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Tracking data highlight the importance of human-induced mortality for large migratory birds at a flyway scale

Juan Serratosa [a,*], Steffen Oppel [b], Shay Rotics [et], Andrea Santangeli [d], Stuart H.M. Butchart [a,e], Luis S. Cano-Alonso [f], Jose Luis Tellería [g], Ryno Kemp [h], Aaron Nicholas [i], Aigars Kalvāns [j], Aitor Galarza [k], Aldina M.A. Franco [l], Alessandro Andreotti [m], Alexander N.G. Kirschel [n], Alex Ngari [o], Alvaro Soutullo [p], Ana Bermejo-Bermejo [q], Andre J. Botha [r], Andrea Ferri [m], Angelos Evangelidis [s], Anna Cenerini [t], Anton Stamenov [u], Antonio Hernández-Matías [v], Arianna Aradis [w], Atanas P. Grozdanov [x], Beneharo Rodríguez [y], Çağan H. Şekercioğlu [z,aa], Catuxa Cerecedo-Iglesias [v], Christina Kassara [ab], Christos Barboutis [s], Claire Bracebridge [ac], Clara García-Ripollés [ad], Corinne J. Kendall [ac], Damijan Denac [ae], Dana G. Schabo [af], David R. Barber [ag], Dimitar V. Popov [ah], Dobromir D. Dobrev [ai], Egidio Mallia [aj,ax], Elena Kmetova-Biro [ak,al], Ernesto Álvarez [am], Evan R. Buechley [an], Evgeny A. Bragin [ao], Fabrizio Cordischi [ap], Fadzai M. Zengeya [aq], Flavio Monti [ar,as], Francois Mougeot [at], Gareth Tate [r,au], Georgi Stoyanov [av], Giacomo Dell'Omo [aw], Giuseppe Lucia [ax], Gradimir Gradev [ah,ay], Guido Ceccolini [t], Guilad Friedemann [az], Hans-Günther Bauer [ba], Holger Kolberg [bb,bc], Hristo Peshev [bd,be], Inês Catry [bf,bg], Ingar J. Øien [bh], Isidoro Carbonell Alanís [bi], Ivan Literák [bj], Ivan Pokrovsky [ba], Ivar Ojaste [bk], Jan E. Østnes [bl], Javier de la Puente [q], Joan Real [v], João L. Guilherme [a,dc], José C. González [bn], José M. Fernández-García [bo], Juan Antonio Gil [bp], Julien Terraube [bq], Karel Poprach [br,bs], Karen Aghababyan [bt], Katharina Klein [bu], Keith L. Bildstein [bv], Kerri Wolter [h], Kjell Janssens [bw,bx], Kyle D. Kittelberger [by], Lindy J. Thompson [r,bz], Mansoor H. AlJahdhami [ca,eu], Manuel Galán [am], Marcin Tobolka [cb,cc], Mario Posillico [cd], Mario Cipollone [ce], Marion Gschweng [cf], Māris Strazds [cg,ch], Mark Boorman [ci], Mark Zvidzai [cj], Marta Acácio [ck], Marta Romero [cl], Martin Wikelski [ba,cm], Matthias Schmidt [cn], Maurizio Sarà [co,cp], Michael J. McGrady [cq], Mindaugas Dagys [cr], Monique L. Mackenzie [cs,ct], Muna Al Taq [cu], Msafiri P. Mgumba [i], Munir Z. Virani [cv], Nicolaos I. Kassinis [cw], Nicolò Borgianni [ce], Nikki Thie [cx], Nikos Tsiopelas [s], Nili Anglister [c], Nina Farwig [cy], Nir Sapir [cz], Oddmund Kleven [da], Oliver Krone [db], Olivier Duriez [dc], Orr Spiegel [ck], Osama Al Nouri [cu], Pascual López-López [dd], Patrik Byholm [de,df], Pauline L. Kamath [dg], Paweł Mirski [dh], Peter Palatitz [di], Pietro Serroni [dj], Rainer Raab [dk], Ralph Buij [an,dl], Ramūnas Žydelis [dm], Ran Nathan [cx], Rauri C.K. Bowie [dn], Rigas Tsiakiris [do], Richard Stratton Hatfield [dp,dq], Roi Harel [cm,dr], Rolf T. Kroglund [bl], Ron Efrat [cz,ds], Ruben Limiñana [dt,du], Salim Javed [dv], Saša P. Marinković [dw], Sascha Rösner [dx], Sasha Pekarsky [cx,cz], Shiv R. Kapila [dq], Simeon A. Marin [dy], Šimon Krejčí [bj], Sinos Giokas [ab], Siranush Tumanyan [dz], Sondra Turjeman [cx,ea], Sonja C. Krüger [eb,ec], Steven R. Ewing [ed], Stoycho Stoychev [u,ee], Stoyan C. Nikolov [u], Tareq E. Qaneer [ef], Theresa Spatz [eg], Thomas G. Hadjikyriakou [eh,ei], Thomas Mueller [ej,ek], Todd E. Katzner [el], Tomas Aarvak [bh],

* Corresponding author.
E-mail addresses: juan.serratosa.lopez@gmail.com (J. Serratosa), vicky.jones@birdlife.org (V.R. Jones).

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Tomáš Veselovský [em], Torgeir Nygård [da], Ugo Mellone [ax,cl], Ülo Väli [en], Urmas Sellis [eo], Vicente Urios [cl], Vladimír Nemček [em,ep], Volen Arkumarev [u], Wayne M. Getz [eq,er], Wolfgang Fiedler [ba,cm], Willem Van den Bossche [es], Yael Lehnardt [ds], Victoria R. Jones [a]

[a] BirdLife International, The David Attenborough Building, Pembroke Street, CB2 3QZ, Cambridge, United Kingdom
[b] RSPB Centre for Conservation Science, David Attenborough Building, Pembroke Street, CB2 3QZ, Cambridge, United Kingdom
[c] Tel-Aviv University, Tel-Aviv, Israel
[d] Animal Demography and Ecology Unit, Institute for Mediterranean Studies (IMEDEA), CSIC-UIB, Esporles, Spain
[e] Department of Zoology, University of Cambridge, Downing Street, CB2 3EJ, Cambridge, United Kingdom
[f] IUCN Species Survival Commission, Rue Mauverney 28, 1196, Gland, Switzerland
[g] Evolution and Conservation Biology Research Group, Universidad Complutense de Madrid, Calle de José Antonio Novais, 12, E-28040, Madrid, Spain
[h] VulPro, Rietfontain, Hartbeespoort, South Africa
[i] Wildlife Conservation Society, Ruaha-Katavi Landscape Program, Tanzania, P.O. Box 1475, Mbeya, Tanzania
[j] Joint Stock Company "Latvia's State Forests", Vaiņodes 1, LV –1004, Riga, Latvia
[k] Aranzadi Science Society, Zorroagagaina 11, San Sebastián, Spain
[l] School of Environmental Sciences, University of East Anglia, NR4 7TJ, Norwich, United Kingdom
[m] Italian Institute for Environmental Protection and Research (ISPRA), Via Cà Fornacetta 9, 40064, Ozzano Emilia (BO), Italy
[n] University of Cyprus, P.O. Box 20537, Nicosia 1678, Cyprus
[o] BirdLife International, Africa Partnership Secretariat, Nairobi, Kenya
[p] Departamento de Ecologia y Gestion Ambiental, Centro Universitario Regional del Este, Universidad de la Republica, Cachimba del Rey entre Bvar. Artigas y Av. Aparicio Saravia., Maldonado, Uruguay
[q] SEO/BirdLife, Melquiades Biencinto 34, 28053, Madrid, Spain
[r] Endangered Wildlife Trust, Private Bag X08, Wierda Park 0149, Gauteng, South Africa
[s] Hellenic Ornithological Society/BirdLife Greece, 52 Ag. Konstantinou Str, GR 10437, Athens, Greece
[t] CERM Endangered Raptors Centre Association, Via Santa Cristina, 6, 58055, Rocchette di Fazio, (GR), Italy
[u] Bulgarian Society for the Protection of Birds/BirdLife Bulgaria, Yavorov District, Block 71, entr. 4, app. 1, 1111, Sofia, Bulgaria
[v] Conservation Biology Group, Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals, Facultat de Biologia and Institut de Recerca de la Biodiversitat (IRBio), Universitat de Barcelona, Av. Diagonal, 643, 08028, Barcelona, Spain
[w] Italian Institute for Environmental Protection and Research (ISPRA), Via Vitaliano Brancati, 60, 00144, Rome, Italy
[x] Department of zoology and anthropology, Faculty of biology, Sofia University, 8, Dragan Tzankov blvd., Sofia, Bulgaria
[y] Canary Islands' Ornithology and Natural History Group (GOHNIC), La Malecita S/N, 38480, Buenavista del Norte, Spain
[z] School of Biological Sciences, University of Utah, Salt Lake City, USA
[aa] Department of Molecular Biology and Genetics, Koç University, Istanbul, Türkiye
[ab] Department of Biology, University of Patras, Panepistimioupoli Rio, GR 26500, Patras, Greece
[ac] North Carolina Zoo, 4401 Zoo Parkway, 27205, Asheboro, NC, USA
[ad] Environment, Science and Solutions SLU, Carrer Les Moreres 14, Esc A, piso 10, pta 29, Valencia, Spain
[ae] DOPPS - BirdLife Slovenia, Trzaska cesta 2, Ljubljana, Slovenia
[af] Conservation Ecology, Faculty of Biology, Philipps-University Marburg, Karl-von-Frisch Str. 8, D-35044, Marburg, Germany
[ag] Acopian Center for Conservation Learning, Hawk Mountain Sanctuary, 410 Summer Valley Road, 17961, Orwigsburg, PA, USA
[ah] Green Balkans, 1A Skopie Blvd., office 10, 4000, Plovdiv, Bulgaria
[ai] Bulgarian Society for the Protection of Birds/BirdLife Bulgaria, 5 Leonardo da Vinci Str., Plovdiv, Bulgaria
[aj] Parco Gallipoli Cognato Piccole Dolomiti Lucane, Via Mazzara 10, San Vito Sullo Ionio, Italy
[ak] Green Balkans, 30, Boruygrad Str., Stara Zagora, Bulgaria
[al] Austrian Ornithological Centre (AOC), Konrad Lorenz Institute of Ethology, University of Veterinary Medicine Vienna, Vienna, Austria
[am] GREFA, Monte del Pilar, s/n, 28220, Majadahonda, Spain
[an] The Peregrine Fund, 5668 West Flying Hawk Lane, 83709, Boise, ID, USA
[ao] Faculty of Natural Science, Kostanay State Pedagogical, Kostanay, Kazakhstan
[ap] Rewilding Apennines, Via Sante Marie 2, Avezzano, (AQ), Italy
[aq] Department of Geography Geospatial Sciences and Earth Observation, University of Zimbabwe, P.O. Box, MP 167, Mt Pleasant, Harare, Zimbabwe
[ar] Institute of Research on Terrestrial Ecosystems (IRET), National Research Council (CNR), Campus Ecotekne, 73100, Lecce, Italy
[as] Maremma Natural History Museum, Strada Corsini 5, 58100, Grosseto, Italy
[at] Instituto de Investigación en Recursos Cinegéticos (IREC), CSIC-UCLM-JCCM, Ronda de Toledo 12, 13005, Ciudad Real, Spain
[au] FitzPatrick Institute of African Ornithology, DST-NRF Centre of Excellence, University of Cape Town, Rondebosch, South Africa
[av] Birds of Prey Protection Society, 23 Golyam Bratan Str., Sofia, Bulgaria
[aw] Ornis Italica, Piazza Crati 15, Rome, Italy
[ax] Mediterranean Raptor Migration Network (MEDRAPTORS), Viale Partigiani 19, 27100, Pavia, Italy
[ay] Department of Agroecology and Environmental Protection, Faculty of Plant Protection and Agroecology, Agricultural University, 12 Mendeleev, 4000, Plovdiv, Bulgaria
[az] Tel-Aviv University, 19 Meller Chaim st., Mazkeret Batya, Israel
[ba] Department of Migration, Max Planck Institute of Animal Behavior, Am Obstberg 1, 78315, Radolfzell, Germany
[bb] Vultures Namibia, P.O. Box 6132, Ausspannplatz, Windhoek, Namibia
[bc] Ministry of Environment, Forestry and Tourism, Private Bag 13306, Windhoek, Namibia
[bd] Fund for Wild Flora & Fauna, 49 Ivan Mihaylov Str., Office 327, P.O. Box 78, Blagoevgrad, Bulgaria
[be] Department of Geography, Ecology and Environmental Protection, Faculty of Mathematics and Natural Sciences, South-West University Neofit Rilski, 66 Ivan Mihaylov Str., 2700, Blagoevgrad, Bulgaria
[bf] CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, InBIO Laboratório Associado, Campus de Vairão, Universidade do Porto, 4485-661, Vairão, Portugal
[bg] CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, InBIO Laboratório Associado, Instituto Superior de Agronomia, Universidade de Lisboa, 1349-017, Lisboa, Portugal
[bh] BirdLife Norway, Sandgata 30 b, NO-7012, Trondheim, Norway
[bi] Saloro, Barruecopardo, Salamanca, Spain
[bj] Department of Biology and Wildlife Diseases, Faculty of Veterinary Hygiene and Ecology, University of Veterinary Sciences Brno, Palackého tř. 1946/1, 61242, Brno, Czech Republic
[bk] Estonian University of Life Sciences, Fr. R. Kreutzwaldi str 1, Tartu, Estonia
[bl] Faculty of Biosciences and Aquaculture, Nord University, P.O. Box 2501, NO-7729, Steinkjer, Norway
[bn] Fundación para la Conservación del Quebrantahuesos (FCQ), Centro las Montañas del Quebrantahuesos finca tullidi s/n, Benia de Onís, Spain
[bo] Hazi Foundation, Granja Modelo, 01192, Arkaute, Spain
[bp] Fundación para la Conservación del Quebrantahuesos (FCQ), Plaza San Pedro Nolasco, n°1, 4-F, Zaragoza, Spain
[bq] Vulture Conservation Foundation, Wuhrstrasse 12, CH-8003, Zürich, Switzerland
[br] TYTO, Nenakonice 500, 78375, Věrovany, Czech Republic

[bs] Palacký University Olomouc, Křížkovského 511/8, 77900, Olomouc, Czech Republic
[bt] BirdLinks Armenia NGO, 87b Dimitrov, apt 14, Yerevan, Armenia
[bu] Natur&emwelt a.s.b.l., 5, route de Luxembourg, Kockelscheuer, Luxembourg
[bv] Acopian Center for Conservation Science, Hawk Mountain Sanctuary Association, 410 Summer Valley Road, 17961, Orwigsburg, PA, USA
[bw] Dutch Montagu's Harrier Foundation, Berkenweg 1, 9471, Zuidlaren, the Netherlands
[bx] INBO Institute for Nature and Forest Research, Havenlaan 88, 1000, Brussels, Belgium
[by] School of Biological Sciences, University of Utah, 257 S 1400 E, 84112, Salt Lake City, UT, USA
[bz] Centre for Functional Biodiversity, School of Life Sciences, University of KwaZulu-Natal, Private Bag X01, Scottsville, 3209, Pietermaritzburg, South Africa
[ca] Office for Conservation of the Environment, Diwan of Royal Court, Oman
[cb] Department of Zoology, Poznań University of Life Sciences, Wojska Polskiego 71C, 60-625, Poznań, Poland
[cc] Konrad Lorenz Institute of Ethology, University of Veterinary Medicine Vienna, Savoyenstraße 1a, 1160, Vienna, Austria
[cd] Reparto Carabinieri Biodiversità Castel di Sangro, Via Sangro 45, Castel di Sangro, (AQ), Italy
[ce] Rewilding Apennines, Via San Giorgio 5, 67055, Gioia dei Marsi (AQ), Italy
[cf] Concepts for Conservation, Postfach 11 01, 89144, Laichingen, Germany
[cg] Laboratory of Ornithology, Institute of Biology, University of Latvia, Jelgavas iela 1–718, LV–1004, Riga, Latvia
[ch] Latvian Ornithological Society, Riga, Latvia
[ci] Vultures Namibia, P.O. Box 1445, Swakopmund, Namibia
[cj] University of Zimbabwe, PO Box, MP 167, Mt Pleasant, Harare, Zimbabwe
[ck] School of Zoology, Faculty of Life Sciences, Tel Aviv University, 69978, Tel Aviv, Israel
[cl] Grupo de Investigación Zoología de Vertebrados, Universidad de Alicante, Campus San Vicente del Raspeig, Edificio Ciencias III, 03080, Alicante, Spain
[cm] Centre for the Advanced Study of Collective Behaviour, University of Konstanz, 78457, Konstanz, Germany
[cn] BirdLife Austria, Museumsplatz 1/10/8, 1070, Vienna, Austria
[co] Department of Biological, Chemical and Pharmaceutical Sciences and Technologies, University of Palermo, Via Archirafi 18, Palermo, Italy
[cp] National Biodiversity Future Center (NBFC), Piazza Marina 61, 90133, Palermo, Italy
[cq] International Avian Research, Am Rosenhugel 59, Krems, Austria
[cr] Nature Research Center, Akademijos st. 2, 08412, Vilnius, Lithuania
[cs] University of St Andrews, College Gate, North Street, St Andrews, United Kingdom
[ct] Namibia University of Science and Technology, Windhoek, Namibia
[cu] BirdLife Middle East Regional Office, P.O. Box 2295, 11953, Amman, Jordan
[cv] Mohamed bin Zayed Raptor Conservation Fund, 129555, Abu Dhabi, United Arab Emirates
[cw] Game and Fauna Service, Ministry of Interior, 1453, Nicosia, Cyprus
[cx] Movement Ecology Laboratory, Department of Ecology, Evolution and Behavior, Alexander Silberman Institute of Life Sciences, The Hebrew University of Jerusalem, 91904, Jerusalem, Israel
[cy] Conservation Ecology, Faculty of Biology, Philipps-University Marburg, Karl-von-Frisch Str. 8, D-35043, Marburg, Germany
[cz] Department of Evolutionary & Environmental Biology and Institute of Evolution, University of Haifa, 199 Aba Khoushy Ave. Mount Carmel, 3498838, Haifa, Israel
[da] Norwegian Institute for Nature Research, P.O. Box 5685 Torgarden, NO-7485, Trondheim, Norway
[db] Leibniz Institute for Zoo and Wildlife Research, Dept. Wildlife Diseases, Alfred-Kowalke-Straße 17, 10315 , Berlin, Germany
[dc] CEFE, Univ Montpellier, CNRS, EPHE, 1919 route de Mende, 34293, Montpellier, France
[dd] Cavanilles Institute of Biodiversity and Evolutionary Biology, University of Valencia, C/Catedrático José Beltrán 2, Paterna, Valencia, Spain
[de] Novia University of Applied Sciences, Raseborgsvägen 9, FI-10600, Ekenäs, Finland
[df] Organismal & Evolutionary Biology, University of Helsinki, P.O. Box 65, FI-00014, Helsinki, Finland
[dg] School of Food and Agriculture, University of Maine, 5735 Hitchner Hall, Rm 342, Orono, ME, USA
[dh] Faculty of Biology, University of Białystok, Ciołkowskiego 1J, 15-245, Białystok, Poland
[di] MME BirdLife Hungary, 1121 Kolto Str. 21, Budapest, Hungary
[dj] Ente Parco Nazionale del Pollino, c.da Santa Maria, 85048, Rotonda, (PZ), Italy
[dk] TB Raab GmbH, Quadenstraße 13, 2232, Deutsch-Wagram, Austria
[dl] Animal Ecology, Wageningen Environmental Research, Droevendaalsesteeg 3A, 6708 PB, Wageningen, the Netherlands
[dm] Ornitela, UAB, Švitrigailos st. 11K-109, 03228, Vilnius, Lithuania
[dn] Museum of Vertebrate Zoology & Department of Integrative Biology, University of California, 3101 Valley Life Sciences Building, Berkeley, USA
[do] Ministry of Environment & Energy, General Secretariat of Forests, Forestry Service of Ioannina, Marikas Kotopouli Street 62, Ampelokipoi, 454 45, Ioannina, Greece
[dp] Wageningen University and Research, Droevendaalsesteeg 3A, 6708 PB, Wageningen, the Netherlands
[dq] The Kenya Bird of Prey Trust, P.O. Box 883, 20117, Naivasha, Kenya
[dr] Department for the Ecology of Animal Societies, Max Planck Institute of Animal Behavior, Bucklestrasse 5, 78464, Konstanz, Germany
[ds] Mitrani Department of Desert Ecology, Jacob Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, 8499000, Midreshet Ben-Gurion, Israel
[dt] Departamento de Didáctica General y Didácticas Específicas, Universidad de Alicante, 03080, Alicante, Spain
[du] Instituto Universitario de Física Aplicada a las Ciencias y la Tecnología (IUFACyT), Universidad de Alicante, 03080, Alicante, Spain
[dv] Environment Agency-Abu Dhabi, Mamoura Building, Tower 1, Maroor Street, Abu Dhabi, United Arab Emirates
[dw] Institute for Biological Research, The Belgrade University, Bulevar Mihajla Pupina 3, Belgrade, Serbia
[dx] Conservation Ecology, Faculty of Biology, Philipps-University Marburg, Karl-von-Frisch Str. 8, D-35045, Marburg, Germany
[dy] Green Balkans, Cherkovna str., 75B, ap.36, 1505, Sofia, Bulgaria
[dz] Hawk Mountain Sanctuary, Khaghagh-Don street 27, apt.33, 0087, Yerevan, Armenia
[ea] Azrieli Faculty of Medicine, Bar-Ilan University, Safed, Israel
[eb] Ezemvelo KZN Wildlife, P.O. Box 13053, Cascades, 3202, Pietermaritzburg, South Africa
[ec] Centre for Functional Biodiversity, School of Life Sciences, University of KwaZulu-Natal, Pietermaritzburg, South Africa
[ed] RSPB Centre for Conservation Science, 2 Lochside View, Edinburgh Park, EH12 9DH, Edinburgh, United Kingdom
[ee] Paisii Hilendarski University of Plovdiv, 4027, Plovdiv, Bulgaria
[ef] The Royal Society for the Conservation of Nature, 1215, Jubaiha, 11941, Amman, Jordan
[eg] Conservation Ecology, Faculty of Biology, Philipps-University Marburg, Karl-von-Frisch Str. 8, D-35046, Marburg, Germany
[eh] Department of Biological Sciences, University of Cyprus, P.O. Box 20537, 1678, Nicosia, Cyprus
[ei] Akrotiri Environmental Education Centre, 4640, Akrotiri, Cyprus
[ej] Senckenberg Biodiversity and Climate Research Centre, Georg Voigt Str. 14-16, Frankfurt, Germany
[ek] Department of Biological Sciences, Goethe-University Frankfurt, Frankfurt, Germany
[el] U.S. Geological Survey, 230 N. Collins Rd., 83702, Boise, ID, USA
[em] Raptor Protection of Slovakia, Trhová 54, 841 01, Bratislava, Slovakia
[en] Institute of Agricultural and Environmental Sciences, Estonian University of Life Sciences, Kreutzwaldi 5D, Tartu, Estonia
[eo] Eagle Club Estonia, Hauka, Polvamaa, Estonia
[ep] Saola - Nature Conservation, Ľubovníková 34, 841 07, Bratislava, Slovakia
[eq] Department of Environmental Science, Policy, and Management, University of California at Berkeley, 130 Mulford Hall, 94720-3114, Berkeley, CA, USA

[er] School of Mathematical Sciences, University of KwaZulu-Natal, Durban, South Africa
[es] BirdLife Europe & Central Asia, c/o Hive5, Cours Saint-Michel 30B, Brussels, Belgium
[et] School of Zoology, Faculty of Life Sciences, and the Steinhardt Museum of Natural History, Tel Aviv University
[eu] Department of Biology, College of Science, Sultan Qaboos University, P.O.Box 36 Muscat 123, Oman

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ABSTRACT

Human-induced direct mortality affects huge numbers of birds each year, threatening hundreds of species worldwide. Tracking technologies can be an important tool to investigate temporal and spatial patterns of bird mortality as well as their drivers. We compiled 1704 mortality records from tracking studies across the African-Eurasian flyway for 45 species, including raptors, storks, and cranes, covering the period from 2003 to 2021. Our results show a higher frequency of human-induced causes of mortality than natural causes across taxonomic groups, geographical areas, and age classes. Moreover, we found that the frequency of human-induced mortality remained stable over the study period. From the human-induced mortality events with a known cause ($n = 637$), three main causes were identified: electrocution (40.5 %), illegal killing (21.7 %), and poisoning (16.3 %). Additionally, combined energy infrastructure-related mortality (i.e., electrocution, power line collision, and wind-farm collision) represented 49 % of all human-induced mortality events. Using a random forest model, the main predictors of human-induced mortality were found to be taxonomic group, geographic location (latitude and longitude), and human footprint index value at the location of mortality. Despite conservation efforts, human drivers of bird mortality in the African-Eurasian flyway do not appear to have declined over the last 15 years for the studied group of species. Results suggest that stronger conservation actions to address these threats across the flyway can reduce their impacts on species. In particular, projected future development of energy infrastructure is a representative example where application of planning, operation, and mitigation measures can enhance bird conservation.

1. Introduction

Across the world, anthropogenic stressors are contributing to the decline of bird populations of many species, resulting in the deterioration of their conservation status (BirdLife International, 2022; Lees et al., 2022; Rosenberg et al., 2019; Şekercioğlu et al., 2004). Some stressors directly kill individuals (e.g., road collision, illegal shooting, or trapping) while others have indirect impacts (e.g., habitat loss and degradation). Annually, millions of birds die from direct anthropogenic stressors (hereafter referred as human-induced mortality), affecting hundreds of bird species worldwide (Calvert et al., 2013; Loss et al., 2015). For some species groups like predatory raptors (Madden et al., 2019), vultures (Ogada et al., 2016b), and bustards (Collar et al., 2017), human-induced mortality can be particularly important, with impacts on their conservation status (Chevallier et al., 2015; Di Vittorio et al., 2018; López-López et al., 2011). Despite its importance, relatively little is known about how human-induced mortality varies geographically and temporally, and the anthropogenic, ecological, and abiotic factors influencing this variation (Loss et al., 2015). For many species with declining populations, reducing direct mortality can help arrest those declines (Etheridge et al., 1997; Oppel et al., 2023; Whitfield et al., 2004). Thus, a better understanding of human-induced mortality is crucial for the effective conservation of birds (Longcore and Smith, 2013).

Tracking technologies have been increasingly used during the last 30 years to gain insights into avian ecology and biology (Kays et al., 2020; Nathan et al., 2022; Wilmers et al., 2015). During the last decade, there has been an increasing interest in understanding bird mortality, with important examples of studies for a variety of species like white stork (*Ciconia ciconia*) (Cheng et al., 2019; Rotics et al., 2021; Rotics et al., 2017; Rotics et al., 2016), black stork (*Ciconia nigra*) (Cano et al., 2013), Egyptian vulture (*Neophron percnopterus*) (Buechley et al., 2021; Oppel et al., 2015), black kite (*Milvus migrans*) (Sergio et al., 2019; Sergio et al., 2018; Sergio et al., 2014), little bustard (*Tetrax tetrax*) (Marcelino et al., 2018), osprey (*Pandion haliaetus*), European honey buzzard (*Pernis apivorus*) and harriers (*Circus spp*) (Klaassen et al., 2014; Strandberg et al., 2010). While a wealth of conservation-relevant data pertinent to understanding bird mortality are generated during tracking projects, these data are often not analysed or published by researchers whose focus is typically on other research questions. The high spatial and temporal accuracy of tracking technologies allow to reduce the biases in detection and reporting of bird mortalities, providing a great opportunity to investigate general trends in avian migrants' mortality in a multi-species framework.

Human socio-economic features, as well as ecological and biological factors, may influence the magnitude of different causes of mortality to bird populations (Buchan et al., 2022) and these can vary geographically throughout their ranges (Oppel et al., 2021; Santangeli et al., 2019). Studies at large spatial and temporal scales are particularly important to analyse this variability and assess how particular causes of mortality impact species (Kirby et al., 2008; Vickery et al., 2014). However, many studies are conducted at national or regional scales or relate to only a single population or species. Multi-species approaches can be helpful in providing information about shared causes of mortality that can be pooled among taxonomic groups and different geographic areas to generate a more complete picture. In this way, tracked individuals can act as sentinels, providing data which, when pooled across many species, contribute to our understanding of spatial patterns and temporal trends.

To assess the relative importance and prevalence of different causes of mortality in the African-Eurasian flyway, we gathered information from multiple researchers/studies on 45 migratory bird species. Specifically, our main objectives were to: i) investigate multi-species tracking data to gain insights into causes of bird mortality, ii) investigate temporal trends in human-induced and natural causes of bird mortality, iii) identify the main causes of human-induced mortality and iv) investigate factors influencing human-induced causes.

2. Material and methods

2.1. Data collation

The study area focused on the African-Eurasian flyway. This flyway has been intensively studied compared with other parts of the world in terms of the number of tracking studies (Guilherme et al., 2023; Kays et al., 2020), making it an ideal focal flyway for this work.

Our analysis was restricted to large bodied terrestrial birds: storks (Family Ciconiidae), cranes (Family Gruidae), and raptors sensu lato (Family Accipitridae, Falconidae and Pandionidae) identified as meeting the Convention on Migratory Species (CMS) definition of 'migratory' (Article I of the CMS convention text https://www.cms.int/en/convent ion-text, and UNEP/CMS 2020) and distributed within the African-Eurasian flyway (see full list of species in Supplementary material – Table S1). The reason for restricting the study to these taxonomic groups was that until recently only larger-bodied bird species could be tagged with the heavier transmitter types that generate accurate positional information (Bridge et al., 2011) that could be retrieved from dead animals. We focused exclusively on data from PTT, GPS, and GPS-GSM since these have the necessary spatial and temporal accuracy for identifying mortality events correctly and transmit the geographical information remotely. Moreover, the selected taxonomic groups comprise many species that have been studied for sufficiently long in the study area that there were enough tagged individuals to permit robust analyses.

To identify potential data holders working on the focal species, we conducted a literature review (scientific and grey) and web search (completed in February 2021). For the literature review we employed Google scholar, using the formula = TITLE-ABS-KEY ("common name" OR "scientific name") AND ("ptt" OR "satellite" OR "gps" OR "tracking"). The web search was done using Google, with a particular focus on tracking databases (e.g., Movebank, Satellitetracking.eu, Birdtelemetry.cz, Birdmap.5dvision.ee). BirdLife International partners (national NGOs) assisted in identifying and contacting potential collaborators. In total, 207 potential collaborators were contacted and requested to contribute data related to mortality events in a standardized data template. This comprised a summary information section and a mortality information section (Supplementary material – Table S2). In the summary section we requested data from each species on i) number of individuals tagged, ii) number of mortality events identified, iii) number of technical failures, and iv) number of unknown causes of tag malfunctioning or transmission failure. Technical failures included events where researchers could confirm the tags fell from the individual or stopped transmitting before the estimated life expectancy of the device. Unknown causes included all those events in which the fate of the bird and/or the tag could not be determined. We estimated the minimum proportion of mortality events from a cohort of tagged birds by excluding unknown causes, and the maximum potential proportion of mortality events by assuming all unknown causes related to mortality of the tagged bird.

In the mortality section, we requested general information about the mortality events for each species. Since mortality events derived from tracking data can be identified using different methods with different likelihoods of a correct assessment, we asked researchers to classify the reported events according to three categories (modified from Klaassen et al., 2014):

- *Possible death of bird*. Loss of signal occurred abruptly and despite preceding good transmission and/or battery performance, or transmitter was continuously transmitting from the same position without indicating movement (activity counter stopped). No further investigation was made using any remote or on the ground method (or if used it did not provide any useful insights into the event); cause of death would be 'unknown' for events in this category most of the time.
- *Very probable death of bird.* Tracking data indicated mortality, and this was categorized as very probable using remote methods (see details below) that helped in the identification of the event (e.g., Sergio et al., 2018). These methods include any type of analysis performed remotely and/or assisted by other devices tagged to the birds (e.g., use of GIS software, statistical analysis of tracking data, accelerometer data, insights from weather conditions, remote sensing, temperature sensors). Since the likelihood of a correct identification varies with the precise method employed, slight differences may be found between methods.
- *Confirmed death of bird*. Tracking data indicated mortality, and this was confirmed by additional in-situ observations (e.g., field observation by researcher or local contacts). Events classified in this category had the highest probability of correctly identifying a mortality event.

Lastly, information was requested about causes of death. The data form included five natural and eight human-induced categories covering the most common causes reported. The natural category included: i) drowning, ii) predation, iii) starvation/exhaustion, iv) disease, and v) other. The human-induced category included: i) illegal killing (i.e., intentional direct killing, considered illegal in some countries of our study), ii) electrocution, iii) power line collision, iv) wind-farm collision, v) road collision (i.e., hit by vehicle), vi) other collision (e.g., building), vii) poisoning, and viii) other. Within the poisoning category we did not distinguish between different types of poisoning (e.g., intentional, accidental, environmental) because of the difficulty in determining the nature of these events. No information was collected on the certainty of the method used to identify the cause of mortality.

2.2. Data analyses

To investigate the relative importance of human-induced, natural, and unknown causes of mortality, we calculated the proportion of each of these three categories in relation to total deaths across different taxonomic groups, geographic areas, and age classes. Moreover, to investigate whether the proportion of human-induced mortality changed over time, we fitted generalized linear models (GLM) with a logit-link function and a binomial error distribution using the R package "stats" (R Core Team, 2023). The response variable was the percentage of human-induced mortality in relation to the total known causes of mortality (i.e., natural mortality + human-induced mortality) pooling all species together, and the year in which the mortality occurred was used as a continuous explanatory variable. To explore the effect of the unknown causes of mortality in the compiled dataset, three different models were developed. The first model included only mortality events with known causes of mortality excluding those with unknown causes of mortality (n = 1026); the second model included mortality events with unknown causes assigned to the category 'human-induced mortality' (n = 1697). The third model included mortality events with unknown causes assigned to the category 'natural mortality' (n = 1697). In this way, we could explore the minimum and maximum proportions between human-induced and natural mortalities. A total of seven mortality events did not include a death date and were excluded from this part of the analysis. To ensure model suitability, we tested uniformity of residuals using the function provided in the R package "DHARMa" (Hartig, 2017).

Different factors may influence the probability of a bird dying from a natural or a human-induced cause. These can be socio-economic factors that affect the prevalence of certain threats like illegal killing (Brochet et al., 2016), the degree of landscape modification (Arrondo et al., 2020), or simply intrinsic biological and ecological traits of the species (De Pascalis et al., 2020). Moreover, these threats can also show geographical gradients that may influence their importance on bird mortality (Buchan et al., 2022; Oppel et al., 2021), and ultimately inform conservation efforts across regions. To analyse this probability and the influence of different socio-economic, ecological, geographical, and biological factors, we fitted random forest (RF) models for classification of the mortality events with an identified cause. To simplify the response variable, we pooled the different mortality causes into two categories: natural and human-induced mortality (n = 1030).

RF is a machine learning algorithm and a powerful statistical classifier that is widely used for statistical analysis of ecological data; the approach creates an ensemble of classification trees and then combines the predictions from all trees (Breiman, 2001; Cutler et al., 2007; Liaw and Wiener, 2002). Moreover, RF can deal with continuous and categorical data as predictor variables in the models. In our analysis, a total of 500 trees were constructed using bootstrap samples from the dataset without replacement (Strobl et al., 2007). To assess the accuracy of the model, c.63 % of the original data are used to construct the trees, the rest of the observations ('out-of-the-bag' sample) were used to assess the classification success of the tree structure. The relative importance of each predictor variable was evaluated as the mean decrease in accuracy of the model if that predictor was randomly permuted (Cutler et al., 2007), and its statistical significance was tested using the permutation algorithm implemented in the library rfPermute using 1000 runs (Archer, 2015).

To build the RF model, we used a combination of categorical and continuous predictor variables that accounted for the main potential drivers of mortality. The categorical variables included in the models were: i) taxonomic group: species were pooled together in 10 taxonomic groups: buzzards (genera *Buteo,* and *Pernis*), cranes (genus *Grus*), eagles (genera *Aquila, Circaetus, Clanga, Haliaeetus,* and *Hieraaetus*), falcons (genus *Falco*), harriers (genus *Circus*), hawks (genus *Accipiter*), kites (genus *Milvus*), ospreys (genus *Pandion*), storks (genus *Ciconia*), and vultures (genera *Aegypius*, *Gyps*, *Gypaetus*, *Necrosyrtes*, *Neophron*, *Torgos*, and *Trigonoceps*), which reflect the different ecological and biological characteristics of the species that may influence the cause of mortality, ii) age: differences in development and maturation of the different species made it difficult to impose consistent sub-categories of age or maturation on non-adult individuals. Therefore, only two generic categories that could be applied consistently were used for an individual's age: 'adult' and 'non-adult', iii) migratory status: even if all species included in our analysis are considered as migratory using the CMS definition (see methods), some populations of these species may be non-migratory or partial migratory (i.e., migratory and non-migratory individuals exist within the same population). To analyse the influence of this factor, we specifically categorized the migratory status (i.e., migratory, non-migratory, and partial migratory) at a population level for each species included through a literature review and information from the data-holders participating in the study (Supplementary material – Table S9), iv) origin: the dataset included wild individuals and individuals that had been reintroduced to the wild from captive breeding programs. The influence of this factor is context-dependent with some studies reporting an effect on bird mortality (Armstrong et al., 2017; Tavecchia et al., 2009), while others have not found any effect (Buechley et al., 2021; Efrat et al., 2022).

Four continuous predictor variables were also employed: i) latitude of mortality event, ii) longitude of mortality event, iii) year, and iv) human footprint index: created by the Wildlife Conservation Society (https://wcshumanfootprint.org/); this index is a proxy for landscape modification and is calculated based on five categories: population density, land cover/land use, built infrastructure, accessibility, and power consumption (Sanderson et al., in press; Venter et al., 2016). Recent versions of the index cover years from 2000 to 2019 and are available at 300 m spatial resolution. This allowed us to calculate the value of the index for the same year in which the mortality event occurred and the specific geographical location. Mortality events from 2020 and 2021 were assigned to the latest information from 2019. Two different generations of maps have been produced, the so-called "first-generation" from 2000 to 2013 and the "second-generation" from 2014 to 2019. To make these two periods comparable we normalised all values from 0 to 1. To check for potential multi-collinearity between continuous predictor variables a variance inflation factor (VIF) analysis was run using the R package HH (Heiberger, 2018). All VIF values were lower than 2 meaning that no collinearity was detected (Supplementary material – Table S4).

Finally, partial dependence plots were constructed to represent the relationship between the predictor and the response variables based on the RF constructed. These plots evaluate the RF model based on the variation within one selected variable while all other variables remain fixed at their actual values. Thus, these plots represent averaged predictions based on a selected variable (Strobl et al., 2008).

3. Results

In total we received 1704 mortality records from July 2003 to August 2021. These records included 45 different species (Supplementary material – Table S1) tagged in 48 countries and dying in 91 countries across the study area (Fig. 1). A total of 376 events (22.07 %) were classified as "possible", 336 (19.72 %) were classified as "very probable", and 992 (58.21 %) were classified as "confirmed". From the 1704 mortality events identified, 1030 (60.45 %) had a known cause of mortality while 674 (39.55 %) had an unknown cause of mortality.

3.1. Frequency of identification of mortality events

From a total of 4097 individual birds tagged, researchers could identify 1704 mortality events (41.6 %) and 497 events of technical device failure or malfunctioning (12.13 %). There were 1124 tags that continued transmitting or that completed their expected life cycle (27.43 %). However, researchers could not determine the fate of the devices/birds in 769 events (18.77 %).

Mortality proportion (i.e., number of dead birds/numbers of total birds tagged) calculated at species and project level was 0.40 (range 0–1) on average. The technical failure proportion (i.e., number of technical failures/total birds tagged) was 0.12 (range 0–1) on average (Supplementary material – Table S3). These different proportions across species and projects were statistically significant ($\chi^2 = 2561.8$, df = 411, $p < 0.01$). These numbers must be interpreted cautiously since tag's manufacturer, project duration, number of tagged birds and scale and type of effort made to identify mortality varied widely between projects.

3.2. Human-induced versus natural causes of mortality

The proportion of mortality events identified as human-induced was consistently higher than the proportion identified as natural mortality across taxonomic groups, geographic areas, and age classes (Fig. 2). When analysing the relationship between human induced and natural mortality (i.e., ratio human-induced/natural), we found that human-induced causes of mortality (37.38 %) were 1.64 times more commonly identified than natural causes of mortality (23.06 %). The ratio between human-induced (31.83 %) and natural mortality (13.28 %) was significantly higher in Africa (2.4 times) than in any other continent ($\chi^2 = 69.61$, df = 4, $p < 0.01$) (Fig. 2B). Non-adult birds showed a higher percentage of natural mortality (24.79 %) than adult birds (17.48 %) ($\chi^2 = 31.33$, df = 4, $p < 0.01$) (Fig. 2C). When considering mortality events with a known cause of mortality (i.e., human, and natural) the probability of a correct identification was as follows: "possible" = 4.56 %, "very probable" = 20.01 % and "confirmed" = 75.34 %. Since the proportion of mortality events with a known cause identified as "possible" was so low, we decided to keep all records in further analysis regardless of this category.

None of the three GLM models investigating the temporal trend in the proportion of human-induced and natural mortality detected any significant effect of year (Fig. 3) (Model 1: $\chi^2{}_1 = 0.88$, $p = 0.35$, Model 2: $\chi^2{}_1 = 1.42$, $p = 0.23$; Model 3: $\chi^2{}_1 = 0.02$, $p = 0.9$) (Supplementary material – Table S5). To reduce the influence of the probability of correct identification of mortality events, we fitted the same GLM model only including the "very probable" and "confirmed" cases of natural and human-induced mortality. Similar to the models using the full dataset, this model could not detect any significant effect of year ($\chi^2{}_1 = 2.88$, $p = 0.09$) (Supplementary material – Table S6).

3.3. Human-induced mortality

When pooling all species together, three main causes of mortality were the most frequently recorded: electrocution (40.5 %), illegal killing (21.66 %), and poisoning (16.33 %) (Fig. 4). For predatory raptors, and storks and cranes, the primary identified cause of mortality was

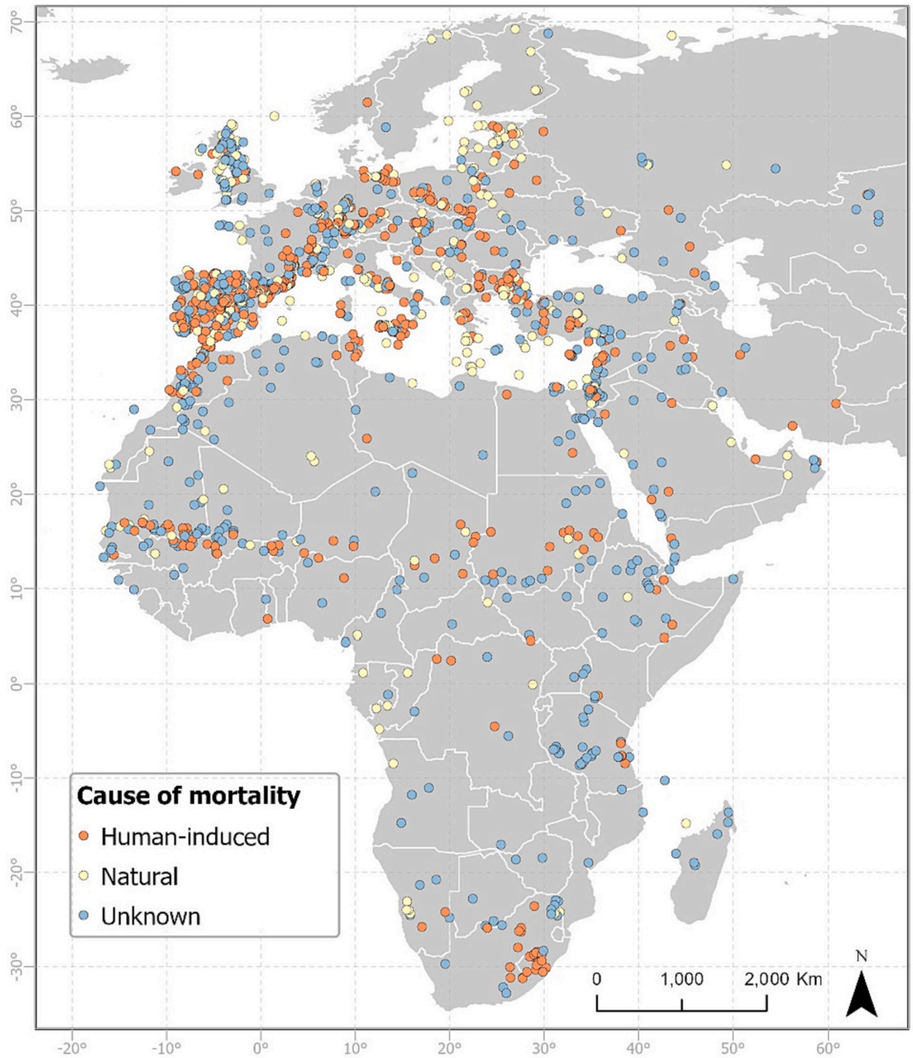

Fig. 1. Spatial distribution of mortality events in the study area, the African-Eurasian flyway.

electrocution (36.25 % and 54.47 %, respectively), followed by illegal killing (23.9 % and 21.27 % respectively). For vultures, poisoning was the main cause of mortality (39.74 %), followed by electrocution (25.83 %) and illegal killing (18.54 %). Illegal killing had the highest prevalence as a cause of mortality in Africa (48.03 %), while electrocution was most prevalent as a recorded cause of mortality in Europe (47.2 %). Energy infrastructure-related mortality (i.e., electrocution, power line collision, and wind-farm collision combined) accounted for 48.98 % of all mortalities across all species combined. Most human-induced mortality events were categorized as "confirmed" (77.86 %) and "very probable" (19.78 %), thus we decided to keep all records regardless of the classification category in subsequent analysis.

The RF model showed an overall accuracy of 73.4 % (Supplementary material – Table S8) in classifying whether a mortality event was natural or human-induced. The most important predictor was taxonomic group, followed by latitude, and human footprint index. Longitude, migratory status and origin had intermediate importance (Fig. 5), but no discernible pattern in the partial dependence plots (Fig. 6). Partial dependence plots showed that buzzards, harriers, and cranes had the lowest predicted probability of human-induced mortality, while eagles showed the highest. Human-induced mortality was highly likely across most latitudes but decreased substantially north of 40° N. Finally, human-induced mortality was highest at intermediate human footprint index values between 0.25 and 0.75, with very low probabilities in undeveloped regions (<0.25) and low probability in highly developed urban regions (>0.75, Fig. 6). Two variables had no significant ($p > 0.01$) influence on whether a mortality event was human-induced or natural: age and year.

4. Discussion

Tracking technologies can be a powerful tool to investigate avian mortality in wild populations. Our study shows how these data can be used to quantify the extent of human-induced mortality among populations of large birds. Investigating mortality can be challenging, both because of the necessary time and expertise to evaluate and analyse this type of data, and because of the cost and time needed to investigate this in the field. However, data on mortality have great value, not only for scientific research but also for conservation. The large numbers of birds tagged in recent years could contribute important information on this topic if additional efforts were made to gather and analyse these data, particularly during the design stage of tagging projects.

Our results agree with previous studies on the high importance of human-induced mortality over natural mortality, but the strength of this importance varies. For instance, De Pascalis et al. (2020) using ringing data, found that natural mortality was just c.5–8 % of total mortality events registered, a much lower percentage than our findings. However, these numbers could be highly influenced by the increased likelihood of finding and reporting a bird dying from human-induced causes close to human settlements. Data on raptor mortality from wildlife rehabilitation

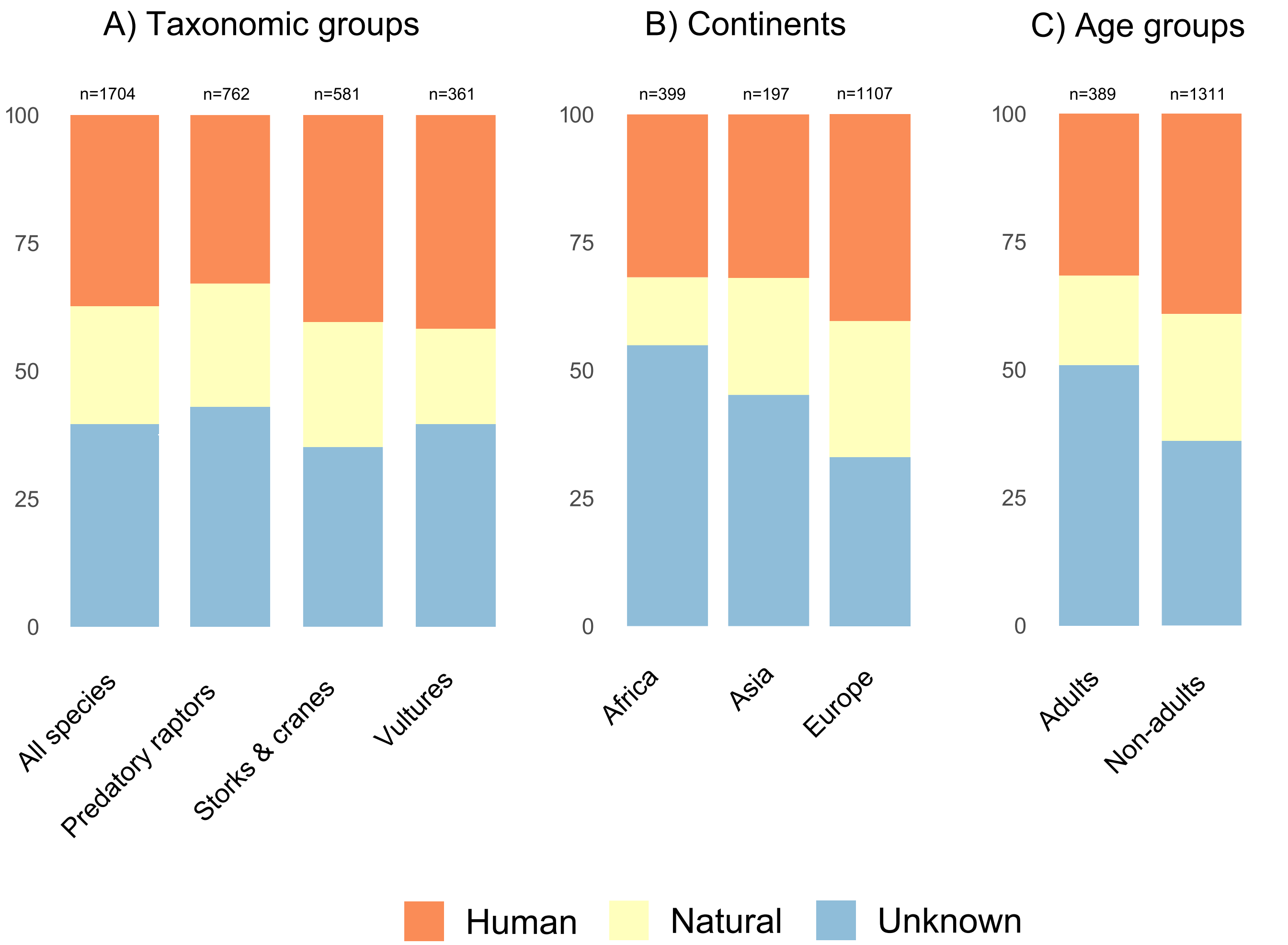

Fig. 2. Percentages of human-induced, natural, and unknown causes of mortality for all mortality events recorded depicted by: A) taxonomic groups, B) continents, and C) age groups. All age classes not considered as adults were classified as non-adults. One mortality event recorded in the middle of the Atlantic Ocean could not be assigned to a continent and four other events did not include age.

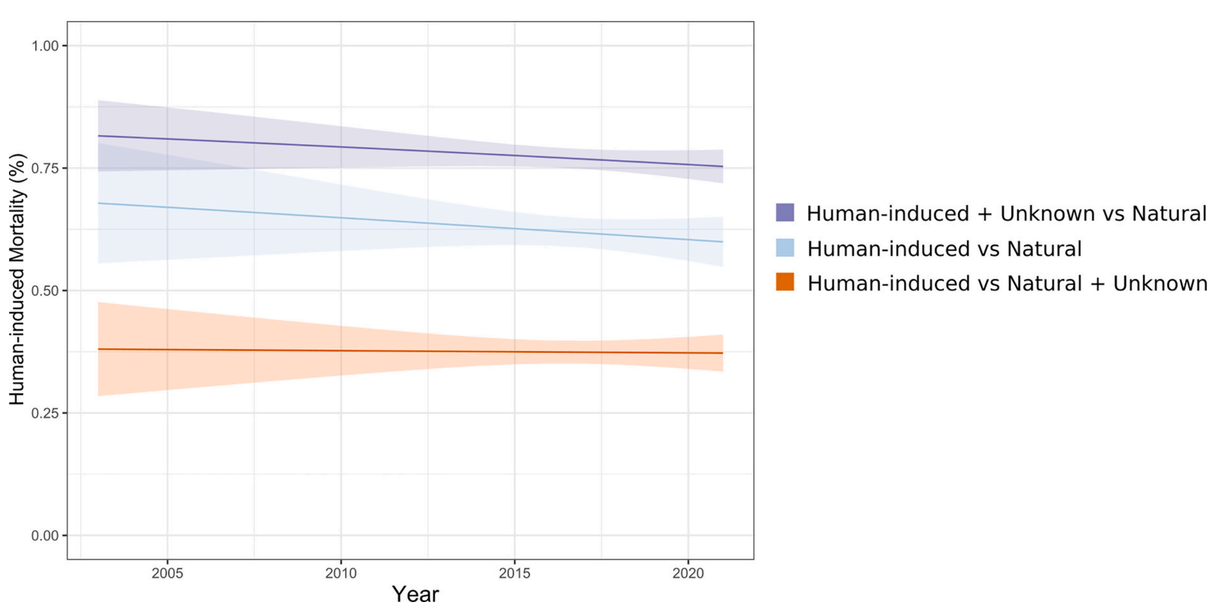

Fig. 3. Probability of human-induced mortality ±95 % CI in relation to year, calculated as the proportion of this kind of mortality in relation to total mortalities. Three different GLM models were built to incorporate unknown causes of mortality in the analysis. None of the resulting models were significant ($p > 0.01$).

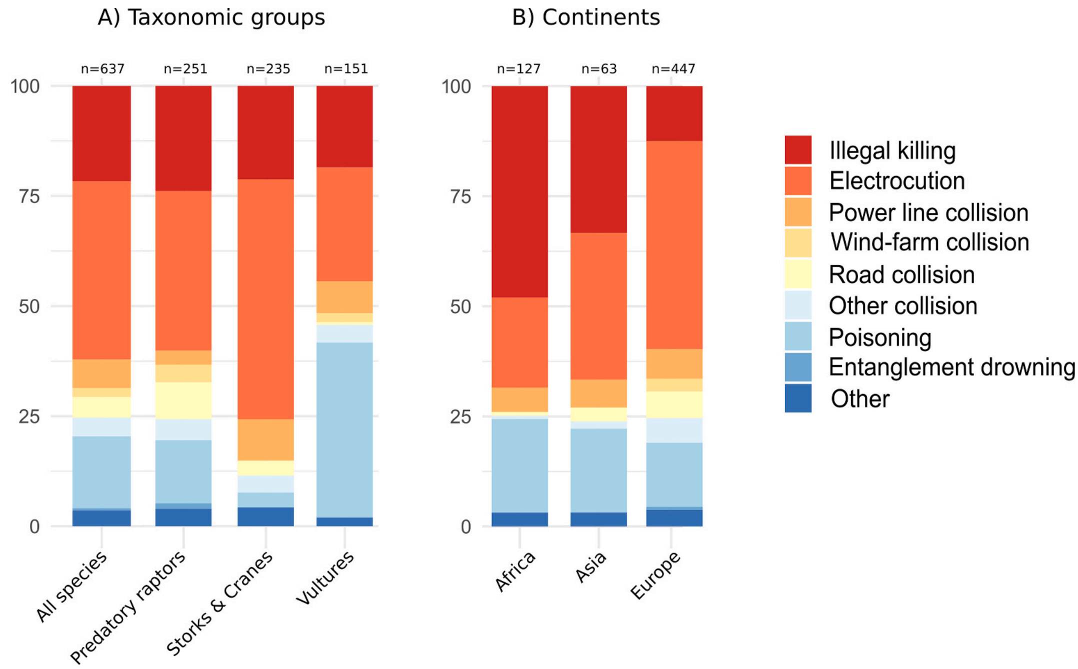

Fig. 4. Percentages of human-induced causes of mortality by: A) taxonomic groups and B) continents, calculated from all known human-induced causes of mortality (n = 637).

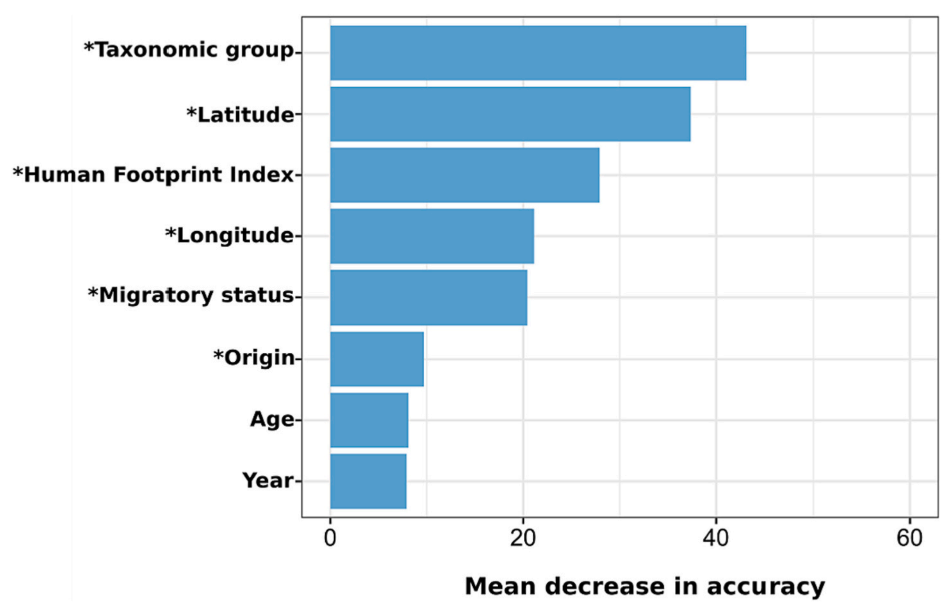

Fig. 5. Relative variable importance influencing a random forest model's accuracy in classifying whether a mortality cause was human-induced or not. Mean decrease in accuracy measures the reduction in the accuracy of the model when randomly permuting that particular variable while maintaining the rest. Variables marked with an asterisk were significant (p < 0.01) after 1000 permutations.

centres in Spain, which could be biased in a similar way, showed similar figures of natural mortality (Martínez et al., 2016). Remote tracking devices provide an opportunity to reduce this bias by revealing locations of dead individuals away from human settlements. Studies carried out using tracking data provide similar results to ours. For instance, Buechley et al. (2021) reported that for Egyptian vultures tracked across the African-Eurasian flyway, 51.1 % of the total known causes of mortality were human-induced, and Monti et al. (2023) found that 60 % of mortality causes for GPS-tracked Griffon vultures in central-southern Italy were also human-induced, like our overall results.

Our models could not detect any change in the frequency of human-induced mortality in the last 15 years. Although events with an unknown cause of mortality generate uncertainty in our results, none of the different scenarios we modelled indicated that human-induced mortality is declining. It is possible that we did not detect any change because both (natural and human-induced) have increased or decreased at the same rate. Likewise, it is also possible that some threats have been replaced by others across time and/or geographical areas. For instance, previous studies from Spain indicate that in recent decades the number of cases of illegal killing has decreased, while fatalities related to energy infrastructure have increased (Martínez et al., 2016; Martínez-Abraín et al., 2009). New threats have also emerged. For instance, intentional

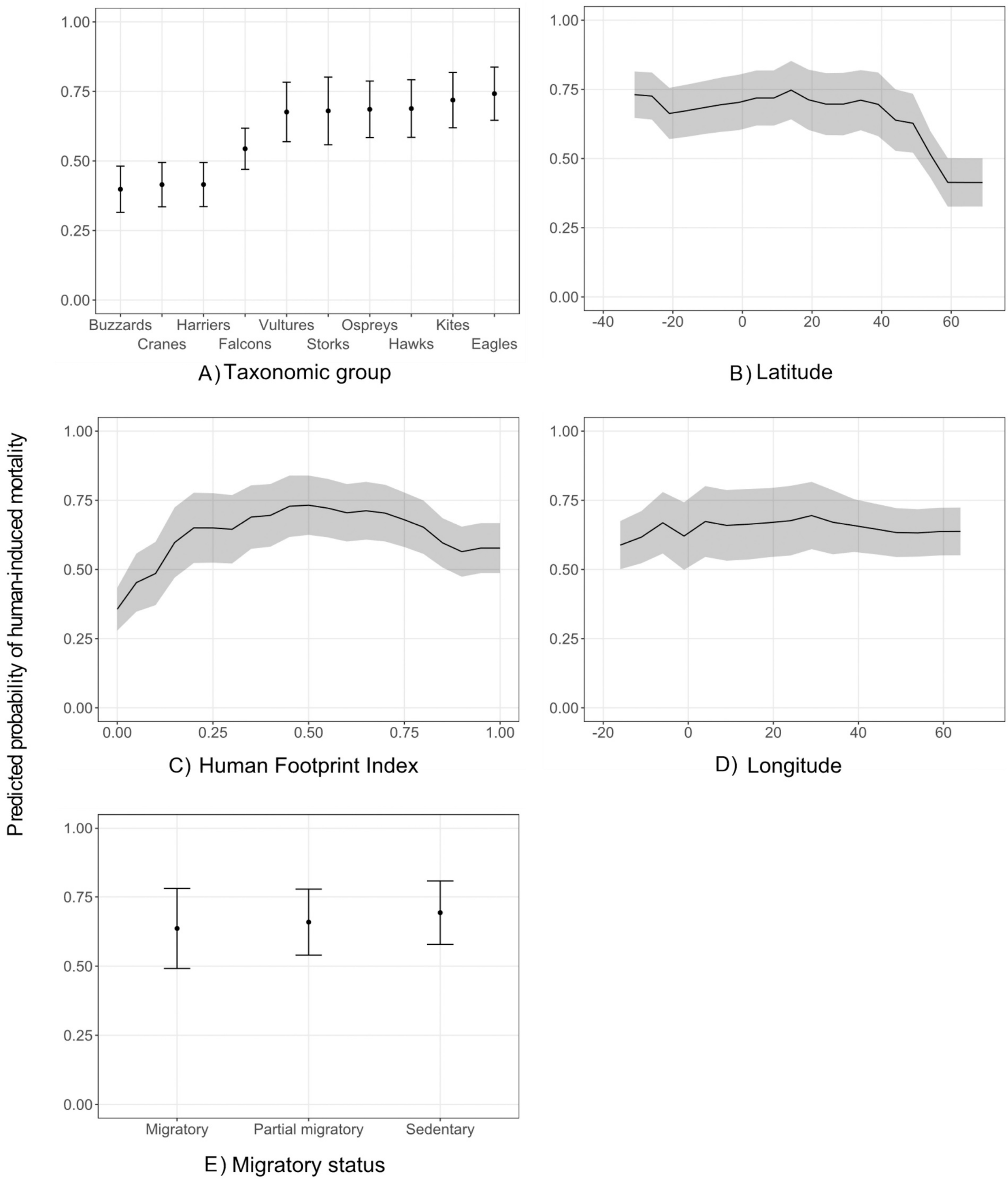

Fig. 6. Partial dependence plots showing the relationship between the most important variables detected by a random forest model and the probability of human-induced mortality if all other variables were held at their actual values. Shadowed areas and error bars represent the standard deviation around predicted mean probability.

poisoning has increased sharply in Africa, having a major impact on vulture populations (Henriques et al., 2020; Ogada et al., 2016a). These new emerging threats may have counteracted the reduction of previous ones.

Our analysis shows that not all bird species are equally at risk of human-induced mortality. The importance of taxonomic groups in our RF model reflects ecological and biological characteristics of species that make them particularly sensitive to certain causes of mortality. Secondly, the importance of latitude indicates that threats are not evenly distributed across space but vary geographically in intensity and persistence (Buchan et al., 2022; Gauld et al., 2022). This is consistent with our findings of a spatial variation in the importance of threats between continents. For instance, according to our results, illegal killing is higher in Africa than in any other continent. This finding could be related to the combination of several factors like direct persecution of vultures for belief-based uses (Ogada et al., 2016b), a high level of hunting pressure in some African countries like Egypt (Brochet et al., 2016), and/or the increasing demand of hunting for bushmeat in sub-

Saharan countries (Whytock et al., 2016). Lastly, the importance of the human footprint index reflects the strong association between human presence and avian mortality. Interestingly, we did not find a monotonic increase in the probability of human-induced mortality with the footprint index, but a peak at intermediate values. This relationship indicates that even moderate human presence can have large impacts on avian mortality, but that human-induced mortality events are not more likely in extremely modified urban landscapes. We speculate that most large bird species simply do not find suitable habitat in highly developed or urbanized areas, and thus limit the time they spent there.

We acknowledge that our study presents some limitations. First, we could not estimate absolute mortality rates and thus quantify demographic impacts. Capture-mark-recapture or recovery models applied to tracking data could be used to estimate mortality rates and relative contributions of mortality causes (Buechley et al., 2021; Schaub and Pradel, 2004; Swift et al., 2020). However, our focus was on identifying broad scale spatiotemporal patterns in mortality rather than estimating species-specific demographic parameters. Our estimates are conditional on the probability of finding and reporting a mortality event from a particular cause, which may lead to bias if certain mortality causes have a higher probability of being detected and diagnosed than others (Tavecchia et al., 2012). However, mortality information derived from tracking data has a higher probability of detection and fewer potential sources of bias than that from other sources (e.g., Bro et al., 2001). Lastly, since we collected data from multiple studies there is a large heterogeneity in the methods used to determine the mortality events. Nevertheless, from all mortality events included in our analysis of known causes of mortality, 95.4 % were classified as "confirmed" or "very probable". We are therefore confident that the main conclusions of our study are robust.

In the coming decades, investment and development in renewable energy is expected to grow substantially worldwide. With much of the expected growth relying on solar and wind energy (70 %), this means that by 2050 we can expect a ten-fold increase in the current total onshore wind energy capacity (IEA, 2021; IRENA, 2019). This massive expansion of renewables will require a proportional growth of the electricity transmission grid to distribute this energy. With almost 50 % of all human-induced mortality events being related to energy infrastructure, our results highlight the impact that this source of mortality already has on birds. Therefore, the expected expansion of this infrastructure could have dramatic consequences for the conservation of these species (Serrano et al., 2020). Currently, the proportion of mortality events that are energy-related is lower in Africa (26 %) than in Europe (57 %). This may be related to the smaller size of the energy infrastructure network in Africa compared to Europe. However, the rapid expansion of electricity networks in developing countries will likely increase energy infrastructure-related mortality. This is already evident in some countries like Kenya and Ethiopia, where collisions/electrocutions have been identified as an important threat for raptors (Ogada et al., 2022; Oppel et al., 2022). Birds could benefit from careful planning to minimise these impacts, and tracking technologies can help us in this task, providing opportunity for energy investors and developers to take account of the important areas and routes for migratory birds, and to build bird-safe infrastructures (Gauld et al., 2022; Oppel et al., 2021).

5. Conclusions

Our study, covering 45 species across 91 countries, reveals that human-induced factors—predominantly electrocution, illegal killing, and poisoning—constitute the major threats to bird mortality, highlighting a critical issue in global biodiversity conservation. Our results further support targeted actions as an important mechanism to combat these threats. For example, insulating power lines and strategically shutting down wind turbines during bird migrations can substantially reduce deaths due to infrastructure (Chevallier et al., 2015; Ferrer et al., 2022; McClure et al., 2021). Tackling illegal killing and poisoning can be based on robust law enforcement, widespread awareness campaigns, and community involvement to instil conservation values (Badia-Boher et al., 2019; Oppel et al., 2023). Comprehensive environmental assessments for new infrastructural projects can prevent potential harm to avian populations. These practical measures will benefit specific species and have wider implications. The insights gained from this extensive study can guide international conservation efforts, informing policy adjustments and fostering cross-border collaborations to safeguard avian species. In doing so, they contribute to broader objectives of maintaining ecological balance and protecting global biodiversity, resonating with the goals of international environmental agreements and conservation strategies.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Authorship contribution statement

Conceptualization: Victoria R. Jones, Willem Van den Bossche, Juan Serratosa, Steffen Oppel, and João L. Guilherme.

Data curation: Juan Serratosa.

Formal analysis: Juan Serratosa, Steffen Oppel, and Shay Rotics.

Methodology: Victoria R. Jones, Juan Serratosa, Steffen Oppel, Shay Rotics, and João L. Guilherme.

Writing - original draft: Juan Serratosa, Victoria R. Jones, Steffen Oppel, Shay Rotics, Andrea Santangeli, Stuart Butchart, Luis S. Cano-Alonso, José Luis Tellería and Ryno Kemp.

Writing - Review & Editing: All co-authors.

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