Current Biology

Report

Active European warzone impacts raptor migration

Highlights

- Greater Spotted Eagles were exposed to conflict while migrating through Ukraine
- Conflict events impacted migratory behavior and stopover site use
- This likely increased energetic cost and risks on migration through conflict zones

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In brief

Russell et al. found that when migrating through Ukraine in 2022, Greater Spotted Eagles were exposed to conflict events, which impacted their migratory behavior. They made route deviations and used fewer stopover sites compared with previous years, potentially increasing the energetic cost of the migration and having sublethal fitness effects.

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Report

Active European warzone impacts raptor migration

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SUMMARY

Human conflicts can have impacts on wildlife, from direct mortality and environmental damage to the displacement of people, changing institutional dynamics and altering economies.[1–3] Extreme anthropogenic disturbances related to conflict may act as a barrier to migrating birds and increase the energetic costs of migration.[4] On February 24th, 2022, the Russian Federation invaded Ukraine, with targeted attacks on Kyiv and the eastern regions.[5] By March 3rd, when the first of 19 tagged Greater Spotted Eagles entered Ukraine on migration, the conflict had spread to most major cities, including parts of western Ukraine.[6] We quantified how conflict impacted the migratory behavior of this species using GPS tracks and conflict data from the Armed Conflict Location and Event Data (ACLED) project[7,8] in a quasi-experimental before-after control-impact design, accounting for meteorological conditions. Migrating eagles were exposed to conflict events along their migration through Ukraine and exhibited different behavior compared with previous years, using fewer stopover sites and making large route deviations. This delayed their arrival to the breeding grounds and likely increased the energetic cost of migration, with sublethal fitness effects. Our findings provide a rare window into how human conflicts affect animal behavior and highlight the potential impacts of exposure to conflict events or other extreme anthropogenic disturbances on wildlife.

RESULTS

Greater Spotted Eagles are a large species of raptor that are of conservation concern and are listed as Vulnerable on the International Union for Conservation of Nature red list.[9] The species has largely been extirpated from western and central Europe, but a key European breeding population persists in Polesia, Belarus.[10] In March and April 2022, 19 GPS-tagged Greater Spotted Eagles migrated through Ukraine on their way north to breeding grounds in southern Belarus during the Russian Federation invasion of Ukraine,[5] exposing them to areas of intense human conflicts. Average flight altitude during this period is relatively low, approximately 350 m above sea level, increasing the risk of exposure to conflict events. Migrations north from 44° latitude through parts of Romania, Moldova, and Ukraine typically take 1–2 weeks, and 90% of birds normally spend several days at three common stopover sites in Ukraine, located in Vinnytsia, Zhytomyr, and the area of Polesia in Rivne and Zhytomyr (Figure 1).

Greater Spotted Eagle migrations through conflict areas in central and western Ukraine had a higher deviation index compared to 65 pre-conflict migrations, with the eagles flying further and less directly to breeding grounds (deviation index defined as the ratio between the distance traveled and straight-line distance; pre-conflict, 1.26 ± 0.03; conflict, 1.39 ± 0.04; $p < 0.001$), traveling on average 85 km further (Figure 2; Table 1). The greatest differences in deviation index were observed north of 48° latitude in Ukraine, where migrations coincided with more military activity (Figure S2). Migrations in 2022 took longer (pre-conflict female, 193 h ± 24; conflict female, 246 h ± 25; p = 0.045; pre-conflict male, 125 h ± 22; conflict male, 181 h ± 21; p = 0.01), with males traveling more slowly (pre-conflict, 9.75 m/s ± 0.73; conflict, 7.66 m/s ± 10.6; p = 0.046) than in pre-conflict years (Table 1). There were no differences in the deviation index or migration performance metrics outside of Ukraine (Figure S1; Table S1).

Stopovers in Ukraine were common from 2018 to 2021, with 18 individuals (90%) making stopovers (identified using 50% utilization distributions in R package track2KBA), defined as days when less than 5 km of progress is made on migration.[13,14] In 2022, fewer individuals stopped in Ukraine before returning to their breeding grounds, with just 6 individuals (32%) making stopovers (probability of stopover pre-conflict, 0.86; conflict, 0.21; t = −1.435; $p < 0.001$). Important stopover sites in Ukrainian Polesia were not used at all in 2022, while in pre-conflict years 11 individuals (55%) used this area (Table S4).

Individuals were exposed directly to conflict areas, with periods of slow migration or deviations in movement associated with these events (Figure 3). Individual responses to conflict varied (Figure S3), with some individuals showing little change

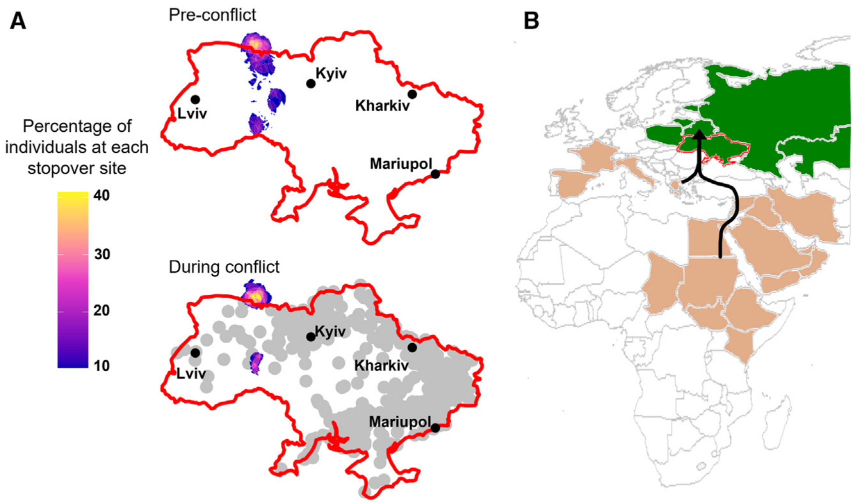

Figure 1. Distribution, migration, and stopover use in Ukraine for Greater Spotted Eagles

(A) Common stopover sites in Ukraine used by more than 10% of Greater Spotted Eagles in pre-conflict years and 2022 shown relative to conflict areas in gray.[11,12]

(B) The European breeding range (green) and wintering range (beige), with typical spring migration routes for individuals breeding in Belarus shown with black lines; Ukraine is highlighted in red. Full details of stopover site use in Table S4.

from previous years. A significant amount of the model variance is explained by the individual term, accounting for differences in migration strategy, routes, and decision making across birds in normal years and how they are differentially exposed to or respond to conflict. One eagle, Borovets (tag: 201402), flew close to Kyiv on migration, similar to previous years, with no obvious deviations or changes in altitude, aided by favorable wind conditions. 15 individuals had a higher deviation index in 2022 than in any of their pre-conflict migrations (Figure S3), including Denisa (Figure 3). Denisa was exposed to multiple conflict events south-west and west of Kyiv, flying within 1 km of reported explosions and battles, which coincided with a slowing of migration, increased deviation index, and westward movement away from these events and more intense conflict zones. We tested if weather conditions explained any of these findings, as changes in weather conditions are known to influence migration routes.[11] Meteorological conditions explained pre-conflict inter-annual variation in migration metrics (Table S3) but did not explain the additional variation observed in 2022 (Table S2).

DISCUSSION

Here, we present findings from a unique dataset, adding key evidence to the record of potential large-scale impacts of conflict and other extreme anthropogenic events (e.g., mining exploration, fireworks, oil drilling, etc.) on wildlife—in particular, on migratory birds. Previous research on the impacts of military activity on wildlife has been limited to resident birds in military training zones[15,16]; our study shows a noticeable impact on Greater Spotted Eagle migration though Ukraine during a period of intense conflict in 2022. Eagles deviated more (∼10%), migrated more slowly (females, ∼20%; males, ∼30%), made fewer stopovers (∼60%), and took longer to migrate (females, ∼25%; males, ∼50%) through Ukraine than in previous years. Our findings show the potential wide-ranging impacts of conflicts on wildlife, as many biodiversity hotspots are in politically volatile countries, with significant conflicts occurring in over two-thirds of biodiversity hotspots between 1950 and 2000.[17] Migratory species can be exposed to a greater range of human conflict events than sedentary species by their ranging behavior throughout the annual cycle, and there are several conflicts in internationally important migration highways.

Artillery fire and jets, tanks, and other weaponry increased potential disturbance to wildlife, including the Greater Spotted Eagles in Ukraine, with unprecedented numbers of soldiers moving through the landscape and more than 10 million civilians displaced.[6,18] Armed Conflict Location and Event Data (ACLED) project data allowed us to investigate conflict events at a daily scale for inhabited areas, providing a coarse measure of conflict intensity and distance to nearest event.[7,8] Greater Spotted Eagles were not observed to circumnavigate conflict areas entirely. Avoidance behaviors occurred on a more local scale, probably around specific short-term events or influenced by their drive to reach nearby breeding grounds. Sporadic and instantaneous extreme anthropogenic disturbance events associated with conflict likely caused diversions or impediments during migration. Abrupt disturbances can trigger immediate panic or escape responses in wildlife.[19] Our data show that individuals exposed to these events may respond by deviating their flight path to flee or seek refugia, increasing the distance traveled. Disruption to stopovers also shows that conflict events influenced trade-off decisions, resulting in individuals potentially migrating when the energetic cost exceeded the potential gain from stopovers.[20,21] Responses varied across individuals and are likely dependent on factors such as energy reserves that limit the individual's ability to quickly avoid or pass through conflict areas and may slow migration. Differences across sexes in flight speed may correspond with migration strategies, with males making longer journeys from wintering grounds in eastern Africa before reaching Ukraine compared to females migrating from Greece.[22]

It is unclear what stimuli Greater Spotted Eagles may have responded to, but it may vary from visual or auditory components of military activities[15,16,23] to traffic, noise, or light, all of which could impact migratory behavior.[24] Many studies report behavioral changes in wildlife when exposed to unpredictable disturbances such as fireworks or other loud noises,[25] so conflict events are likely to trigger similar responses. These effects are reported to be greater over large open habitats,[25] such as the wetland systems used by Greater Spotted Eagles in Belarus and Ukraine. Isolating the direct impacts of conflict on fine-scale decisions is difficult without high-resolution and accurate conflict data, as we cannot determine what stimuli birds are exposed to and what influences individual decisions.

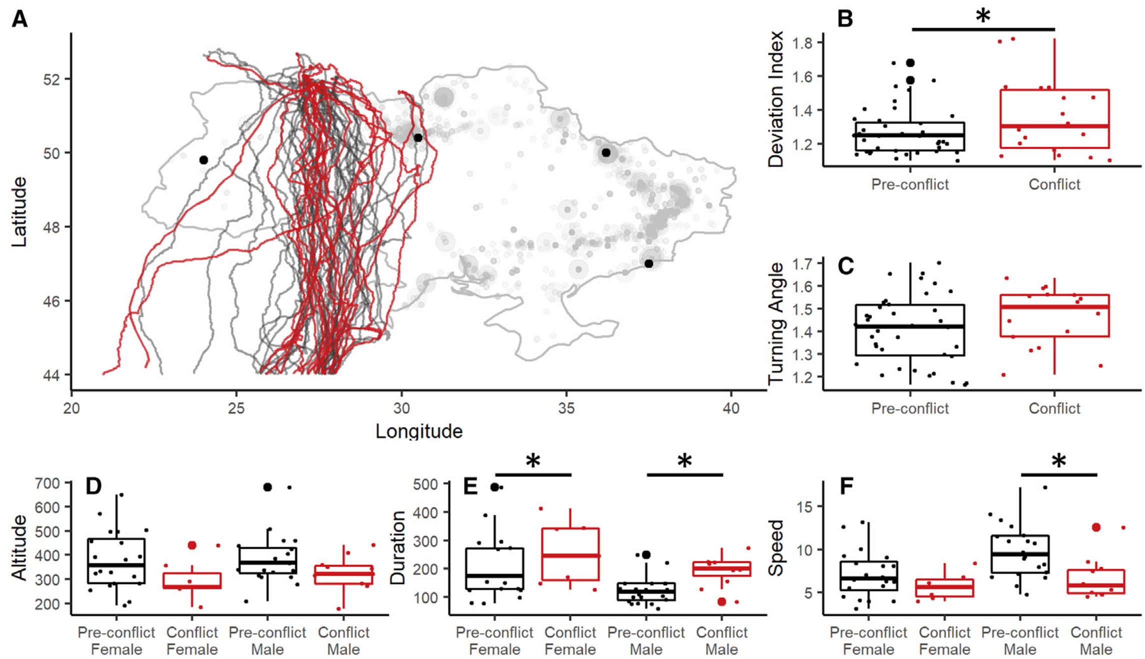

Figure 2. Pre-conflict spring migration (2019–2021, black, *n* = 41) and spring migration during the Russia-Ukraine conflict (2022, red, *n* = 19) routes and performance metrics for 22 Greater Spotted Eagles passing through Ukraine from 44° latitude to their breeding grounds

(A) Migration routes are shown in relation to major cities (points) and areas of conflict (gray[11,12]).

(B–F) Migration performance metrics comparing pre- and during-conflict migrations including: (B) route deviation index; (C) average turning angle (radians); (D) average altitude of migration (meters); (E) time taken to cross Ukraine (hours); and (F) average migration speed (meters per second). Significant differences are indicated with asterisks and models described in Table 1. Analysis including data from 2018 is shown in Figure S4. Metrics are compared at a finer scale in the supplementary materials.

The behavioral changes associated with the conflict in 2022 likely had sublethal fitness effects and increased the energetic costs of migration and the risk of mortality.[20,26] Long-distance migratory raptors have an elevated mortality rate during migration due to natural causes and exposure to anthropogenic threats.[24,27] Changes in flight behavior cause immediate increases in energy expenditure,[25,28] and the physiological impacts of stress responses can carry over for several hours after exposure to the stressor ceases,[29] influencing behavior during this period. Cumulatively, these responses may result in large impacts to individuals, with some studies reporting over a week of compensatory foraging activity following firework displays.[30] Greater Spotted Eagles regularly use a small selection of fragmented wetland areas as stopover sites on their migration through Ukraine, and reduced access to these sites may also limit an individual's ability to improve their body condition before returning to their breeding grounds, impacting their recovery time to reach optimal breeding condition.[12,26]

Greater Spotted Eagles in Belarus and Ukraine represent an important subpopulation of Greater Spotted Eagles (~15% of the European population), with 150 breeding pairs located in Polesia, a large wetland region spanning northern Ukraine and southern Belarus.[31,32] Greater Spotted Eagles are raptors with slow life histories,[33] producing a single chick each year with relatively low breeding success (~60%).[34] Soaring raptors have high energetic flight costs when weather conditions are not favorable, so the impacts of conflict events on decision making may be more costly than in other birds.[27,35,36] Parent fitness and delays in onset of breeding to recover fitness can impact chick provisioning as well as fledgling date, negatively affecting breeding success,[26] and any impacts on this population are significant for the global conservation of the species. These impacts are probably greater for individuals that migrated through more intense conflict areas.[32] Elevated levels of disturbance from conflict and increased military activity may also directly impact reproductive success of individuals breeding in conflict zones, such as populations in Ukraine and the Chernobyl Exclusion Zone (CEZ).[37–39] The CEZ has become an increasingly important breeding area for Greater Spotted Eagles, associated with the impacts of rewilding and reduction in disturbance,[38] but this population, including several monitored pairs of breeding Greater Spotted Eagles, has now been exposed to military activity reported within the Belarusian portion of the CEZ.

In addition to the direct impacts of conflict on wildlife, the longer-term impacts on governance and NGOs could cause immeasurable damage to conservation efforts in the region.[1–3] In Ukraine, the current conflict limits the capacity to protect active Greater Spotted Eagle nests from activities such as logging, as resources for surveys and conservation activities are reduced. Military activity, such as widespread reported mining by Russian troops in Ukraine, could degrade the wetlands that Greater Spotted Eagles depend upon and hamper wetland restoration efforts, threatening the declining population in Polesia.[40,41]

This study increases our understanding of the impacts of extreme anthropogenic disturbance and conflict on migratory

Table 1. Outputs from mixed-effects models comparing pre-conflict and conflict migration performance metrics and route deviation of Greater Spotted Eagles

Response	Model	Predictor	Effect size	Std. error	t	*p*	$R^2_{(m)}$	$R^2_{(c)}$
Deviation index	Conflict + (1 | individual)	Pre-conflict	1.265	0.033	38.832	<0.001	0.07	0.60
		Conflict	+0.099	0.032	+3.108	0.003*		
Duration (hours)	Conflict + conflict × sex + (1 | individual)	Pre-conflict : female	192.75	24.16	7.978	<0.001	0.19	0.66
		Conflict : female	+49.85	24.30	+2.052	0.047*		
		Pre-conflict : male	124.58	22.18	5.616	<0.001		
		Conflict : male	+67.24	20.91	+3.216	0.003*		
Altitude (m)	Conflict + conflict × sex + (1 | individual)	Pre-conflict : female	381.819	29.122	13.111	<0.001	0.08	0.53
		Conflict : female	−72.750	33.248	−2.188	0.075		
		Pre-conflict : male	373.953	27.085	13.807	<0.001		
		Conflict : male	−53.944	28.556	−1.889	0.066		
Turning angle (rad)	Conflict + (1 | individual)	Pre-conflict	1.407	0.028	51.505	<0.001	0.03	0.32
		Conflict	0.051	0.036	1.389	0.173		
Speed (m/s)	Conflict + conflict × sex + (1 | individual)	Pre-conflict : female	7.185	0.652	11.012	<0.001	0.23	0.31
		Conflict : female	−1.376	1.151	−1.195	0.239		
		Pre-conflict : male	9.766	0.643	15.201	<0.001		
		Conflict : male	−3.14	0.983	−3.163	0.003*		

Models selected had the greatest model fit by Akaike's information criterion corrected for small sample sizes (AICc). Model intercepts are pre-conflict years, and effect sizes for conflict year are relative to the intercept. Asterisks indicate significant differences. Models including sex were relevelled to allow direct comparison of pre-conflict females to conflict females and pre-conflict males to conflict males.

raptors, demonstrating decreased route efficiency and highlighting potential sublethal fitness costs. Previous research has found that responses to loud activity such as artillery fire are greater compared with responses to the movement of people,[16] and that other anthropogenic activities such as oil drilling,[42] mining,[43,44] traffic,[45] fireworks,[25] and wildfires[46] might also impact migrations. Few anthropogenic disturbances are likely to be as invasive and intense as armed conflicts, and while effects may not directly cause mortality, we observe prolonged exposure to these events causing significant behavioral changes that may have fitness costs. Our work highlights the potential wider impacts of extreme anthropogenic disturbances and conflict on other migratory and sedentary species in Ukraine or in other internationally important flyways that are similarly impacted; such disturbances could have detrimental effects on hundreds of threatened species and millions of migratory birds.

STAR★METHODS

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

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- EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS
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- METHOD DETAILS

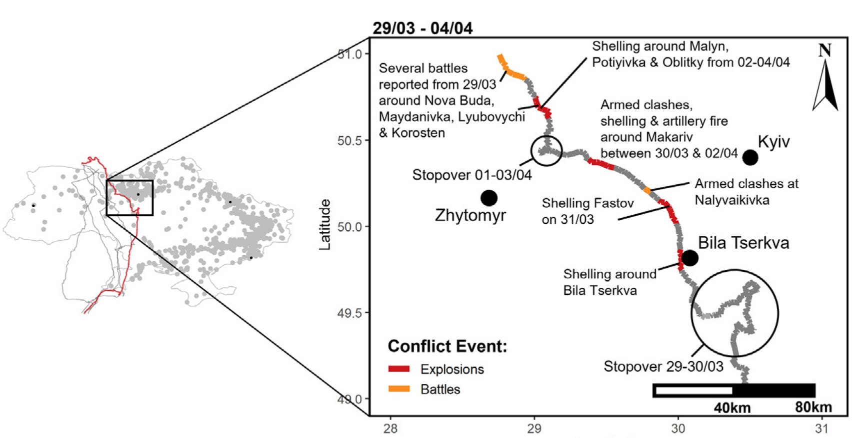

Figure 3. Migration tracks for Denisa

Migration tracks for Denisa (tag: 171034) showing the 2022 spring migration (red) and pre-conflict migrations (gray) in relation to conflict areas from ACLED project data (gray[11,12]) highlighting exposure to specific conflict events (inset). Differences in individual responses are shown in Figure S3.

- Data processing
- QUANTIFICATION AND STATISTICAL ANALYSIS

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.cub.2024.04.047.

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AUTHOR CONTRIBUTIONS

A.A.-B., A.F., and C.R. conceived the study. A.A.-B., P.A., and Ü.V. collected and curated the data. C.R. analyzed the data and wrote the original manuscript. A.A.-B., P.A., A.F., C.R., and Ü.V. reviewed and edited the manuscript.

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		
Processed data and code to reproduce the data analysis and figures	This paper	https://doi.org/10.5281/zenodo.10619944
Raw tracking data	Movebank	Study identifier: 283964859
Software and algorithms		
R Project for Statistical Computing	R Core Team	R 4.2.1; RRID: SCR_001905

RESOURCE AVAILABILITY

Lead contact

Further information and queries should be directed to and will be fulfilled by the lead contact, Charlie Russell (charlie.russell@uea.ac.uk; charliejgr@gmail.com).

Materials availability

There are no newly generated materials associated with this study.

Data and code availability

- The data that support the findings of this study are stored on Movebank (ID: 283964859) but are not publicly available due to the sensitive nature of tracking data for threatened species. To request access, please contact Adham Ashton-Butt, British Trust for Ornithology.
- All original code, and processed datasets to reproduce analyses, have been deposited on Zenodo (https://doi.org/10.5281/zenodo.10619944) and is publicly available as of the date of publication. DOIs are listed in the key resources table.
- Any additional information required to reanalyse the data reported in this paper is available from the lead contact upon request.

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

Data collection

We analysed tracking data from twenty-two adult Greater Spotted Eagles from Belarusian Polesia. Individuals were fitted with OrniTrack-30 GPS transmitters (Ornitela; www.ornitela.org) between 2017 and 2021 as part of a study on breeding behavior and migration of the population. Transmitters were fitted using a Teflon ribbon harness in a backpack configuration weighing ~30 g, less than 2% of the birds' body mass. The tags recorded the location of each bird, speed and altitude every 5 min between 04:00 and 21:00 (Minsk-Time) over a period of several years. Data were downloaded via the Global System for Mobile communication network and deposited in Movebank (www.movebank.org).

METHOD DETAILS

Data processing

Movement data were pre-processed to filter out grossly unrealistic movements using criteria for ground speed, step length and turning angle using the R packages amt and atlastools.[47,48] Tracking data for the pre-breeding migration period was then extracted by defining the start of each migration as the first day an individual travels >10km north[49] and the end of the migration as the first day when a bird reached its known breeding grounds. Migrations were separated into two groups: within Ukraine (north of 44° latitude, the southernmost point of Ukraine, where the impacts of conflict were hypothesised to occur) and the entire migration. There were an average of 137 GPS locations (± 54) per day across 77 separate spring migrations. Seventeen eagles had data for migrations in pre-conflict years and 2022, three eagles only had data for pre-conflict years and two eagles only had data for 2022. Tracking data for 2018 was a lower resolution, so excluded from analysis in the main text. Inclusion of this data does not impact results (Figure S4; Table S4).

QUANTIFICATION AND STATISTICAL ANALYSIS

Stopover sites in Ukraine were identified using the R package track2KBA[11] for spring migrations in pre-conflict years (2018–2021) using 50% utilisation distributions at a resolution of 1km^2 for each migration with a smoothing parameter of 10km to identify the spatial scale at which birds spend the most time, representing stopover sites.[14] Frequency and duration of stopovers at each common site were calculated from observing migration paths in DYNAMOVis.[50]

Migration performance metrics including: altitude, turning angle and speed were calculated for each individual in pre-conflict years and in 2022 across the pre-breeding migration at three temporal scales (hourly, daily & overall). Migration duration was compared for the whole period. Route deviation was determined as the ratio of the cumulative distance travelled over the straight-line distance between the first and last GPS locations for each day, across Ukraine and overall. Differences in hourly, daily and overall averages of each migration performance metric and route deviation index between pre-conflict migrations and 2022 were analysed using mixed models, selected by Akaike information criterion (AIC) and parsimony, accounting for individuals as a random effect. Sex was modelled as an additional fixed effect and interaction term to test whether responses to conflict differed between sexes. Variation across individuals was also explored (Figure S3) as well as across latitudinal bands (Figure S2).

There are high levels of variation in migration routes and other variables which might explain the differences observed in 2022. To isolate the potential effects of conflict on Greater Spotted Eagle migration a conflict-free control zone was used outside of Ukraine (between 41.7° and 44° latitude; the point where the migration of African and European wintering populations meets up to the southern border of Ukraine; Figure S1; Table S1) where no significant differences were observed. All flight fixes were annotated with precipitation and wind using the R package RNCEP[51] to interpolate u- and v-wind components from the NOAA NCEP global atmospheric reanalysis model from the 970 mb pressure level, equivalent to a flight height of approximately 350 m above sea level (the average flight height of Greater Spotted Eagles migrating through Ukraine). During pre-conflict years, weather was a significant predictor explaining natural inter-annual variation in migration metrics (Table S3) but did not explain all of the variation observed in 2022. In mixed models including meteorological conditions and conflict, conflict explained a greater proportion of the variation observed (Table S2). Individual identifiers were included in all models as a random effect and influential data points tested.