Several large-bodied birds and mammals moved farther than Kirtland's warblers during forays or alternative space-use strategies, but all had much larger normal daily movements, resulting in small relative movement distances. Thus, the distances moved by Kirtland's warblers stood out as unusually long in terms of both absolute and relative distances. Two possible conclusions can be drawn; either these long-distance movements are unique to Kirtland's warblers or similar movements have gone undetected in other species.

Kirtland's warblers depend on fragmented and ephemeral stands of jack pine forest to breed. Dispersal and prospecting are more likely to evolve when resources show predictable spatiotemporal variation [25–28]. Thus, it is possible that long-distance prospecting evolved in Kirtland's warblers because of their habitat specialization. However, the fragmented nature and limited geographic extent of their breeding habitat is also what allowed us to use automated telemetry to study their long-distance movements. Similarly, Ward [29] was able to document one of the other longest distance examples of prospecting behavior because the rare and fragmented nature of yellow-headed blackbird (*Xanthocephalus xanthocephalus*) breeding marshes allowed for re-sighting at distant locations. Thus, it remains unclear whether long-distance prospecting is more likely to evolve under these circumstances or merely easier to detect. Nonetheless, many other birds and mammals are capable of long-distance travel and depend on resources that are found in fragmented or ephemeral habitats. Regardless of the purpose, we argue that long-distance movements within the breeding season are more common than currently recognized.

Why Have Long-Distance Movements Been Underestimated?

Long-distance forays and alternative space-use strategies may have gone undetected because of limitations in tracking

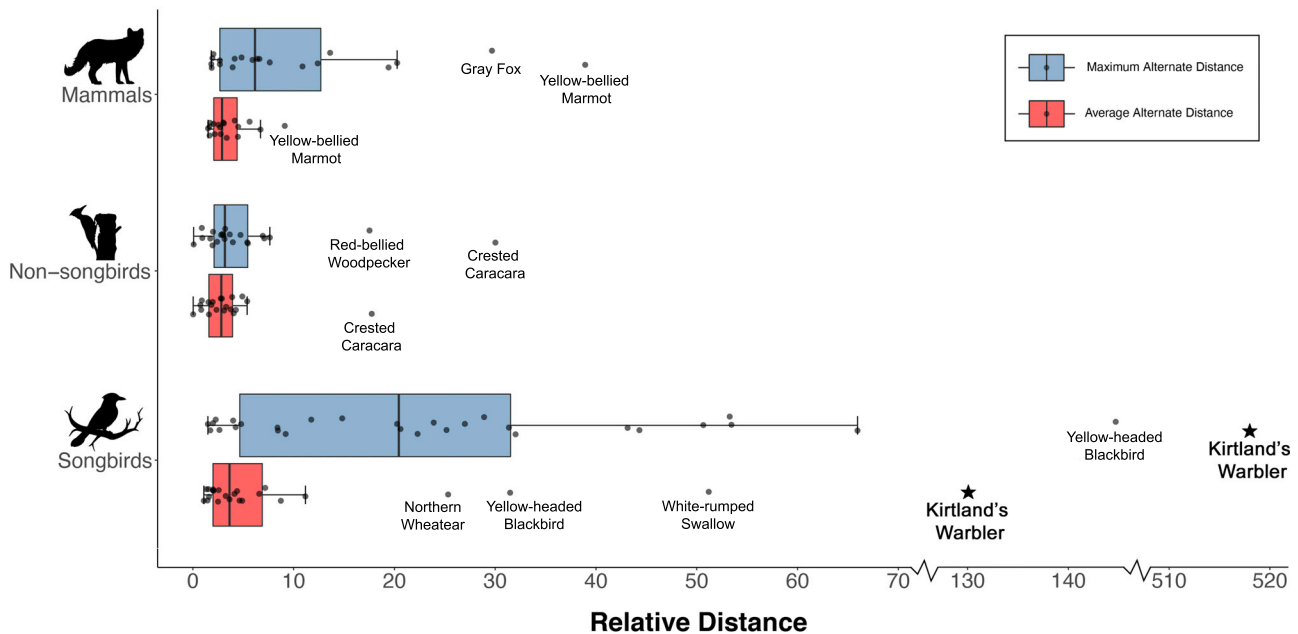


Figure 2. Comparison of Relative Movement Distances across Taxa

Relative average and maximum distances moved by animals during forays or alternative space-use strategies. Closed circles show data points for individual species. Boxes show median \pm inter-quartile range (IQR), whiskers show $1.5 \times$ IQR, and all values above or below whiskers are statistical outliers. Note the two breaks in the x axis. Stars indicate values for Kirtland's warblers. [Tables S1](#) and [S2](#) show summary and raw data.

technology and a bias toward studying adults and breeders rather than juveniles and non-breeders. Most (59%) studies in our review used handheld radio-telemetry or direct observations to track animals, which are strongly biased toward the detection of short-distance movements and require an active observer, limiting temporal resolution. Correspondingly, several studies reported not being able to find radio-tagged individuals despite extensive searches, suggesting movement outside of the study area [30–33]. The use of tracking methods with a higher probability of detecting long-distance movements was less frequent (36%), but they were used in all studies that documented longer absolute movement distances than Kirtland's warblers. Even when these technologies are used, high cost and logistical challenges often result in small sample sizes. Moreover, the low position acquisition rates required to increase battery life on smaller devices can result in missing relatively rare movements. Together, this suggests that many studies in our database would have failed to detect long-distance movements if they were present.

In addition to technological limitations, the study of foray behavior and alternative space-use strategies has suffered from a research bias and logistical challenges. Several factors have led to a severe bias toward tracking reproductive adults [34], but most alternative space-use strategies in our literature review were carried out by non-breeders. Regardless of breeding status, individuals exhibiting alternative space-use strategies are difficult to capture and track. Such individuals may respond less aggressively to capture techniques that take advantage of territorial behaviors, and they are often secretive, not physically identifiable by plumage or markings, and may move over long distances. Thus, many studies of alternative

space use have relied upon incidental captures, resulting in small sample sizes. Together, we believe that these technological limitations, research biases, and logistical challenges have resulted in a widespread underreporting of the frequency and scale of forays and alternative space-use strategies. With continued advances in tracking technology [35, 36], researchers will likely detect similar and perhaps even longer non-migratory movements in other species in the future.

Implications

Underestimating the frequency and spatial scale of forays and alternative space-use strategies has implications for the ecology and conservation of animals. Broadly speaking, if animals move at larger scales than currently understood, managers may not protect all necessary locations and habitat types [37–41]. Further implications of underestimating the frequency and spatial scale of forays and alternative space-use strategies depend on the purpose of the movements and the identity of the individuals moving.

Forays and alternative space-use strategies frequently involve prospecting, and yet prospecting is poorly understood, with little attention devoted to its spatial scale [34]. The prospecting trips observed in our study were as large as many dispersal events in birds [42, 43] and mammals [44], suggesting that long-distance dispersal may be commonly informed through prior visitation. Understanding the frequency of long-distance prospecting is important because failure to account for informed dispersal in population models results in inaccurate predictions [45–47]. Because dispersal has such profound effects on a species' population dynamics, potential for range expansion, and extinction risk [47–49], it is critical that models more realistically incorporate

dispersal and the behaviors that inform it, if their aim is to predict how animals will respond to large-scale environmental changes, such as global climate change.

Our literature review showed that non-breeders frequently exhibit foray behaviors and adopt alternative space-use strategies, and non-breeders often make up a substantial portion of avian populations (30%–70%) [11, 50, 51]. Similar estimates are not available for mammals, but non-breeders impact avian and mammalian population dynamics [51–53], sexual selection [11], and conservation [50, 54, 55]. Despite their importance, information about non-breeders is rarely available. Monitoring programs often only count breeders or do not determine breeding status, and even when they attempt to do so, accurately censusing non-breeders is difficult. For example, recent estimates from a marking and re-sighting effort suggested that only 8% of male Kirtland's warblers were non-breeders [3], much lower than our estimate (32%). Our method of randomly radio-tagging individuals on the wintering grounds and later relocating them on the breeding grounds likely provides a more accurate estimate but will be difficult to replicate in most other species until tracking technology improves. Devising improved methods for estimating the non-breeding portion of animal populations should therefore be a priority.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

Supplemental Information can be found online at <https://doi.org/10.1016/j.cub.2020.07.056>.

A video abstract is available at <https://doi.org/10.1016/j.cub.2020.07.056#mmc5>.

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AUTHOR CONTRIBUTIONS

N.W.C. and P.P.M. conceived of the project, designed the study, and acquired funding. N.W.C. collected and analyzed the data. The manuscript was written by N.W.C. and edited by P.P.M.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited Data		
Raw and analyzed data and associated code	Mendeley Data	http://dx.doi.org/10.17632/ycnx37zj4b.2
Experimental Models: Organisms/Strains		
<i>Setophaga kirtlandii</i>	Wild	N/A
Software and Algorithms		
geodist 0.0.3	[56]	https://github.com/hypertidy/geodist
motus 3.0.0	[57]	https://github.com/MotusWTS/motus
moveVis 0.10.5	[58]	https://github.com/16EAGLE/moveVis
suncalc 0.5.0	[59]	https://github.com/datastorm-open/suncalc
R 4.0.0	[60]	https://www.r-project.org/

RESOURCE AVAILABILITY

Lead Contact

Further information and requests for resources should be directed to and will be fulfilled by the Lead Contact, Nathan W. Cooper (nathanwands@gmail.com).

Materials Availability

This study did not generate unique reagents.

Data and Code Availability

Original data and code have been deposited to Mendeley Data: <http://dx.doi.org/10.17632/ycnx37zj4b.2>.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

We used mist nets and conspecific song playback to capture 163 Kirtland's Warblers (137♂, 26♀) on their wintering grounds on Cat Island, The Bahamas (24.33° N, 75.45° W). All handling of birds was approved by a Smithsonian Institute for Animal Care and Use Committee Permit to P.P.M.

METHOD DETAILS

Study species and sites

Kirtland's Warblers winter in scrub forests in The Bahamas and Turks and Caicos from October through late April or early May [61]. Nearly all of the population (~97%) breeds in young (5–15 year old) jack pine forests in the northern Lower Peninsula of Michigan, USA, with small populations in Michigan's Upper Peninsula, Wisconsin, and Ontario, Canada [3]. Kirtland's Warblers are usually single-brooded, but if nests fail early in the season, they will often build replacement nests, with the latest known nest initiation date in Michigan being July 2 [3]. Individuals initiate their annual molt sometime between late July and their departure for the wintering grounds in late September and October [3, 62].

Following control of Brown-headed cowbird (*Molothrus ater*) populations and creation of breeding habitat, the population recovered from 167 males in 1987 to over 2300 males in 2015 and was subsequently removed from the endangered species list in 2019. Current breeding habitat in Michigan consists of 15,000 ha of jack pine forest spread across the northern Lower Peninsula in spatially disjunct areas located within a habitat matrix consisting of various other forest types, agricultural lands, and rural settlements (Video S1).

Field Methods

In March and April 2017–2019, we used mist nets and conspecific song playback to capture 163 Kirtland's Warblers (137 ♂, 26 ♀) on their wintering grounds on Cat Island, The Bahamas (24.33° N, 75.45° W). We sexed each individual using plumage characteristics [63] and then affixed three plastic color bands and one USGS aluminum band. We attached a 0.35 g coded radio tag (model = NTQBW-2, Lotek Wireless) using a modified leg-loop harness [64]. Tags weighed on average $2.4 \pm 0.17\%$ (SD) of body mass (Range: 2.0%–3.3%). Each tag emitted a coded pulse every 29.3 (2017–2018) or 24.1 s (2019) that allowed for individual identification by

telemetry receivers [35]. Estimated battery life was a minimum of 140–165 d depending on the year and even the earliest deployed tags lasted at least through the end of July and often into September.

In Michigan, we relocated 99 (61% total; 87♂ [64%], 12♀ [46%]) of the 163 Kirtland's Warblers (137♂, 26♀) radio-tagged in The Bahamas from 2017–2019. We removed radio-tags from a total of 6 breeding birds in late May or early June of 2018 and 2019. In addition, shortly after arrival to Michigan, two individuals were depredated, one individual likely died due to a trematode parasite (*Collyriclum faba*), and three individuals likely moved outside of the main breeding range or had their tags fall off or fail. These 12 individuals were removed from the analysis when calculating the proportion of breeders and non-breeders that made long-distance movements.

Each season, we erected 11 (2017–2018) or 12 (2019) solar-powered, automated radio towers at all major breeding areas found in the northern Lower Peninsula of Michigan (Video S1). Each of the two, directional 9-element Yagi antennas (Laird Connectivity) attached to the towers had a maximum detection range of approximately 15–20 km [35]. However, maximum detection range is only achieved when individuals are up in the air column well above the forest canopy, which likely only occurred when birds arrived or departed from a breeding area. As individuals arrived at a breeding area, towers would usually detect them for at least 90 s and up to a few minutes before they dropped down into the breeding habitat and out of detection range. Simultaneous observation of radio-tagged birds using handheld and automated telemetry indicated that the detection range of the towers was at best 2 km and usually much lower (< 500 m) while birds were in breeding habitat.

When radio-tagged individuals were first detected by a tower, we systematically searched the surrounding area by vehicle and foot, using car mounted or handheld telemetry. We also carried out systematic searches in the few breeding areas not well covered by the towers at least every three days in May and June, but often more frequently. Once a bird was located, we attempted to re-sight it at least once per week, from arrival through the end of the breeding season to determine territorial, pairing, and breeding status through direct observation. We attempted to find nests of all radio-tagged individuals and monitored nests at least once every three days until completion.

Interpreting Movement Data

To estimate the frequency, timing, and starting and ending locations of long-distance movements, we used the “motus” package [57] in Program R [60] to manually inspect detection data from the towers for all radio-tagged individuals and also used any detections acquired through handheld telemetry that were then followed by direct observations in the field. We defined a long-distance movement as any movement between two towers (min = 6.3 km). Movements detected by handheld telemetry ≥ 5 km were also included. Most long-distance movements (47 of 62; 76%) were first detected only through automated telemetry, while the remaining 15 (24%) were detected through handheld telemetry followed by direct observation. Detections at a tower were considered valid when at least three consecutive detections were recorded [35]. Of the 47 movements detected only through automated telemetry, 9 (19%) consisted of fewer than 10 consecutive detections (median = 4, interquartile range [IQR] = 3–7), while the remaining 38 movements (81%) had 10 or more consecutive detections (median = 47, IQR = 21–132, range = 10–6367).

For each long-distance movement, we attempted to confirm that the individual involved occupied breeding habitat after it moved. Occupancy of breeding habitat was confirmed in 46 of 62 (74%) cases either through direct observations or large numbers of consecutive detections during daylight hours. For the remaining 16 (26%) movements, occupancy of breeding habitat was considered highly likely given the number and timing of detections, but in some cases could have represented birds simply passing through a breeding area with a tower to other breeding areas or to locations without breeding habitat. Ten of 19 (53%) individuals that made long-distance movements returned at least once to their original breeding area and 5 (26%) resettled at their original breeding area before ceasing long-distance movements. Detection histories for some individuals included detections in quick succession (i.e., within 0.5–2 hr) at two or more towers and were therefore indicative of individuals flying through one breeding area on the way to another breeding area. Accordingly, these movements were treated as a single movement from the area of departure to the area of eventual settlement, rather than as multiple independent movements.

Literature Review

We used the “Web of Science Core Collections” database to find studies of foray behavior and alternative space-use strategies in birds and mammals. We defined foray behavior as round-trip movement outside of the territory or home range. We defined an alternative space-use strategy as any other movement exhibited by a portion of the overall population that differed in pattern and spatial scale from the majority of the population. To search for studies of foray behavior we used different combinations of the search terms: “foray,” “excursion,” “excursional,” “extra-territorial,” “extraterritorial,” “extra territorial,” “off-territory,” “off territory” and “prospecting.” To search for studies on alternative space-use strategies, we used combinations of the search terms: “alternate,” “alternative,” “space use,” “non-territorial,” “nonterritorial,” “transient,” and “floater.” We then inspected all studies and appropriate references cited therein to extract information related to the scale of normal daily movements (e.g., territory size, home range size, or foraging distance), average and maximum scale of movement for forays or alternative space-use strategies, the age, sex, and breeding status of individuals involved, season of study, type of tracking technology used, proposed purpose of the movements, and sample sizes. Six species appear twice in the database. This occurred when we found two studies on the same species that met our search criteria, or when studies found that space use differed significantly by sex.

Study design and information reported varied widely, but foray studies typically reported territory or home range size as a measure of distance moved during normal daily activity, and distance traveled from a central location (e.g., nest, burrow, territory center) as a measure of foray distance. Studies of alternative space-use strategies generally reported the typical territory or home range size and either the home range size of individuals exhibiting the alternative space-use strategy, or the distance they traveled from a central location. When typical territory or home range size was not reported, we attempted to find these values from the same study population, or at least from the same regions using other published sources. Some species (e.g., Yellow-headed Blackbirds, *Xanthocephalus xanthocephalus*) do not hold all-purpose territories and forage primarily outside of their small nesting territories. For these species, we used information about foraging distance away from the territory to estimate distance moved during normal daily activity. For all studies in which territory or home range sizes were reported, we assumed the areas used were roughly circular and calculated the radius. This allowed for direct comparison between studies reporting areas used and those reporting distances traveled. This resulted in three distances for each species; distance moved during normal daily activities, and the average and maximum distance moved during foray or alternative space-use strategy (hereafter average and maximum alternate movement distance). In 10 cases, the average alternate distance moved was not reported, and only maximum values were available. In an additional 10 cases, the maximum values were not reported, and we therefore estimated the maximum by adding the reported measure of dispersion to the estimate of central tendency.

We found 34 examples of foray behavior (20 birds, 14 mammals) and 37 examples of alternative space-use strategies (31 birds, 6 mammals), across 65 species (47 birds, 18 terrestrial mammals; [Tables S1](#) and [S2](#)). Sample sizes were generally small (median = 12, IQR = 5-21, range: 1-141). Ground based radio-telemetry was used in 37 of 71 (52%) cases, followed by transmitting GPS or satellite tags ($n = 11$, 15%), archival GPS tags ($n = 9$, 13%), direct observations ($n = 6$, 8%), aerial radio-telemetry ($n = 6$, 8%), automated radio-telemetry ($n = 1$, 1%), and passive integrated responder (PIT) tags ($n = 1$, 1%). Irrespective of period of the annual cycle, extra-territorial forays were most often carried out by individuals known to be breeders ($n = 24$, 71%), and less frequently by both breeders and non-breeders ($n = 5$, 15%), non-breeders alone ($n = 3$, 9%) or individuals of unknown breeding status ($n = 2$, 6%). In contrast, alternative space-use strategies were most commonly carried out by non-breeders ($n = 29$, 78%), followed by individuals of unknown breeding status ($n = 7$, 19%) and breeders ($n = 1$, 3%). Regardless of movement type, prospecting was suggested as the motivation behind the movements in most cases ($n = 44$ of 71, 62%), followed by mating and extra-pair copulations ($n = 21$, 30%), foraging ($n = 18$, 25%), and unknown ($n = 5$, 7%; percentages total > 100% because of multiple proposed purposes).

Across all taxa, the normal daily and alternate movements varied by nearly five orders of magnitude. We first compared absolute distances moved between Kirtland's Warblers and all other songbirds, and then made limited comparisons with other groups. To make meaningful comparisons across our diverse dataset, we then put all distances on a relative scale by dividing the average and maximum alternate distances moved by the distance moved during normal daily activities. The distributions of normal and alternate distances moved were highly right-skewed, and therefore we report medians and interquartile ranges. For all other variables we report means \pm 1 SE.

QUANTIFICATION AND STATISTICAL ANALYSIS

Due to small sample sizes, we used Fisher's Exact Test to investigate differences in both breeding status and the likelihood of long-distance movement by breeding status. Movement distances were estimated by calculating great circle distances between consecutive observations or tower locations using the "geodist" package [56], and we animated movement data using the "moveVis" package [58] in Program R [60]. To relate the timing of movements to the stage of nesting in the surrounding Kirtland's Warbler population, we first estimated the start date of the incubation, nestling, and fledging periods for all Kirtland's Warbler nests found in the Lower Peninsula of Michigan ($n = 308$, 2017-2019) as part of this and a related study [61]. For nests found after incubation had already begun, we backdated to determine the start date of incubation using the average incubation period length [3]. For nests found in the fledgling period, we estimated the age of young to the nearest day using species-specific plumage characteristics (N.W.C. et al., unpublished data) and then backdated to find the start of the nestling and incubation periods using those ages and the average length of the incubation period. The mean start dates for the incubation, nestling, and fledgling periods varied non-significantly by 1-2 d each year (all $p > 0.05$) and therefore, we pooled nests across all years to estimate average start dates for each period.

To estimate the time of day that each movement took place, we manually inspected all detection data. We could only definitively determine the time of the movement when an individual was detected within the same day both at the area it departed from and the area it moved to, which was the case for 20 of 62 (32%) movements. We calculated the time after sunrise for movements that took place during the day, and we calculated the time after sunset and the time after nautical dusk for movements that took place at night using package "suncalc" [59] in Program R [60]. For all remaining movements, the interval between detections at the two areas spanned more than one day, and therefore we could only infer the time of day that the movement occurred by using the start and end times for each movement. For these latter movements, it is possible that the start and end times only reflect the time when the bird moved locally within the area and became available for detection by the tower and not the actual times of the long-distance movement between towers.

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Supplemental Information

Hidden Long-Distance Movements by a Migratory Bird

Nathan W. Cooper and Peter P. Marra

	Normal Daily Movements (km)	Average Alternate Movement (km)	Maximum Alternate Movement (km)	Relative Average Alternate Movement	Relative Maximum Alternate Movement
Kirtland's Warbler	0.15	19.4	77.3	130.1	517.9
All other songbirds (n = 29)	0.07 (0.04 - 0.10)	0.2 (0.1 - 0.9)	1.4 (0.4 - 2.4)	3.6 (2.0 - 7.2)	20.6 (4.5 - 37.6)
Non-songbirds (n = 22)	5.02 (0.80 - 26.12)	14.7 (0.9 - 68.8)	33.5 (1.6 - 91.8)	2.8 (1.6 - 4.0)	3.2 (2.0 - 5.8)
All other birds (n = 51)	0.12 (0.06 - 2.6)	0.7 (0.2 - 12.9)	1.7 (0.8 - 27.0)	3.1 (1.6 - 4.9)	6.9 (2.8 - 25.2)
All mammals (n = 20)	1.40 (0.49 - 4.8)	4.6 (1.1 - 10.0)	8.6 (3.4 - 26.1)	2.9 (2.0 - 4.5)	6.2 (2.7 - 13.3)
All other animals (n = 71)	0.37 (0.07 - 4.28)	1.5 (0.3 - 10.2)	3.5 (1.0 - 27.0)	3.0 (1.8 - 4.6)	6.4 (2.7 - 20.6)

Table S1. Summary movement distances for Kirtland's Warblers and other groups.

Related to Figure 2.

The spatial extent of normal daily movements (e.g., territory or home range size, foraging distance) and average and maximum distances moved during forays or alternative space use.

Average and maximum alternate distances are also shown in relation to normal daily movements to facilitate comparison across this diverse group of birds and mammals.

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