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Induced breeding failure alters movements, migratory phenology, and opportunities for pathogen spread in an urban gull population

Juliet S. Lamb^{1,2*} and Thierry Boulinier¹

Abstract

Background Annual-cycle movements of wildlife are driven by a combination of intrinsic and extrinsic factors. In urban systems, management strategies to reduce human-wildlife interactions could also alter wildlife movement and distribution, with potential effects on key ecological processes such as pathogen spread.

Methods To better understand how management actions interact with existing spatial dynamics to mediate wildlife movement patterns, we experimentally subjected urban-nesting yellow-legged gulls to induced breeding failure via egg-oiling. We then followed their movements using bird-borne GPS transmitters throughout the treatment season as well as the following annual cycle and compared them to the movements of tracked gulls whose nests were not oiled, while also accounting for individual and temporal factors known to influence movement patterns including sex, body size, and breeding stage.

Results Gulls with oiled nests had smaller breeding-season home ranges, spent more time at breeding sites, made fewer foraging trips, and traveled shorter distances than gulls with non-oiled nests during the treatment season but not during the following breeding season. Gulls were partially migratory, with individuals showing a variety of migratory strategies from year-round residency to long-distance migration to inland urban centers. Although egg-oiling delayed the onset of post-breeding migration, individual migration strategies remaining consistent between years regardless of treatment. Antibody titres against three common pathogens varied among pathogens but not by migration distances or individual characteristics.

Conclusions Our results show that induced breeding failure via egg-oiling may have unintended short-term consequences including smaller home range areas, altered habitat use, delayed migration, and longer breeding-site residency, suggesting that management actions aimed to reduce breeding success could increase opportunities for human-wildlife conflict and spread of spatially heterogeneous pathogens at local scales. At the landscape scale, the migration patterns and wintering distribution of yellow-legged gulls are unlikely to be affected by egg-oiling.

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However, long-distance inland migrations of a portion of the population present a novel pathway for pathogen transmission between and among marine habitats and terrestrial human, livestock, and wildlife populations. **Keywords** Foraging, Frioul, Human-wildlife conflict, *Larus michahellis*, Mediterranean, Yellow-legged gull

Background

Individual heterogeneity in movement strategies is an important, though often cryptic, driver of demographic and distributional patterns in mobile wildlife [1]. Within seasonal habitats, individual habitat specializations may lead to differences in fitness or risk exposure [2]. At the annual scale, resident and migratory individuals may cooccur within the same breeding population, with corresponding variation in survival and condition [3-5]. Both localized movements and migratory strategies depend on a complex suite of factors including sex, age, morphometrics, and genetics [6, 7], individual physiology and reproductive success [8-10], environmental conditions [11, 12], and intra- and interspecific interactions [13, 14]. Seasonal movement decisions may also affect one another through carry-over effects, with heterogeneity in migratory strategies and wintering locations driving individual variation in phenology, condition, and reproductive success during the breeding season, and vice-versa [15-17]. Since movement strategies can influence demographic structure and drive resilience to short- and longterm changes in external conditions [18–20], an accurate understanding of variation is important to developing accurate predictions of ecological and population processes [21]. However, due to their complexities and intensive data requirements, drivers of individual variation in intra- and interseasonal movement patterns remain poorly understood in many wildlife populations [21, 22].

Understanding individual variation in patterns of movement and migration is particularly vital when such movements mediate specific processes of interest, such as the spread of pathogens [23]. If distribution of infectious agents is spatially heterogeneous, individual variation in movement and migratory strategies may affect exposure rates and thus potential for hosts to contract and spread pathogens [24]. In turn, the scale and extent of host migration structures pathogen metapopulations, driving the frequency and intensity of disease outbreaks [25–27]. Individual heterogeneity in movement can thus affect both the likelihood and spatial extent of key epidemiological processes. For example, in a simulation study, higher variability in individual home range sizes of urban raccoons Procyon lotor increased the rate of spread of rabies virus, reducing the effectiveness of vaccination programs [28]. Similarly, non-breeding brown skuas Stercorarius antarcticus range more widely than breeding individuals and frequently carry bacterial infections, making them potential spreaders of pathogens among sympatric seabird species with disjunct breeding locations [29]. Thus, failing to account for individual variability in movement can limit the effectiveness of predictions related to pathogen spread.

Although a variety of migratory wildlife are involved in spreading pathogens at various scales, species that interact with humans and livestock in urban areas are of particular interest [30, 31]. At the same time, public health concerns often motivate efforts to relocate or control urban wildlife populations [32]. Such efforts may interact with disease transmission by shifting activity patterns and altering rates of pathogen exposure and interaction with humans, livestock, and other wildlife, often with unintended consequences. Strategies that remove animals from anthropogenic areas, such as translocations and culling, may result in increased dispersive movements and spread of pathogens to novel human, livestock, and wildlife populations [33, 34]. Changes in movement patterns resulting from strategies that reduce reproductive output while leaving wildlife on the landscape (e.g., sterilization) are less well understood, but likely depend on factors such as habitat configuration and underlying intrinsic variation among individuals [35]. In order to achieve desired outcomes of management interventions, it is therefore necessary to understand how underlying factors driving movement patterns of target organisms are likely to interact with management strategies.

Urban-adapted birds such as gulls (Laridae) can play an important role in disease transfer at the wildlife-human interface due to their wide-ranging movements, foraging behavior, and exploitation of anthropogenic and nonanthropogenic habitats across various ecosystems [36]. Scavenging on carcasses and discards exposes gulls to a variety of pathogens [37], which they can then carry and spread during migration and dispersal [38]. Such pathogens can have severe public health, economic, and conservation consequences [36, 39, 40]. Understanding the movement patterns of gulls can therefore help to identify potential routes and opportunities for pathogen transmission, which can in turn inform conservation and policy recommendations related to management of disease and other sources of human-wildlife conflict [41]. Since many species of gulls are partially migratory [42-44], the extent of their migratory movements is often unknown or underestimated. Recently, bird-borne tracking data have helped to elucidate how gull habitat use and migration mediate both exposure to and potential transfer of disease [45, 46]. However, additional information is needed on the influence of within- and among-individual variation in migration on these spatial processes, including how management efforts interact with existing spatial dynamics [9, 47].

To help fill these information gaps, we examined the impact of induced breeding failure on breeding-season foraging movements and migratory patterns of urban yellow-legged gulls Larus michahellis breeding on an island colony in Marseille, France. Yellow-legged gulls host and spread a variety of infectious diseases [48, 49], making them valuable sentinels for disease dynamics. Prior studies in this species have demonstrated spatial and individual heterogeneity in both breeding season foraging movements [50, 51] and occurrence and spread of pathogens [52, 53]. However, with the exception of encounter histories of individuals ringed as juveniles [54–56], movement patterns of yellow-legged gulls away from the breeding colony and outside the breeding season remain poorly described. Meanwhile, yellow-legged gulls frequently come into conflict with human populations and are targets of management actions to reduce numbers and limit conflict [41, 57]. We experimentally manipulated breeding success using egg oiling, a common control technique to reduce breeding success and relocate bird populations [58-60] that is regularly employed to control yellow-legged gulls in the study area [57]. We then evaluated breeding and non-breeding movements of gulls with oiled and non-oiled nests during the season of treatment, as well as during the subsequent non-breeding period and the following breeding season. Our goals were to estimate the likelihood and interannual consistency of different migratory strategies, evaluate exposure to three pathogens with potential effects on human and livestock health (avian influenza, Toxoplasma gondii, and infectious bronchitis virus), and examine the effects of egg oiling on breeding-season foraging patterns, migratory timing and destinations, and potential pathogen spread. Based on prior studies, we expected that (1) gulls with oiled nests would show changes in movements and habitat use and increased prospecting behavior compared to gulls with non-oiled nests during the breeding season immediately following treatment but not during the subsequent breeding season [61, 62]; (2) migration strategies would vary among individuals and would be influenced by intrinsic characteristics such as sex and body size but not by nest oiling [6, 13]; and (3) migratory gulls would have higher concentrations of antibodies to focal pathogens, indicating greater exposure [30]. Ultimately, we aimed to improve understanding of how intrinsic and extrinsic factors combine to affect urban gull movements, habitat use, and opportunities for pathogen transmission.

Methods

Study system

We focused our study on yellow-legged gulls nesting on the islands of Pomègues and Ratonneau, which are linked by a dyke and function as a single colony, collectively called Frioul. Frioul is located in the Mediterranean Sea (43° 16' 32" N, 5° 18' 24" E), 2.7 km offshore from the city of Marseille, France (pop. 870,000 [63]). Approximately 8,000 pairs of yellow-legged gulls, or about half of the breeding pairs in the region, nested on Frioul in the study year ([64]; C. Brunet, pers comm.) in breeding habitats composed of limestone rock interspersed with patches of grass and shrubs. Breeding activity occurs primarily from mid-March to late June, with most eggs hatching in mid to late April. Adults continue to attend nest sites for several weeks after hatch, and nestlings generally remain close to the original nest site for 35–40 days before fledging.

Capture and tracking

We captured 30 adult yellow-legged gulls between 15 and 24 April 2021, targeting incubating adults with a full clutch of three eggs but no hatched chicks, since gulls at this stage are unlikely to abandon nests if disturbed. We captured gulls on nests using a walk-in wire mesh box trap with a treadle-activated door prop. If the adult did not enter the trap within 15 min, we reoriented the trap for a second attempt; if the second attempt was also unsuccessful, we removed the trap and targeted a different nest. Before beginning captures, we randomly selected 50% of nests for the egg-oiling treatment, while the remaining 50% were non-oiled.

Upon capture, we restrained the gull in a fabric sack, banded it on the right tarsus with a uniquely-numbered metal band, collected morphometric measurements to evaluate sex (culmen and skull lengths), size (wing chord, tarsus), and body condition (mass), and drew a 1 mL blood sample from the brachial vein using a heparinized 28-gauge needle and syringe, which we stored on ice until processing was complete. We subsequently centrifuged all blood samples within 2 h of capture and separated plasma, which we then stored frozen until subsequent laboratory analysis. We then attached a~12 g GPS-UHF transmitter (UvA-BiTS: Amsterdam, Netherlands [65]) weighing < 3% of body mass (mean: 1.1%; range: 0.9-1.3%). Transmitters were secured dorsally between the gull's wings using a cross-body harness [66] made of Teflon ribbon (Bally Ribbon Mills: Pennsylvania, USA) reinforced with nylon twine, knotted and secured with cyanoacryate. Similar harnessing techniques did not detrimentally affect breeding performance in this species [67]. After harness attachment, we released the gull and monitored the nest until it returned. For nests assigned to the oiling treatment, we removed each egg from the nest, fully immersed it in vegetable oil, and wiped off any excess oil before replacing it in the nest. During the four weeks following transmitter deployment and egg oiling, we checked oiled and non-oiled nests every 5–7 days and recorded nest contents.

We determined sex of captured gulls using head length (i.e., the measurement from the tip of the culmen to the back of the skull), which has previously been shown to be > 99% effective in sexing yellow-legged gulls in this region [68]. Based on these established criteria, we classified all gulls with head lengths below 124.54 mm as females and all others as males.

Spatial data collection and processing

Transmitters were configured to collect and store a GPS location every five minutes. We downloaded data from transmitters using a system of three antennas arranged in a triangle around the 0.15 km² target capture area: one main antenna mounted at the top of a semaphore tower at the southern edge of the gull colony area (89 m above sea level) and two relay antennas on rocky slopes overlooking the northeast and northwest corners of the colony area (60 m). All capture sites were within 150 m of an antenna and had direct sight lines to at least one of the antennas. Data uploaded automatically to a continuouslyoperating base station whenever birds were in range of the antenna array, and we accessed data via the University of Amsterdam's Virtual Lab for Bird Movement Modeling [65]. We initially screened GPS data to remove spurious locations using a speed filter corresponding to the maximum expected flight speed (30 m/s [69]).

We conducted all spatial data analysis and statistical tests in R 4.2.0 [70]. To compare individual breeding-season home ranges between gulls with oiled and non-oiled nests, we limited location data to the period of colony attendance (i.e., at least one location/day within the breeding colony footprint). Since we captured all gulls after 15 April in Year 1, we included only data collected after 15 April in Year 2; thus, estimates from both breeding seasons include the late incubation and chick-rearing periods, and may include some post-breeding movements for individuals who continued to attend the colony after nest failure or chick fledging. To minimize inclusion of post-breeding foraging movements for residents that occupied their breeding sites throughout the year, we included only tracks with return dates on or before 30 June for all individuals, based on the observation that most chicks on the island have fledged by that time (C. Brunet, pers. comm.). We then used the track2kba R package [71] to calculate basic foraging metrics including trips/day, trip duration, and maximum distance from the colony for the treatment year (Y1: 15 April - 30 June 2021) and the subsequent breeding season (Y2: 15 April - 30 June 2022). We also calculated 50% and 90% kernel density estimates (KDEs) for each individual by year to determine the size and position of their core and full home range areas, using the canonical bandwidth estimator (href) as a smoothing parameter [72], and visually assessed tracks to determine whether gulls visited nearby breeding colonies [52, 54] during the breeding or post-breeding seasons.

To evaluate colony attendance and use of anthropogenic habitats by breeding gulls, we first defined the colony area as the minimum convex polygon surrounding all nest locations and classified all locations during the breeding season (i.e., 15 April – 30 June) as either within or outside the colony area polygon. We then superimposed breeding-season GPS locations of tagged gulls with the European Union's Copernicus Land Monitoring Service 2018 Corine Land Cover (CLC) dataset [73] which classifies land use and land cover at a 100 m grid square resolution from satellite data collected over a 6-year period, and assigned each point classified as outside the colony area to the CLC land cover category in which it occurred. Finally, we extracted the proportion of breeding-season locations for each individual and treatment group classified as either urban (continuous urban fabric; discontinuous urban fabric; green urban areas; sports and leisure facilities), agricultural (non-irrigated arable land; permanently irrigated land; rice fields; vineyards; fruit trees and berry plantations; olive groves; pastures; annual crops; complex cultivation patterns; land permanently occupied by agriculture with significant areas of natural vegetation), dump sites (dump sites), or industrial (industrial or commercial units; construction sites). Within the breeding-season home range footprint of tracked gulls, we visually compared landcover classifications based on CLC data to current satellite images to verify that primary use areas were accurately classified. To ensure robust sample sizes in each category, we calculated proportional use of anthropogenic habitats across the entire breeding season. Three additional anthropogenic habitat categories (mining, road/rail, and port) comprised < 5% of locations for any individual/year; we did not compare these between groups.

To evaluate migratory strategies, we classified all individuals with at least one full year whose breeding and non-breeding areas did not overlap as migrants, individuals whose breeding and non-breeding areas overlapped but who left the colony for at least one consecutive month (750 h) as locals, and all other individuals who remained at the colony throughout the year as residents. For migrants and locals, we defined the departure and return dates as the start and end dates of the longest trip away from the colony. For individuals with >1 year of data, we separately evaluated migratory strategy, distance, duration, and departure and return dates in both the year of nest oiling (Y1) and the subsequent non-oiled year (Y2).

Antibody testing

To evaluate background levels of pathogen circulation in tracked adults with varying movement strategies, we screened plasma samples for antibodies against three common pathogens: avian influenza virus (AIV), a complex of viruses that has caused recent widespread mortality events in livestock and wild birds with spillover to wild mammal and human populations, for which gulls act as an important reservoir [74]; Toxoplasma gondii (TOX), a parasite that causes the disease toxoplasmosis in wildlife and humans that is present at varying rates across yellow-legged gull populations in the region [52]; and infectious bronchitis virus (IBV), a gammacoronavirus that can develop into destructive epidemics in livestock [75]. These three pathogens are of widespread interest due to their effects on livestock and human health and represent a range of underlying prevalence in the system [76]. Antibody assays do not provide information on current infection rates; however, they offer a window into infection history and long-term dynamics of pathogen transmission in the system.

To test for antibodies in plasma samples, we used enzyme-linked immunosorbent assay (ELISA) kits (ID Screen[®] Avian Toxoplasmosis Indirect, TOXOS-MS-2P; ID Screen[®] Influenza A Antibody Competition Multispecies, FLUACA-5P; and ID Screen[®] Infectious Bronchitis Indirect, IBVARSV2-5P; Innovative Diagnostics SARL, Grabels, France). These kits and associated methods have been successfully used to evaluate antibodies against the target pathogens in wild gull populations in several previous studies [52, 77]. While they do not measure current infection rates or provide information on specific strains or subtypes of the target pathogens, they do offer a standardized metric for comparing prior infection histories among individuals.

We diluted and analyzed plasma samples following kit instructions. Each tray included four controls (two positive and two negative), as well as four standards selected from among our samples to represent a range of antibody concentrations. We read absorbance at 450 nm on a microplate reader (Tecan Infinite[®] 200 Pro; Tecan Group Ltd., Mannendorf, Switzerland) to determine final antibody titres. We standardized raw titres by subtracting the average value of the negative controls in the same tray and dividing by the difference between the averages of the positive and negative controls. For all assays, the intra-assay coefficient of variation was >10% (2.9% for AIV, 1.8% for TOX, and 1.1% for IBV), and the inter-assay coefficient of variation was >15% (9.2% for AIV, 10.6% for TOX, and 6.8% for IBV).

Statistical analyses

To compare parameters between treatments, we constructed generalized linear mixed models using the nlme package [78]. For breeding-season foraging metrics, we built separate models for each trip-level and colony attendance variable (distance, duration, trips per day, and proportion of time spent at the colony). Each model included a random effect of individual ID and fixed effects of mass, wing chord, sex, nest status (oiled or non-oiled), year (Y1 or Y2), day of year, and the interaction of nest status with year. We did not attempt to select a best-fitting model, but rather compared the full models among the different foraging metrics to assess the relative contributions of individual factors and treatment groups to observed responses. We evaluated breeding home range areas (50% and 90% KDEs) and proportions of locations in each anthropogenic habitat category (urban, industrial, dump, and agricultural) across the entire breeding season using the same suite of random and fixed predictors minus the effect of day of year. For migrants with multiple years of data (n = 11), we compared migration departure and return dates, distances, and destinations for oiled and non-oiled nests. Finally, we modeled antibody titres against the three tested pathogens (AIV, TOX, and IBV) as a function of fixed effects of mass, wing chord, sex, migratory status, and average breeding season home range size and proportions of each of the four anthropogenic habitat types (urban, industrial, dump, and agricultural), averaged across years. If the 95% confidence estimate of the coefficient value for a covariate did not overlap zero in a given model, we considered that predictor to be significant for that response.

Results

Of 30 yellow-legged gulls fitted with transmitters, 27 (non-oiled: n = 13; oiled: n = 14) provided data throughout at least one breeding season (Table S1). The remaining three gulls abandoned their nest sites shortly after capture and did not return to the colony. Of the 27, we identified 8 (30%) as female and 19 (70%) as male based on body measurements. During the 3–4 weeks following oiling, adults with oiled nests continued attending their nest sites, and we did not observe any evidence of either re-nesting or hatching at oiled nests. In contrast, all nonoiled nests hatched within 3 weeks of capture.

Breeding-season movements

During the breeding season, gulls averaged 1.9 foraging trips per day (SD = 1, range = 1–7), with an average duration of 2.1 h (SD = 4.9, range = 0.5–124.0) and a maximum distance of 19.2 km (SD = 10.9, range = 0.5–83.2) (Fig. 1). Trips were primarily oriented north-northeast of the colony in the direction of the city of Marseille and surrounding areas (Fig. 2). Across all birds and years, breeding-season core home ranges averaged 166 km² in size (SD = 59, range = 58–284), and full home ranges averaged 737 km² (SD = 335, range = 242–1476). Across



Fig. 1 Changes in foraging trip metrics with significant year-nest oiling interactions (coefficients of interaction terms in GLMM did not overlap 0; Table 1) between 2021 (Y1) and 2022 (Y2) for tracked yellow-legged gulls nesting on Frioul, Marseille, France: **a**) distance, **b**) duration, **c**) trips per day, **d**) proportion of locations in urban habitat, **e**) core home range (50% KDE), and **f**) full home range (90% KDE). Shaded bands indicate 95% confidence intervals of trendlines. The oiled group (Y1: n = 14; Y2: n = 13) received egg-oiling treatment in Y1 but not Y2, while the non-oiled group (Y1: n = 13; Y2: n = 7) did not receive egg-oiling treatment in either year

both breeding seasons, an average of 18.7% of locations per individual outside the breeding colony were at dump sites (SD = 7.7%, range = 2.6-44.6%), 10.2% in agricultural areas (SD = 8.7%, range = 0.4-40.4%), 9.0% in areas with urban land cover (SD = 4.7%, range = 2.9-24.5%), and 6.8% in industrial areas (SD = 5.8%, range = 0.5-22.9%).

The interaction of treatment group with year significantly affected foraging trip duration, maximum distance traveled, number of trips per day, colony attendance, and home range sizes (Table 1; Fig. 1). Compared to gulls with non-oiled nests, gulls in the oiled treatment group travelled shorter distances (Fig. 1a), made longer foraging trips (Fig. 1b) but fewer trips per day (Fig. 1c), spent more time at the breeding colony (Fig. 2a) and more time in urban areas (Fig. 1d), and had smaller core and full home range areas (Figs. 1e-f and 3a-b) in the year of nest oiling than during the subsequent year. Foraging trip parameters and home range sizes did not differ between years for the non-oiled treatment group (Figs. 1, 2b and 3c-d). Foraging trip duration and number of trips per day significantly increased over the course of the chick-rearing period (Table 1a), while colony attendance declined (Fig. 2). Sex was also a significant predictor of foraging trip duration and colony attendance, with males making shorter-duration foraging trips and spending more time at the colony than females (Table 1a). Weight and wing chord were not significant predictors of any foraging parameters. Proportions of time spent in agricultural, dump, and industrial habitats varied among individuals and years, but were not affected by treatment (Table 1c). In the year of nest oiling, 4/14 gulls with oiled nests (29%) and 4/13 gulls with oiled nests (21%) visited at least one of the known breeding colonies in the region (range = 1–5 colonies per individual).

Migratory movements

Of 20 gulls tracked through at least one full annual cycle, 7 (35%: 4 males, 3 females) were migrants, another 6



Fig. 2 Breeding-season kernel density home ranges for yellow-legged gulls on Frioul, Marseille, France, 2021 (Y1; **a**) oiled, n = 14; **b**) non-oiled, n = 13, **b**) non-oiled, n = 7). Darker polygons show the cumulative footprint of all individual 50% contour areas, and lighter colors show 90% contours. Yellow stars indicate the breeding colony location. The interaction of year with oiling status was a significant predictor of both 50% and 90% contour areas (see Table 1)

(30%: 3 males, 3 females) were locals, and the remaining 7 (35%: 7 males, 0 females) were residents (Table S2). Migrants traveled an average maximum distance of 661 (\pm 50 SD) km from the breeding colony during a migration cycle, while locals traveled 65 (\pm 14) km, and residents traveled 52 (\pm 15) km. Overall, migrants departed the colony on 3 July (\pm 15 days) and returned on 13 November (\pm 14 days), while locals left the nesting area on 8 July (\pm 9 days) and returned on 19 September (\pm 27 days). Principal migratory destinations of migrants were distributed between three inland agricultural regions in north-central and western France: the Paris Basin, the Loire Valley, and areas to the north of Bordeaux (Fig. 4). Locals occupied inland territories to the northwest of the colony site near Salon de Provence.

Of 17 gulls tracked through at least two full annual cycles, none changed migratory status, route, or destination between years (Table S2, Figure S1). Migrants from the oiled treatment group departed an average of 22 days later in the year of treatment than the subsequent nontreated year (SD = 13 days, n = 5), while for the non-oiled group departure dates did not change between the first and second years (mean difference = 1.5 days, SD = 14 days, n = 2) (Fig. 5a). There were no apparent changes

between years in either return dates or migration distances for either treatment group (Fig. 5b-c).

Pathogen exposure

Regardless of individual characteristics or migratory strategies, gulls had high and consistent levels of antibodies to TOX, and lacked antibodies to IBV (Fig. 6). More resident gulls tended to have lower titres for antibodies against AIV and higher titres for antibodies against TOX compared to more migratory individuals (Fig. 6); however, migratory status was not a significant predictor for any of the antibody titres (i.e., all coefficient values overlapped 0; Table S3). None of the individual or habitat variables we tested were significant predictors of antibody levels against AIV or IBV. TOX titres were negatively related to use of urban habitats, dump sites, and agricultural areas (Table S3).

Discussion

We found that induced nest failure via egg-oiling affected breeding-season movements and migratory departure dates of yellow-legged gulls, with individuals attending oiled nests exhibiting more concentrated movements, **Table 1** Coefficient values and [95% confidence intervals] estimated from generalized linear mixed models of breeding-season (a) daily foraging metrics; (b) seasonal home range areas, and (c) seasonal habitat use for yellow-legged gulls nesting on Frioul, Marseille, France, 2021–2022. Bold values indicate coefficients that were significant predictors for a given response (i.e., whose 95% confidence intervals did not overlap zero)

, , ,								
[Duration (hours)		Distance (km)		Trips per day		Colony attendance	
Intercept (ID)	7.23	[-28.5-44.0]	-2.55	[-74.0–68.9]	3.97	[-6.73–14.7]	0.49	[-1.14-2.12]
Year (vs. 2021)	0.58	[0.21–0.95]	0.3	[-0.52-1.12]	-0.12	[-0.190.04]	-0.07	[-0.080.06]
Oiled (vs. non-oiled)	1.02	[-0.47-2.51]	-1.87	[-4.84–1.09]	-0.77	[-1.220.31]	-0.04	[-0.09-0.01]
Year * Oiled -	0.57	[-1.080.07]	2.83	[1.69–3.96]	1.09	[0.98–1.20]	0.09	[0.07–0.11]
Weight 0	0.009	[-0.003-0.022]	0.0002	[-0.02-0.02]	0.08	[-0.08–0.25]	-0.001	[-0.005-0.003]
Wing -	0.04	[-0.14-0.06]	0.05	[-0.16–0.26]	-0.48	[-1.90–0.94]	-0.002	[-0.03-0.03]
Sex (M vs. F) -	3.36	[-6.220.51]	-0.92	[-6.55–4.72]	0.04	[-0.84–0.93]	0.19	[0.05–0.32]
Julian day (0.03	[-1.08 – -0.07]	-0.001	[-0.01-0.01]	0.001	[0-0.002]	-0.003	[-0.0030.003]
b. Seasonal Home Rang	es							
E	50% UD (km ²)		90% UD (km²)					
Intercept (ID)	120	[-362–762]	2449	[-1129–6027]				
Year (vs. 2021)	4.77	[-25.8–35.3]	21	[-167–209]				
Oiled (vs. non-oiled) -	-31	[-62.2-0.21]	-192	[-387–2.65]				
Year * Oiled	43.1	[3.23-82.9]	231	[12.9–476]				
Weight 0	0.08	[-0.11-0.28]	0.81	[-0.44-2.06]				
Wing -	0.42	[-2.03-1.19]	-6.32	[-16.6–3.95]				
Sex (M vs. F) -	10.5	[-53.6-32.7]	-98.6	[-375–178]				
c. Seasonal Habitat Use								
ί	Urban (%)		Agricultural (%)		Dump (%)		Industrial (%)	
Intercept (ID) -	-30.3	[-59.2–1.3]	-72.7	[-141.93.5]	141	[80.7–201.1]	-50.2	[-95.25.2]
Year (vs. 2021)	0.02	[0.001–0.029]	0.04	[0.01–0.08]	-0.07	[-0.100.04]	0.03	[0.003-0.05]
Oiled (vs. non-oiled)	34.6	[43.7–125.6]	43.3	[-54.5-141.2]	-90.9	[-176.0–5.7]	39.9	[-23.7–103.5]
Year * Oiled -	0.04	[-0.060.02]	-0.02	[-0.07-0.03]	0.04	[-0.03-0.08]	-0.02	[-0.05-0.01]
Weight -	0.0001	[-0.0004-0.0002]	0.0002	[-0.0003-0.0007]	-0.0002	[-0.0005-0.0004]	0.0002	[-0.0002-0.0005]
Wing (0.0003	[-0.002-0.003]	-0.0008	[-0.0005-0.0003]	-0.0008	[-0.004-0.002]	-0.001	[-0.004-0.002]
Sex (M vs. F)	0.05	[-0.16–0.26]	-0.48	[-1.90–0.94]	-0.002	[-0.03–0.03]	-0.42	[-2.03–1.19]

altered habitat use, and longer residencies in and around the breeding area. Outside the breeding season, however, individuals showed high fidelity to their migration strategies, routes, and endpoints regardless of management strategy, suggesting that large-scale movement patterns are robust to short-term breeding outcomes and management actions. Finally, we found that yellow-legged gulls in this population have similarly high rates of exposure to avian influenza virus but that exposure to *Toxoplasma gondii* varies based on habitat use, meaning that the effects of management actions on movement patterns could have consequences for the spread of pathogens of conservation and economic concern.

Egg-oiling substantially decreased the frequency and footprint of yellow-legged gull movements during the breeding season in the treatment year. Compared to gulls with non-oiled nests, gulls with oiled nests, which were neither provisioning nor guarding young, made longer-duration and more localized foraging trips, fewer trips per day, and had smaller overall home range areas. As a result, the proportion of time spent at the colony remained high throughout the breeding season in the oiled group in the treatment year of oiling, rather than declining as in the non-oiled group. In the second year of tracking, both groups of gulls were similar across all foraging trip metrics, suggesting that egg-oiling rather than underlying individual specialization was responsible for the patterns observed in the first year. Prior studies of management impacts on yellow-legged gulls have found little change in foraging patterns following culling [33] and increased dispersal distances following landfill capping [79]. However, effects of egg-oiling have not previously been assessed in this species despite its widespread use. In comparable species, experimental egg-oiling treatments showed no effect on colony presence in ringbilled gulls Larus delawarensis [80], but this study used a relatively coarse measure of colony attendance (presence on the colony at night) and did not examine foraging behavior. The use of individual tracking improves on these prior studies by allowing us to relate space use to management actions at the individual level over fine spatiotemporal scales, revealing short-term increases in time spent away from the colony that may not otherwise have been observed.



Fig. 3 Proportion of time spent at the nest by day of year for tagged yellow-legged gulls on Frioul, Marseille, France during the breeding seasons of 2021 (Y1; solid lines and darker points) – 2022 (2022; dashed lines and lighter points). Shaded bands indicate 95% confidence intervals of trendlines. The oiled group (Y1: n = 14; Y2: n = 13) were subject to egg-oiling treatment in Y1 but not Y2, while the non-oiled group (Y1: n = 13; Y2: n = 7) did not receive egg-oiling treatment in either year. The interaction of year with oiling status was a significant predictor of colony attendance (see Table 1)

Regardless of oiling status, breeding yellow-legged gulls adopted a predominantly terrestrial foraging strategy directed toward the urban perimeter, with ~50% of locations in anthropogenic habitats. Oiled gulls spent more time in urban habitats in the treatment year than in the subsequent year but did not differ in use of other anthropogenic habitats. However, we also observed interindividual and interannual variation in proportional use of all anthropogenic habitat types, suggesting both individual specialization on specific resources and year-toyear changes in resource distribution. For instance, use of urban habitats increased sharply between years in gulls with non-oiled nests, possibly because movement restrictions enacted during the COVID-19 pandemic were lifted between the 2021 and 2022 breeding seasons. The fact that we observed the opposite pattern in in gulls with oiled nests could indicate elevated use of urban habitats near the breeding area following nest oiling compared to the subsequent year; however, this result should be interpreted with caution as unmeasured intrinsic and extrinsic factors likely played an important role. Observed foraging trip distances, durations, and frequencies were similar to studies from yellow-legged gulls elsewhere in their range. However, gulls on Frioul did not show extensive use of marine foraging habitats in either study year, in contrast to other regions [50, 51]. Prior studies have linked interannual variation in foraging patterns to varying marine conditions; thus, the comparative stability of the terrestrial food resources favored by the gull population on Frioul may have contributed to a relative lack of interannual variation in habitat use. Gulls in this study also made shorter foraging trips than gulls foraging on marine resources in prior studies despite traveling similar or longer distances (e.g., mean values of 3.6 h and 11.7 km [50], vs. 2.1 h and 19.2 km in this study), which also suggests that access to stable and predictable anthropogenic food resources may increase foraging efficiency and colony attendance by chick-rearing adults. Further evaluation of the factors driving variation in habitat use and overlap with anthropogenic areas among years and individuals would be a valuable avenue for further analysis.

We observed a difference in departure dates between migratory individuals with oiled and non-oiled nests, with egg-oiling delaying the onset of migration and increasing the duration of colony attendance. All longdistance migrants with oiled nests remained at the colony longer in the year of nest oiling than in the subsequent



Fig. 4 Migration routes of yellow-legged gulls breeding on Frioul, Marseille, France, 2021 (Y1)– 2022 (Y2). Gulls with oiled nests (solid lines) received nest oiling treatment in Y1 and not in Y2. Gulls with non-oiled nests (dashed lines) did not receive nest oiling treatment in either study year. Blue lines represent riparian corridors and grey dots show the locations of major cities (> 30,000 inhabitants). Insets show main wintering areas near a) Paris, b) Tours/Orleans, and c) La Rochelle/Bordeaux, with areas classified as urban (based on Copernicus Land Monitoring Service 2018 Corine Land Cover classes) shown in grey



Fig. 5 Difference in **a**) departure date, **b**) return date, and **c**) migration distance for migratory yellow-legged gulls from oiled (n = 6) and non-oiled (n = 5) nests on Frioul, Marseille, France, 2021 (Y1)-2022 (Y2). Shaded bands indicate 95% confidence intervals of trendlines. The oiled group were subject to egg-oiling treatment in Y1 but not Y2, while the non-oiled group did not receive egg-oiling treatment in either year. The interaction of year with oiling status was a significant predictor of departure date, but not of return date or migration distance (see Table S2)



Fig. 6 Antibody concentrations against **a**) avian influenza virus (AIV), **b**) Toxoplasma gondii (TOX), and **c**) infectious bronchitis virus (IBV) for resident (blue, n = 9), local (pink, n = 4) and migratory (yellow, n = 7) yellow-legged gulls on Frioul, Marseille, France, 2021. Titers are reported as a proportion of the range between positive and negative controls

year, and three of five individuals migrated at least three weeks later. In contrast, egg-oiling has been found to decrease the duration of the colony attendance period in Canada geese Branta canadensis [60] and double-crested cormorants Phalacrocorax auratus [58, 59]. We did not re-oil nests after the initial treatment and did not observe any evidence of re-nesting in the treated group in the month following nest oiling, suggesting that gulls either continued attending nests and incubating non-viable eggs beyond the normal incubation period or re-nested at nearby sites or after the one-month observation window. The increase in residence times of breeding adults following nest-oiling could limit the effectiveness of this management strategy for reducing localized conflicts. However, we did not see apparent patterns in return dates or distance traveled for long-distance migrants, suggesting that effects of egg oiling on distribution are primarily local to the breeding area.

Although migratory strategies varied across the study population, individual migratory strategies were consistent between years regardless of induced nest failure, suggesting that intrinsic factors may play a greater role than external conditions in shaping migratory movements. All yellow-legged gulls that remained resident at the breeding site year-round were males, a result that supports similar findings from other partially migratory marine birds [13, 81]. Males may prioritize remaining at and defending a favorable breeding site, while females may prioritize finding high-quality food resources to replenish the energetic reserves required for egg-laying [81]. Our results also highlight the coexistence of multiple migratory strategies in this population, as well as dependence of yellow-legged gulls on Frioul on terrestrial urban and agricultural habitats throughout the annual cycle. Both local and long-distance migrants made northward migrations toward inland urban areas, returning to the colony in late fall or early winter. The migratory patterns we observed mirror observations from band recoveries of Adriatic yellow-legged gulls, which also show a partially migratory strategy with long-distance migrants traveling inland during the post-breeding period [55]. Overall, it appears that management actions during the breeding season are unlikely to substantially alter the overall distribution of this population during the non-breeding season, while individual drivers may be a useful avenue for future study.

From an epidemiological perspective, breeding season movements and long-distance inland migrations of yellow-legged gulls on Frioul present pathways for transmission of pathogens from marine and coastal habitats in the Mediterranean basin to inland urban and agricultural centers throughout France. Individual physiology and movements were poor predictors of variation in antibodies against the two viruses we tested, AIV and IBV. Gulls in our study had low antibody titres to IBV, suggesting universally low exposure; in contrast, titres to AIV were high and trended higher in migratory individuals, although not significantly. Since these viruses are transmissible among individuals through multiple pathways including direct contact, respiratory transfer, and environmental exposure [74, 82], exposure might be expected to be consistent among gulls breeding in proximity to one another regardless of individual habitat use. While we did not test for specific strains of avian

influenza and thus could not distinguish among virus subtypes, evidence from the wildlife disease surveillance scheme suggests that most wild bird exposure to highly pathogenic avian influenza in France occurred post-2022 [83], meaning that the antibodies we observed were more likely due to low-pathogenicity strains. However, gulls are known to act as a reservoir for a wide variety of avian influenza strains, including low-pathogenicity and gull-specific subtypes as well as highly pathogenic strains that have caused recent mass mortality events in poultry farms and in wild bird and mammal populations [84, 85]. In contrast, TOX antibody titres varied among individuals, including a negative relationship to use of urban areas, dump sites, and agricultural habitats. Exposure to T. gondii depends largely on contact with cats, which are the definitive host for and transmit oocytes through their feces [86]; thus, in line with previous studies, exposure is likely to be spatially heterogeneous depending on individual contact with areas used by feral cats [52, 76]. Since the archipelago of Frioul has a large feral cat population, exposure rates could be higher for gulls that stay near the colony to forage than for those that commute to mainland urban and agricultural habitats. Thus, egg oiling could potentially increase the prevalence of pathogens like TOX with sources close to the colony area by increasing local residency, but might have little effect on pathogens like AIV that are readily transmitted among individuals regardless of habitat use. Overall, the movements of our study population suggest that yellow-legged gulls may play an important role in transmitting pathogens among human, livestock, and wildlife populations across marine and terrestrial biomes, and that management actions that alter breeding-season habitat use could affect transmission of spatially heterogeneous pathogens.

Conclusions

While egg-oiling can decrease reproductive success and, eventually, population size [87], we found that it also resulted in longer residency periods, increased colony attendance, and more constrained habitat use near the breeding colony following treatment compared to individuals that bred normally. This suggests that eggoiling may increase rather than decrease opportunities for localized human-wildlife conflict in the short term, making it more suited to some applications than others. For example, among frequent human-gull conflicts [41], egg-oiling might reduce aggressive defense of hatched chicks in and around nesting areas but increase noise or damage caused by nesting gulls on residential buildings. Since egg-oiling increases the intensity and duration of gull presence near the breeding site and affects use of anthropogenic habitats, it could increase or shift localized pathogen transmission by gulls. In addition, nest failure due to oiling could affect the propensity of gulls to prospect for potential breeding sites. Although we observed few prospecting movements in this study and no differences between oiled and non-oiled nests, increased prospecting behavior has previously been reported following egg loss [88] and local nest failure [61] as well as occasionally during active breeding [89], which could in turn increase opportunities for interaction and disease transmission among breeding colonies. If the primary management goal is immediate resolution of short-term conflict, complete nest destruction or deterrence might be a more effective option. However, strategies that relocate gulls away from their existing nest sites may change distribution patterns over larger spatiotemporal scales than egg-oiling, which appears to impact primarily localized and short-term movements. Ultimately, understanding annual-cycle movement patterns of target species may help to identify potential unintended consequences of management actions and select methods that effectively achieve the desired outcomes.

Supplementary Information

The online version contains supplementary material available at https://doi.or g/10.1186/s40462-025-00535-8.

Supplementary Material 1

Acknowledgements

We thank David Grémillet for supplying the transmitters used in this study; Yvan Satgé for assistance with field sampling; the staff of the Parc National des Calanques (Lorraine Anselme, Alain Mante, Aurélien Robin and Camille Brunet) for field site access and help with logistics; and Valentin Ollivier for assistance with ELISA analyses.

Author contributions

Funding acquisition: JL, TB; study conception and design: JL, TB; data collection: JL; analysis and interpretation of results: JL; draft manuscript preparation: JL; review of results and approval the final version of the manuscript: JL, TB.

Funding

This work was conducted under a Marie Skłodowska-Curie Actions Individual Fellowship to J.S.L. under the European Commission's Horizon 2020 program (Project SENTIMOUV; H2020-MSCA-IF-2018 #843470), with additional funding from the Waterbird Society (Nisbet Research Award) and OSU OREME.

Data availability

The datasets generated and/or analysed during the current study are available in the Zenodo data repository (https://doi.org/10.5281/zenodo.14233397), and movement data are available for viewing via Movebank (http://www.mov ebank.org, Study ID 1732940583).

Declarations

Ethics approval and consent to participate

All experiments were performed in accordance with relevant guidelines and regulations, under permits from the Préfecture des Bouches-du-Rhône (Arrêté préfectoral n°13-2020-06-22-00), Parc National des Calanques (Avis Conforme No. DI-2020-046), French Ministry of Research (APAFIS #23794_2020071214191592), Ministère de la Transition Écologique et Solidaire (NOR: TREL20025085/308) and Centre de Recherches sur la Biologie des Populations d'Oiseaux (CRBPO; Project #1094, Permit #19313) and the CEFE's Animal Experimentation Ethics Committee.

Consent for publication

Not applicable.

Competing interests

The authors declare no competing interests.

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Received: 4 December 2024 / Accepted: 30 January 2025 Published online: 06 March 2025

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