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Crossing artificial obstacles during migration: The relative global ecological risks and interdependencies illustrated by the migration of common quail *Coturnix coturnix*



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HIGHLIGHTS

GRAPHICAL ABSTRACT

- The urban sprawl can impact migration and the spread of diseases.
- Urbanization puts health at risk and jeopardizes wildlife populations.
- We found a decrease in the return paths of quail with respect latitude and artificial soil.
- A global ecology perspective helps understand the relationships of migration and One Health.

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ABSTRACT

The increase of urban expansion, whereby soils become altered or filled with buildings through human action, presents a global threat to biodiversity and the spread of disease. Many of the factors determining bird migration routes and disease spread are poorly understood. We studied the migration routes of common quail *Coturnix coturnix* in western Europe. We examined the recoveries of ringed birds to characterize their migration trajectories to understand how this nocturnal migrant crosses artificial areas and predict the risk of migration collapse and disease transmission. We evaluated the possible consequences of quail collisions with human infrastructure elements (i.e., buildings, cranes, overhead cables and wires, and wind farm structures) to assess disease transmission in relation to the amount of urban soil. Our results show that variations in the amount of artificialized soil in central Europe are correlated with the relative absence of quail migratory routes. Conceptual models incorporating environmental ecology showed the relations ships between climate warming, agroecosystems, and urban ecosystems as well as human health and economic growth. We predict a drastic loss of biodiversity and spread of disease if we do not curb the spread of land consumption. Taking a broad view of the interrelations discussed here allows predictions of global vulnerability and increased risks to health due to losses of biodiversity and ecosystem services. Lessons drawn from migration route maps of quail in relation to the distribution of urbanized soils provide tools for global conservation political decision making.

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1. Introduction

Soil urbanization refers to the processes whereby the actual state of an agricultural, forest or natural area change towards artificial surfaces, i.e. urban fabrics, industrial and commercial areas, transport infrastructures and their dependencies, open-cast mines and quarries, landfills and construction sites (Cortinovis et al., 2019). The occurrence of urbanized surfaces, is correlated with ecosystem type and socioeconomic factors (van Vliet et al., 2017). Similarly, human health is impacted by environmental factors. Urban spaces present threats and barriers to wildlife migration and also increase the probability that pathogens can be transmitted by a vector, often linked to the degree of soil artificialization. Four invasive Aedes mosquito species have become established in Europe, potentially increasing the transmission of the diseases for which they are the key vectors. Birds and humans are both hosts of these mosquitoes (Cebrián-Camisón et al., 2020). Invasive species often benefit from the resulting biotic homogenization and the reduction in overall biodiversity, which enables them to further increase their range and abundance (Wilke et al., 2020). Various diseases are periodically transmitted between mosquitoes and birds (Zhou et al., 2021) and increases in these diseases in agricultural systems depends on climate change parameters and the details of the host-pathogen system (Altizer et al., 2013). For example, another mosquito Culex pipiens transmits four Plasmodium lineages which are in active circulation in Europe (Gutiérrez-López et al., 2020). One environmental model in which mosquitoes are the vectors and birds form the host reservoir, can explain the outbreaks of the virus causing West Nile fever in Europe, when the migration routes and environmental characteristics of the bird host populations are taken into account (García-Carrasco et al., 2021).

A high proportion of zoonotic enteropathogens have shown resistance to at least one antimicrobial agent (Antilles et al., 2021), a fact that is associated with human activities. Global changes affect disease transmission and spread, and this in turn influences ecosystem services (Paseka et al., 2020). As the birth rate falls the number of households has increased at a faster rate than the human population size. As a result, socioeconomic, political, demographic, and cultural characteristics have encountered different ecological issues in urban, semi-urban and rural areas, altering a variety of ecosystem services and bringing different environmental problems (Liu et al., 2007). One of the main issues is the energy transition in Europe, and the increase in the use of renewable energy resources could well threaten biodiversity as they are often provided at the expense of high ecological value soils (Serrano et al., 2020).

Despite their importance, bird migration routes still remain relatively poorly studied (Newton, 2007). Although remote tracking systems are providing relevant information for large bird species, some technological limitations for some small species obliges the use of alternative methods. For example, there have been relatively few quantitative attempts to identify migration routes using ringing data (Musitelli et al., 2019). A better understanding of migratory patterns and their relationship to anthropogenic landscapes could provide information to improve ecosystem function through optimal management and conservation practices.

In this study, we identified the migration routes of the common quail Coturnix coturnix in western Europe, in order to understand how anthropogenic landscapes (e.g. cities, buildings, electric transmission and mobile towers) affect quail population dynamics, within the One Health risk paradigm. Global change increases the interdependence between human, animal, and environmental health (Rodrigues et al., 2021). Humans, wild animals, parasites and pathogens are undergoing changes in how they interact due to the effects of increasing urbanization, pollution, and global trade (Mcewen and Collignon, 2017). Globalization has exponentially increased human health risks and, as a response, international organizations like the Food and Agriculture Organization (FAO) and the World Health Organization (WHO) are putting in action the One Health approach with the objective of increasing disease control and prevention. We predicted that urban areas act as potential obstacles for migratory birds, increasing the probability of their contacting arthropod disease vectors and so enhancing the transmission of certain diseases. We used Spanish ringing data to reveal

quail migration routes, creating flowcharts to clarify the effects of magnification (stopover bottlenecks), spread (collisions between birds and infrastructure while crossing urban areas) and transmission (contact with arthropod vectors). Empirical testing of quail migration provides a key model understanding global ecology and human well-being. Urban areas in central Europe can limit migration flow and facilitate disease transmission, and we set out to test how areas of artificialized soils impact the migration routes of this species and increase the risk of the spread of disease.

2. Methods

2.1. Global ecology and quail migration

Ecological processes provide ecosystem services, which in turn affect human health and have consequences for economic growth and global change. Taken overall these factors link climate warming, agroecosystem intensification, and growing urbanization which further impact ecological processes (Fig. 1).

Quail' annual cycle includes four biological stages: wintering, spring migration (arrival), breeding stays, and autumn migration (departure). In Iberian Peninsula, arrivals take place in February–April, breeding stays last through May–July and departures occur in August–October (Nadal et al., 2019). Quail link habitat quality to population demography via movement patterns (Taylor et al., 2016), what initially follows green up for breeding but then abandons reproduction sites when fields are harvested. During their European summer, quail alternates breeding activity with movements searching good quality habitat and conspecifics. The sequential breeding of quail begins in Africa and southern Iberian Peninsula, followed by second and third breeding attempts in Iberian Peninsula and Central Europe. In middle of august, begin birds' autumn migration to return to their African wintering grounds (Newton, 2007).

2.2. Data collection

We used quail ringing data consisting of 2595 recovery records obtained from Spanish ringing schemes SEO/BirdLife (ICONA rings), hunting associations (FEDENCA rings) and two autonomous communities (Junta de Castilla y León and Cabildo de Tenerife rings), and the Sociedad de Ciencias Aranzadi (ARANZADI rings) also some from French, Italian, Dutch and Belgians schemes covering the 1933–2015 period. We filtered and homogenized these datasets to generate standardized information that included Julian date, longitude, and latitude. Given that this study does not attempt to evaluate quail abundance using ringing data and the fact that we study routes that cross the Iberian Peninsula, the differences in recovering effort should not affect our results.

We classified quail ringing recoveries into eight categories: *stopover* (less than five days between ringing and recovery), *sedentary* (ringing and recovery at the same site), *wintering* (recovery between September–February), *direct* trip (less than 180 days between ringing and recovery) and recovery) and reproduction (less than 180 days between ringing and recovery) and reproduction (less than 180 days between ringing and recovery, and a distance travelled <85 km). Reproduction was divided into three subcategories: *reproduction1* (ringing between March–May), *reproduction2* (ringing between June–July), and *reproduction3* (ringing between August–September) (Spina and Volponi, 2008). The three trip categories (*stopover*, *direct* and *return*) represent 32.4% of the observations and the reproduction categories represent 64.6%, with *reproduction2* being the most frequent (Table 1).

2.3. Statistical analysis

We mapped the trajectories between the ringing and recovery points. Each category of trajectories was subdivided into northerly (direction of the azimuth $0^{\circ}-90^{\circ}$ and $270^{\circ}-360^{\circ}$) and southerly groups (direction of the azimuth $90^{\circ}-270^{\circ}$). The directional vector was calculated for each category as the average of all the trajectories included. We used the Rayleigh Test to



Fig. 1. Diagram of the ecological processes showing the relationships between components that create a global ecological system that includes processes, services, goods (health), economics, global changes (anthropogenic changes), ecosystems, and the risks and spread of diseases (red dotted line). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

compare the uniformity of the directions taken (the null hypothesis being no preferred direction), against the unimodality (the alternative being a single preferred direction) within each category. We applied Hotelling's Paired Test to contrast the difference between the northerly and southerly trajectories in each category (the null hypothesis being no difference between the two directions).

We calculated the mean Julian date of ringing and recovery, and the ringing date of the quail that remained in the same location, in each category and trajectory subcategory. We then used Eurostat (https://www.eea.europa.eu/data-and-maps/dashboards/land-cover-and-change-

statistics) to obtain the percentage occurrence of urbanized surfaces in each locality. Finally, we calculated the correlation between locality and the occurrence of urbanized surfaces for the trip categories, using JMP15, Arcgis, and Oriana. We drew diagrams of the spring and autumn migration routes, and for the three reproduction stages, synthetizing the data on trajectories, and ringing and recovery localities to produce standard deviations, frequencies, and ellipses representing their distributions. The diagrams showing migration routes represented the trajectories of movements greater than those of stopover localities alone. The diagrams showing the reproduction stages showed trajectories shorter that those between staging localities.

Table 1

Categories of quail recoveries (1933-2015) from the Spanish bird ringing scheme.

Recovery	Ν	%
Stopover	169	6.51
Sedentary	68	2.62
Wintering	10	0.39
Direct trip	413	15.92
Return trip	259	9.98
Reproduction1	621	23.93
Reproduction2	979	37.73
Reproduction3	76	2.93
Total	2595	100

2.4. Conceptual models

Previous studies (Becker et al., 2020; Blagodatski et al., 2021; Fecchio et al., 2021) have suggested that bird migratory routes are important entry points for the spread of disease. Therefore, following Giere (2010), we schematized previous findings regarding global changes and the ecology of arthropod disease vectors and migratory bird host reservoirs, to derive models to understand the potential for disease outbreaks in Europe. We hypothesized that migration route diagrams would be useful in understanding the relationships between migration and health risks, bird abundance and distribution, urbanized soils, and disease propagation. To test these hypotheses we built models of quail migration routes using the ringing and recovery data. Fig. 2 shows a conceptual feedforward and feedback model using the positive and negative relationships between climate warming, agroecosystems, urban ecosystems, human health, and economic growth. This conceptual model includes different feedforward and feedback circuits that can aid recognition of causes and effects in global ecological systems. Our hypothesis is that urban landscapes (with artificialized soils) can be a hurdle to bird migration that increases the risk of disease spread and hinders species distribution.

3. Results

Ringing recoveries since 2000 comprise 95% of the total recoveries since the Spanish scheme began in 1930 (Fig. 3). Trips accounted for 38.5% of recoveries (without *stopover*, *sedentary* and *wintering* categories), and 86.2% of the *direct* trips started and finished within Europe. Figs. 4 and 5 show that *return trips* constituted 45.7% of the trips. *Direct* trips with northerly trajectories comprised 4.04% of the trips (Rayleigh Test Z = 30.7, P < 0.0001, N = 69 and $350.5^{\circ} \pm 51.6$ degrees with respect to North), and those with southerly trajectories comprised 20.12% of the trips (Rayleigh Test Z = 279.9, P < 0.0001, N = 344 and $234^{\circ} \pm 26$ degrees with respect to North). *Return* trips with northerly trajectories comprised 4.97% of the trips (Rayleigh Test, Z = 25.11, P < 0.0001, N = 85



Fig. 2. Global ecological conceptual feedforward and feedback model showing the relationships between ecosystems transformed by human activities, human health, economic growth, and climate warming. Negative-negative relationships are shown in red; positive-positive relationships are shown in blue; possible negative or positive relationships are shown in blue; and dotted lines indicate discontinuous relationships. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

and 12.2° \pm 63.3 degrees respect to North), and those with southerly trajectories comprised 9.36% of the trips (Rayleigh Test Z = 80, P < 0.0001, N = 160 and 224.3° \pm 47.7 degrees respect to North).

Reproduction1 northerly trips (ringing from March-May, Supplementary materials) were observed almost twice as often as southerly trips. Trips with northerly trajectories comprised 13.22% of the trips (Rayleigh Test Z = 84.9, P < 0.0001, N = 226, and 19.1° \pm 56.7 degrees with respect to North), and those with southerly trajectories comprised 6.96% of the trips (Rayleigh Test Z = 24.5, P < 0.0001, N = 119 and 191.8° \pm 67.7 degrees with respect to North).

Reproduction2 (ringed from June–July, Supplementary materials) movements were more often southerly than northerly in direction. Trips with northerly trajectories comprised 17.6% of all trips (Rayleigh Test Z = 69.3, P < 0.0001, N = 301 and 2° ± 69.4 degrees with respect to North), and those with southerly trajectories comprised 20.94% of all trips (Rayleigh Test Z = 99.6, P < 0.0001, N = 358 and 197.5° ± 64.8 degrees with respect to North). Regarding *reproduction3* (ringed from August–September), more southerly trips were made than northerly ones. Trips with northerly trajectories comprised 1.11% of all trips (Rayleigh Test Z = 4.3, P < 0.01, N = 19 and 332.5° ± 69.8 degrees with respect to North), and those with southerly trajectories comprised 1.7% of all trips (Rayleigh Test Z = 7.3, P < 0.0005, N = 29, and 184.6° ± 67.5 degrees with respect to North).

Significant differences were found between the observations of northerly and southerly trajectories within each category; *direct* trips (Hotelling's Paired Test, F = 263.3, P < 0.0001, N = 413) and *return* trips (Hotelling's



Fig. 3. Dataset of quail recoveries by year.

Paired Test, F = 277.7, P < 0.0001, N = 245). The same results were found for the three phenological reproduction stages considered: *reproduction1* (Hotelling's Paired Test, F = 465.4, P < 0.0001, N = 345), *reproduction2* (Hotelling's Paired Test, F = 757.4, P < 0.0001, N = 659) and *reproduction3* (Hotelling's Paired Test, F = 36.16, P < 0.0001, N = 48).

As the quail route diagrams show (Fig. 6), trips with northerly trajectories were divided between two general routes; one towards central Europe, and the other towards the Mediterranean area, with the Alps as the dividing line between them. As latitude increased from the Iberian Peninsula to central Europe, so did the percentage of urban surfaces. The latitude of the ringing locations of southerly trips was positively correlated with the percentage occurrence of urbanized soil (F = 627.7, P < 0.0001, N = 504, $r^2 = 0.56$, b = 0.02 ± 0.0009, Figs. 6 and 7).

4. Discussion

Migration routes depend as much on genetics as physiology and ecology. For example, birds use innate biological time-keeping mechanisms to predict upcoming changes in environmental cycles. Both predictive anticipation and flexibility are important for determining the timing, direction, and distance components of migration. On the other hand, the routes of night migration are variable and affected by hyperphagia, fat deposition as fuel, and information from stars and the geomagnetic field (Åkesson and Helm, 2020). In this sense, simulation models suggest that birds migrate in response to seasonal variations in climate (Somveille et al., 2019). The seasonal movement of animals has also been linked to seasonal variation in ecological productivity. In fact, primary consumers synchronize migration with vegetation phenology, and bird species often track the phenology of vegetation greenness during spring migration (La Sorte and Graham, 2020). This supports our findings that during reproduction1 the average movement is northwards, in agreement with the general pattern for Afro-Palaearctic land-bird migration across Europe, which is determined by ecological factors driving the timing of vegetation greening in the spring, and senescence in autumn. Migrants therefore track vegetation greening in spring but depart for the winter quarters before vegetation senescence in autumn (Briedis et al., 2020). Our results indicate that the average movement is southwards during the reproduction2 and 3 stages. We found that direct and return trip trajectories coincide, and this result provides support for the theoretical framework regarding the benefits of breeding-site fidelity. In fact, site fidelity to familiar breeding locations is a primary adaptive driver of spring migration (Winger et al., 2019).

In migration models the distribution of landmasses, mountain ranges, and weather conditions can explain bird migration routes. Geographic



Fig. 4. Quail migratory trajectories for each category. Red arrows show the trajectories of individual birds. Yellow arrows show the average trajectory of each category. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

barriers (coastlines, mountain ranges) and wind direction are the principal factors influencing the fine detail of migration routes (Aurbach et al., 2020). Our findings show that in the Iberian Peninsula, the preferred destination of quail is the Northern plateau. After crossing the Pyrenees, quail follow both the central and Mediterranean European routes, avoiding the Alps. This could be due by the atmospheric conditions that strongly affect bird route selection (Becciu et al., 2020); Haest et al., 2019). When and where birds stop to rest and refuel is governed by the weather experienced during the flight (Clipp et al., 2020). When going to, and returning from Europe, quail stop to refuel in the Iberian Peninsula, suggesting the importance of the Northern plateau and Ebro valley habitats for population conservation. Migratory birds rely on a network of habitats along their migration routes as temporary stopover sites between the breeding and wintering grounds. The extent to which the breakdown of migration retworks, due to changes in land use, impacts the population sizes of migratory

birds is poorly understood. The use of radar in aeroecology is advancing rapidly and can show continent-scale patterns of nocturnal migration and illustrate migrant flow rates and timing (Lin et al., 2019). Population sizes decline significantly when the functional connectivity of migration routes is reduced or destroyed. If migration routes contain bottlenecks at stopover sites – through which a large proportion of the population travels – habitat loss in these areas increases the potential negative impact on population levels (Iwamura et al., 2013).

Migration routes represent a trade-off between the costs associated with distance travelled and the gains in terms of better access to resources (Somveille et al., 2019). But migration behavior exposes a population to a wide range of increasing anthropogenic threats with direct mortality effects (Buchan et al., 2021). The results of this study indicate that few quail actually reach central Europe. Anthropogenic factors are also known to change waterfowl movements as habitat availability and quality decreases, and



Fig. 5. Representation of the Rayleigh tests for each category. Blue bars show group trajectories, and red arrows show the average trajectory. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

movement patterns at stopover sites are impacted (Newton, 2007). Changes in environmental factors can be used as indicators of the probability that a site will disappear from a migration network (Xu et al., 2021). Billions of birds migrate across the continents by night through airspaces increasingly altered by human activity, resulting in the deaths of millions of birds every year through collisions with man-made structures (Tschanz et al., 2020). In the US, it has been estimated that 500 million individual birds migrate each night during peak passage, and many collide with buildings, airplanes, and wind turbines (Van Doren and Horton, 2018). In Spain, politically driven environmental plans on renewables are due to double the land area under wind farms and quadruple that with photovoltaic panels by 2030 (Serrano et al., 2020). As a result, bird migratory strategies must respond to global changes – both in climate and land use – and increasing urbanization modifies the mechanisms driving bird migration (Bonnet-Lebrun et al., 2020). Artificial light at night (ALAN) and urban landcover have negative impacts on nocturnal migrant birds, and it is important to reduce ALAN during migratory periods (Cabrera-Cruz et al., 2020; La Sorte and Horton, 2021). Nocturnally migrating birds fly higher over urban areas compared with rural ones (Cabrera-Cruz et al., 2019). We found that on the quail migration routes, latitude and the presence of urbanized soil can have significant effects, confirming the notion that urban land presents a dangerous barrier obstructing migration, and increasing the probability that arthropod vectors will spread diseases as they come into increased contact with bird disease hosts. Northward spring migrants J. Nadal et al.



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Fig. 6. Route diagrams. Top: the trip routes; left: the northerly routes; and right: the southerly routes. The number is the percentage of trajectories. Below: the reproduction stages; left: *reproduction1*; and right: *reproduction2* and *3*. The number is the percentage of trajectories.

travelling at higher latitudes needs to compensate for wind drift (Horton et al., 2018); seasonal winds exacerbate the variations in migration flow rates and dates (Newcombe et al., 2019) and can have lethal effects when birds cross barriers such as seas or cities, with inexperienced juvenile birds at greater risk than adults (Santos et al., 2020).

Habitat loss can trigger migration network collapse by isolating migratory birds. Stopover sites are most vulnerable to habitat loss and can cause migration network collapse (Xu et al., 2020). Accordingly, management of migratory birds should consider their wide fluctuations in interannual abundance (Fink et al., 2020), as well as the implications of global warming (La Sorte and Graham, 2020) and transboundary management (Nadal et al., 2020; Xu et al., 2021). We have identified the migration routes of quail and how they are compromised by areas of urbanized soil (Gerten et al., 2019). The growing occurrence of urban soil has consequences for the loss of migration routes and ecosystem services, and for health and the quality of life (Zheng et al., 2019). Since artificialized soil disrupts migration and increases the probability of disease spread, land planning managers and politicians should consider the interactions between the spread of urbanized soil and bird migration and health, because of their ecological interdependencies.

This problem is not easy to reverse because the reduction of urban soil is unpopular and hardly compatible with a liberalized market. However, it currently represents the greatest threat to global biodiversity and humanity. Economic growth has ecological costs in terms of the quality of life, public health, ecosystem services, and biodiversity loss. Because urban spaces present potential threats to wildlife migration and also increase the probability of pathogens transmission, we need holistic and relevant political and management decisions that will properly harmonize ecological development and conservation, taking into account health vulnerability, dynamic interactions between ecosystems, biodiversity, ecosystem services, and human population growth.

Fig. 7. Relationship between the percentage occurrence of urbanized soil and the latitude of the departure locality of southerly quail migration trips.

5. Conclusions

Bird migration potentially influences the transmission of infections because birds often carry diseases that can jump to humans using a vector. Our data suggest that quail migration to central Europe is likely to increase the probability of contact with humans and increase the likelihood of mortality, in this highly urbanized landscape where night time impacts with the built environment are likely. We identified a decrease in the return paths of the quail with increasing latitude and anthropogenic landscapes in central Europe. In light of these findings, global ecology needs to better understand the effects of the built environment on the interactions between humans and wildlife.

CRediT authorship contribution statement

Jesús Nadal: Conceptualization, Data curation; Formal analysis, Methodology, Supervision; Validation; Visualization, Writing – original draft, review & editing.

David Sáez: Data curation; Formal analysis, Methodology, Software, Writing – original draft.

Antoni Margalida: Writing - review & editing.

All authors contributed critically to the drafts and gave final approval for publication. The authors declare to be accountable for the aspects of the work that they conducted and ensuring that questions related to the accuracy or integrity of any part of their work are appropriately investigated and resolved.

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.

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Appendix A. Supplementary data

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