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Increased adult movements and decreased juvenile apparent survival of urban crows during COVID-19 lockdowns

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The increasing abundance of animal species thriving in urban environments is a source of conflicts with managers and users of public spaces. Although opportunistic urban species often use resources originating from human food leftovers, the potential impact of a reduction in these resources on their demography is hard to quantify. The COVID-19 epidemic, which led many countries to set up lockdowns, gave us the opportunity to estimate the impact of a drastic reduction in such food resources and human activities on the demography of an urban bird population. Based on 7 years (2015–2021) of capture-mark-recapture of carrion crows (*Corvus corone*) in the city of Paris, France, we used multi-state models to examine the intra-annual (3-month time steps) apparent survival and movement patterns of crows during and outside COVID-19 lockdowns. We showed that the apparent survival of juvenile carrion crows decreased down during lockdown, while adult movements increased during this period, with more adult crows moving out of the urban district. Lockdown modified the demography of this urban crow population, suggesting that the reduction in food resources was sufficient to affect fitness and reduce carrying capacity.

Keywords Carrion crow, *Corvus corone*, Movement, Pandemics, Survival

The global processes of land alteration by humans and urbanization have considerably modified ecosystem functioning, and led to frequent conflicts between humans and wildlife[1]. In urban environments, along with the increase of human population densities, a few plant and animal species become dominant within homogenized biological communities[2]. Some opportunistic species benefit from abundant and predictable human food resources in cities to maintain or expand their populations, such as crows and feral pigeons, while their increase in numbers often results in frequent conflicts with humans[3].

In this context, the COVID-19 pandemic and associated lockdowns provided an opportunity to study the relationship between food provided by human activities in populated areas and the fate of urban bird populations[4]. Following the pandemic, many countries throughout the world implemented lockdowns in February-March 2020, resulting in a sharp reduction of human activities[4], noise and air pollution[5]. However, the consequences of lockdowns on synanthropic bird species can be many and diverse, with e.g. hypotheses on impacts on movements or demography being potentially antagonistic. On the one hand, birds may have benefited from a temporary strong reduction in human disturbance[6] and road traffic[7,8], while on the other hand they may have suffered from a drastic reduction in food resources[4]. The end of lockdowns also induced an increase in recreational activities which potentially disturbed wildlife, for example impacting the breeding success and dispersal of some animals[9,10].

We aimed at studying the impacts of COVID-19 pandemic-related lockdowns on the movement and survival probabilities of an urban-dwelling bird benefiting from food provided by human activitiesin cities. The Carrion Crow *Corvus corone* is an opportunistic omnivorous corvid bird, inhabiting various open habitats, including urban environments even in city centres, where it frequently feeds on human food waste. During the day, large flocks of crows gather in urban places where food is abundant and predictable[11], for example public gardens and parks where humans often consume food outdoor. In Paris, France, carrion crows are a common sight and have been monitored by ringing at Jardin des Plantes (hereafter JDP) since 2015[12]. Three successive lockdowns were implemented in France in 2020 and 2021, the most stringent one occurring from 17 March to 11 May 2020, with forbidden outdoor activities and closure of all urban parks and gardens, schools and restaurants, while most

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workers were requested to work from home. As a consequence, all public bins in public parks and gardens were empty for weeks, and food waste was stored in household garbage bins rather than in public street bins. The spring 2020 lockdown provided therefore a valuable opportunity to test how much urban crows depend on food provided by human activities. We thus explored the effects of lockdown on survival and movement probabilities as compared to non-lockdown periods. If access to food resources decreased during lockdowns, we expected lockdowns to negatively affect apparent survival, and especially for young crows than for more experienced older individuals. Indeed, in relatively long-lived animal species, the theory predicts that juvenile survival varies more with environmental variations than adult survival, the so-called "environmental canalization"[13].

We used a capture-mark-recapture approach with a seasonal time step (corresponding to four sessions per year) to study movements and survival in combination. All individuals were captured and marked at JDP. Following this first capture, subsequent recapture events (mostly observations of ringed individuals) took place either within the JDP, or outside the JDP, in the city of Paris or beyond the limits of Paris. We used a multi-state model, with two possible states for each recapture event of each bird: bird recaptured in the JDP or outside the JDP. The study of transitions between these states enabled us to estimate the probabilities of bird movement from the JDP or towards the JDP, as well as the differences in apparent survival among areas, while taking into account the different recapture probabilities between the two locations. The dataset covers the period 2015–2021 and therefore also enabled us to test the existence of possible differences between the year of lockdown following the COVID-19 pandemic (year 2020) and the other years used as references to test our hypotheses on the effect of lockdown on survival and movement patterns.

Results

Parametrization of a global multi-state capture-mark-recapture model

The overall test for multi-state capture-mark-recapture models revealed a significant but moderate deviation from the Jolly-Move model (for the group of birds marked as juveniles: $\chi^2_{218} = 392.7$, P-value $< 10^{-3}$; for the group of birds marked as adults: $\chi^2_{149} = 196.2$, P-value $= 0.006$). This deviation was mainly related to a memory effect and a transience effect for birds marked as juveniles (WBWA test, $\chi^2_{33} = 83.5$, P-value $< 10^{-3}$, 3G.SR test, $\chi^2_{24} = 36.7$, P-value $= 0.04$) but not for the birds marked as adults. These results suggest that……. Futhermore, we highlighted an immediate trap-dependence for both age groups (birds marked as juveniles: $\chi^2_{26} = 153.9$, P-value $< 10^{-3}$; birds marked as adults: $\chi^2_{24} = 69.8$, P-value $< 10^{-3}$), suggesting that…… To incorporate these deviations in our model selection, we (1) incorporated and tested an age effect for birds marked as juveniles for parameters Φ (survival probability), p (recapture probability), and Ψ (transition probability, corresponding to movement probability), and (2) incorporated a correction coefficient corresponding to the overall c-hat ($\hat{c}$) (overdispersion coefficient) of the group of birds marked as adults ($\hat{c} = 196.2 / 149 = 1.3$).

Table S1 in supplementary materials reports model selection (without lockdown effect) for Φ, p and Ψ, while Tables 1 and 2 report model selection to study the impact of lockdown on survival and movement probabilities, respectively. The best model without lockdown effect was Φ (season × age class) p (time + location) Ψ (time*location) (model 1, Table S1). This model assumed that Ψ and p are time- and location-dependant, with an additive effect between time and location for p and a non-additive effect for Ψ.

Ψ varied over time (model 21 vs. 22, ΔQAICc = 10.3, Table S1) and time was more appropriate than season to explain movement variations (model 11 vs. 18, ΔQAICc = 68.6, Table S1). Adding an age effect on Ψ improved model fit when combined with season (model 12 vs. 18, ΔQAICc = 61.2, Table S1) but not when combined with time (model 13 vs. 14, ΔQAICc = 1.7, Table S1).

Φ did not vary between locations (models 5 vs. 6, ΔQAICc = 1.9 and models 1 vs. 2, ΔQAICc = 6.3, Table S1), but it was season and age dependant (model 1 vs. 5, ΔQAICc = 23.1, Table S1). Time explained survival

Model number	Model description	Δ QAICc	Number of parameters	QDeviance
23	Φ (season*Age class + COVID[1y, SF]) p (time + location) Ψ (time*location)	0	85	3764.45
24	Φ (season*Age class + COVID[1y, F]) p (time + location) Ψ (time*location)	1.47	84	3768.04
25	Φ (season*Age class + COVID[1y, SFW]) p (time + location) Ψ (time*location)	1.57	86	3763.90
26	Φ (season*Age class + COVID[1y + Ad, SF]) p (time + location) Ψ (time*location)	2.53	87	3762.74
27	Φ (season*Age class + COVID[1y, FW]) p (time + location) Ψ (time*location)	3.04	85	3767.49
28	Φ (season*Age class + COVID[1y + Ad, F]) p (time + location) Ψ (time*location)	3.58	85	3768.03
29	Φ (season*Age class + COVID[1y, S]) p (time + location) Ψ (time*location)	4.26	84	3770.83
1	Φ (season*Age class) p (time + location) Ψ (time*location)	4.95	83	3773.64

Table 1. Survival selection for models on capture-recapture histories of 667 carrion crows captured from 2015 to 2021 in Jardin Des Plantes (JDP) in central Paris. The model effects of age class, time, season, location on survival (φ), recapture (P) and movement (Ψ) probabilities were tested. Starting from the best model of the general selection (model 1), lockdown effect was applied on survival of adults (ad) only, juvenile birds (1y) only or both of them (respectively COVID[Ad], COVID[1y] and COVID[1y + ad]), and its effect was tested during summer (S), fall (F), winter (W) 2020 or combinations of several seasons. For φ, "location" models assume that survival is different between JDP and the rest of Paris; for Ψ, "location" models assume that movements depend on the direction of the transition. Models are based on $\hat{c}$ = 1.3. Best model is Model 23 with QAICc = 6436.97. The complete set of models tested is presented in Table S2 (supplementary materials)

Model number	Model description	Δ QAICc	Number of parameters	QDeviance
35	Φ (season*Age class + COVID[1y, SF]) p (time + location) Ψ (season*location*Age class + COVID[Ad, FW])	18.39	53	3849.99
36	Φ (season*Age class + COVID[1y, SF]) p (time + location) Ψ (season*location*Age class + COVID[Ad, W])	20.90	51	3856.65
37	Φ (season*Age class + COVID[1y, SF]) p (time + location) Ψ (season*location*Age class + COVID[Ad, F])	21.48	51	3857.23
38	Φ (season*Age class + COVID[1y, SF]) p (time + location) Ψ (season*Age class + COVID[Ad, SFW])	21.94	55	3849.39
39	Φ (season*Age class + COVID[1y, SF]) p (time + location) Ψ (season*location*Age class + COVID[1y + Ad, W])	23.74	53	3855.34
40	Φ (season*Age class + COVID[1y, SF]) p (time + location) Ψ (season*location*Age class)	24.16	49	3864.05

Table 2. Models of transition probability applied to capture-recapture histories of 667 carrion crows captured from 2015 to 2021 in Jardin Des Plantes (JDP), Paris The effects of age class, time, season, location on survival (Φ), recapture (p) and movement (Ψ) probabilities were tested. Starting from the best model from the survival selection (model 40), lockdown effect was applied on movement of adults (ad) only, juvenile individuals (1y) only or both of them (respectively COVID[Ad], COVID[1y] and COVID[1y + ad]), and its effect was tested during summer (S), fall (F), winter (W) 2020 or combinations of several seasons. For φ, "location" models assume that apparent survival is different between JDP and the rest of Paris; for Ψ, "location" models assume that probability of movements depend on the direction of the transition. Models are based on $\hat{c} = 1.3$. Best model is Model 35 with QAICc = 6455.36. The complete set of models tested is presented in table S3 in supplementary materials

variations better than season (model 8 vs. model 9, ΔQAICc = 10 and model 1 vs. model 17, ΔQAICc = 129.7, Table S1), suggesting that temporal variation in survival was more explained by inter-season than inter-year variation.

Movement probabilities out of JDP were higher for birds in their first year (1y) than for adults (Ad) in two seasons, summer (Ψ = 0.19 [0.14; 0.26] for Ad and 0.50 [0.42; 0.59] for 1y, model 12) and fall (Ψ = 0.29 [0.22; 0.36] for Ad and 0.56 [0.48; 0.64] for 1y, model 12, Figure S1). Movement probabilities towards JDP were higher for juveniles than for adults in summer (Ψ = 0.11 [0.08; 0.16] for Ad and 0.33 [0.15; 0.56] for 1y, model 12, Table S1, Figure S1).

Assessing lockdown effects on apparent survival and movement

Including a lockdown effect on survival of 1y birds improved model fit (model 1 vs. models 23, 24, 25, respectively ΔQAICc = 4.9; 3.5; 3.4, Table 1), especially in spring and fall. The estimates showed that survival of 1y birds drastically decreased between summer and fall 2020 (Φ = 0.85 [0.77; 0.91] for 1y between summer and fall of years without lockdown, and Φ = 0.59 [0.38; 0.78] for 1y between summer and fall 2020, Fig. 1). In contrast, the lockdown did not seem to induce variation in the survival of adults (model 1 vs. model 33, ΔQAICc = 2.5; model 1 vs. model 34, ΔQAICc = 3.4, Table S2).

Lockdown affected movements, estimated by transition probabilities, of adults (models 35 to 38 vs. model 40, respectively ΔQAICc = 5.8; 3.3; 2.6; 2.2, Table 2), but not of 1y birds (model 40 vs. models 43, 44, 46, 50, 51, Table S3). Between summer and fall, adult movements from JDP to Paris increased during lockdown (Ψ = 0.18 [0.12; 0.25] without lockdown, versus Ψ = 0.21 [0.15; 0.30] during lockdown, model 35, Table 2; Fig. 2). The same result was obtained between fall and winter (Ψ = 0.38 [0.22; 0.36] without lockdown, versus 0.46 [0.30; 0.62] during lockdown, model 35, Table 2; Fig. 2). Adult movements from Paris towards JDP were not influenced by lockdown in summer and fall (Table S3).

Discussion

Overall, our results revealed that the lockdowns implemented in France in 2020 during the COVID-19 pandemic had demographic consequences on the crow population in Paris, with different effects according to the age of the birds. In particular, the transient reduction in apparent survival probabilities for juvenile birds at a critical stage of their life cycle (the first complete moult occurs during the first summer) is consistent with the hypothesis of a predominant effect of the reduction in available resources on demographic rates. A decrease in the food that human activities made available for the crows due to lockdowns during the COVID-19 pandemic was sufficient to significantly reduce apparent survival during the first year of life. Indeed, the apparent survival dropped from 0.85 to 0.59 during lockdowns for young birds, as compared to the same seasons without lockdown. By contrast, we failed to find a corresponding increase during lockdowns for adult crows.

The probabilities of movements between the JDP and the rest of Paris estimated by our models illustrate that urban crows are rather mobile. Juvenile individuals displayed movement frequencies approximately two times higher than adults, during their first summer and fall. This difference probably depends on the territorial behaviour of adults during the breeding season, while adult moving out from the main study site increased during winter. This pattern was however modified during lockdowns, with increased movements of adults out of the main study site. Lockdowns drove adult crows to move outside the JDP at higher rates in summer and fall 2020. However, contrary to individuals in their first year of life, adults did not suffer from a higher apparent mortality. Taken together, these two findings may result from higher propensity of territorial adults to forage outside of their usual territories, in the context of an absence of human food provision in urban parks during lockdowns. We could also attribute these broader movements to a reduction in human disturbance outside parks and gardens during lockdowns, leaving more space available for wildlife to forage in the city and along streets.

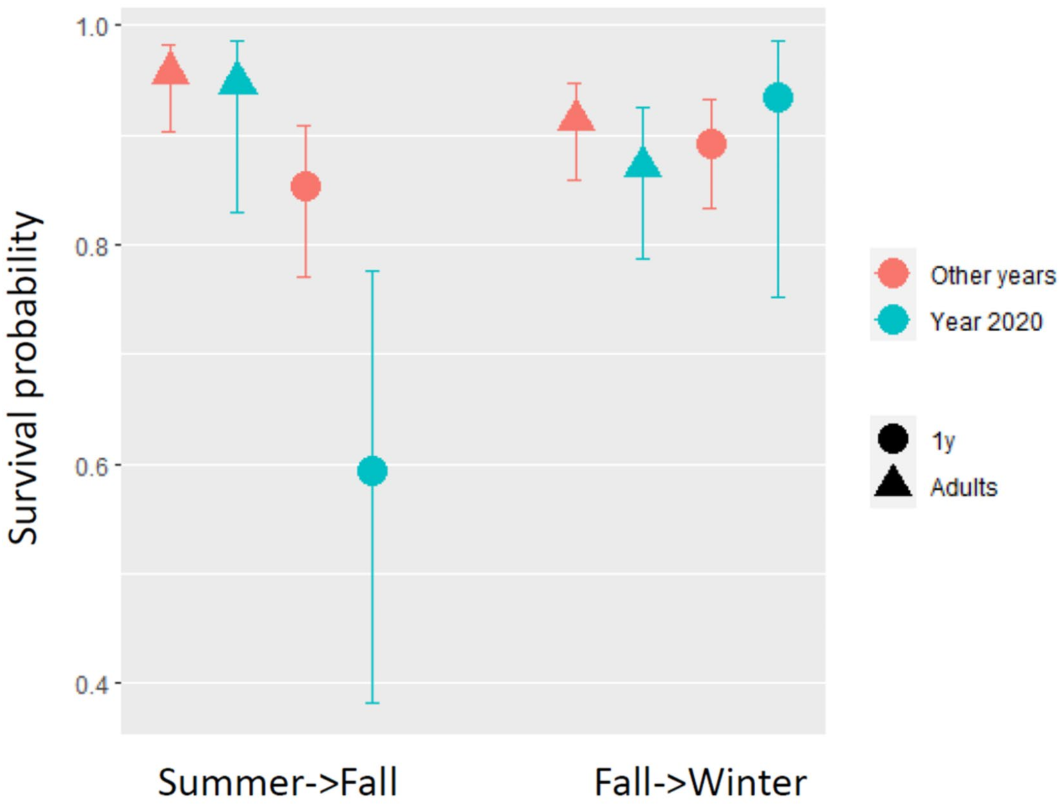

Fig. 1. Apparent survival estimates (95% confidence intervals) of adults (Adults) and juvenile (1y) carrion crows, for the year of lockdown (2020) and the other years (2015–2019 and 2021). Estimates are derived from model 30 in Table S2.

Such changes in movements of urban birds during lockdowns have also been reported in Torresian crows *Corvus orru* in Australia, which moved from cities to beaches in response to the rarefaction in urban food resources[14], while feral pigeons *Columba livia* from Singapore changed their feeding hotspots during a lockdown[10].

As early as 2020, scientists[4] highlighted how the scientific community could use the tragic circumstances of the COVID-19 pandemic to provide important insights into human–wildlife interactions in a human-dominated biosphere. Lockdown effects have been drastic, sudden, and widespread. The reduction in human mobility on land and at sea during this so-called anthropause is unparalleled in recent history, and led to numerous reports of an increase in the mobility of wild animals. Globally, mammals displayed larger home ranges and moved closer to human infrastructures during lockdowns[15,16]. Positive effects on survival have also been reported, as the global reduction of road traffics dramatically reduced road casualties[7,17,18].

Some urban-dwelling animals have become so reliant on food discarded or provided by humans that they struggled to find food during lockdowns, while humans gathering at urban green spaces potentially disturbed resident wildlife[4]. Our results further highlight the role of carrion crows as urban scavengers. As a consequence, the demography of urban crows can be impacted by a drastic reduction in the availability of waste food, while the natural large-scale quasi-experimental setting provided by lockdowns in 2020 allowed to quantify the degree to which crow survival in cities depends on food provided by human activities. In Paris, large flocks of non-breeding immature crows gather in parks and gardens, and a dedicated management of food waste in the public space could largely and rapidly decrease the survival of these immature individuals. Whether this would further induce a decrease in crow numbers in the city would probably depend on the movement dynamics at large spatial scales, like the source-sink or fusion-fission dynamics described for other corvid species[11,19].

Methods

Study site and data collection

Carrion crows were captured and colour-ringed at JDP (48,84°N, 2.36°E) since 2015. This urban park located in Paris city, France, near the Seine River, covers 23.5 ha and is mainly frequented by families, tourists and schools for recreational and cultural activities. We trapped crows using a baited cage trap (8 m^3), which crows can enter through a horizontal ladder along the roof, but cannot escape. The trap was visited every day and birds were processed within 20 h of capture. From 2015 to 2021, we captured and ringed 667 carrion crows (496 juvenile individuals, hereafter 1y crows, and 171 adults). All procedures performed in this study involving animals were in accordance with the ethical standards of the French government guidelines. Authorization to capture and mark carrion crows was obtained from CRBPO at Museum National d'Histoire Naturelle, as the national licensing

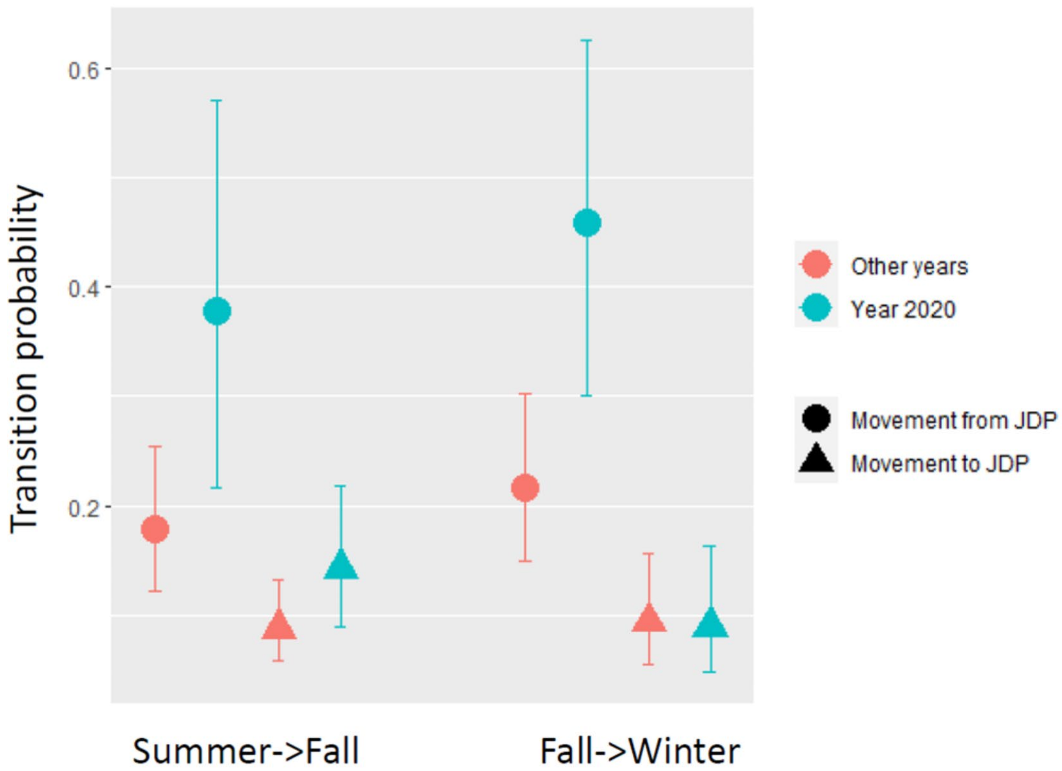

Fig. 2. Estimates of movement probabilities (transition probabilities, 95% confidence intervals) from and to Jardin des Plantes (JDP) for adult carrion crows, estimated during two seasons (summer and fall) during the lockdown period (year 2020) and outside the lockdown period (years 2015–2019 and 2021). Estimates are derived from model 35 in Table 2.

committee delivering such authorizations, under file reference PP883. We confirm that the study is reported in accordance with ARRIVE guidelines (https://arriveguidelines.org). Once captured, we ringed each crow with a unique-coded metal ring from the national ringing scheme (CRBPO), and also with a pair of plastic colour coded rings (one on each tarsus), displaying a unique individual code, allowing distant individual identification. Age was evaluated using the colour pattern of the palate (pink for 1y crows and blackish for older birds) and moult contrasts between body and flight feathers[20]. In France, the most stringent lockdown occurred from 17 March to 11 May 2020, while two further lockdowns (from 30 October to 15 December 2020, then from 3 April to 3 May 2021) were less stringent, with schools and public parks remaining open to the public.

Capture-recapture histories

Individually marked crows were re-observed thanks to a participatory science scheme: any observer identifying a ringed bird (ring number) could report the observation, with bird identity, location and date, on a dedicated website (www.corneilles-paris.fr). Each record submitted to the platform was checked and eventually validated. We used this validated database, together with recaptures at the cage traps, to produce the recapture histories of ringed individuals. Recaptures were made continuously (from 2015 to 2021), which deviates from traditional capture-mark-recapture frameworks, as capture sessions should be very short compared to intersessions. However, this duration assumption can be violated if recapture probability is higher than 20%[21], which was the case in our study. We captured and ringed 667 individuals, of which 516 have been reobserved generating 18,785 observations.

Capture-mark-recapture survival and movement analysis

Individual Capture-Mark-Recapture multi-state histories (CMR) were constructed by considering two states, which corresponded to the spatial location of birds at capture and at each recapture event: the JDP state (for all first captures as well as recaptures occurring within a radius of 500 m from the trap cage) and the Paris state, for recaptures occurring outside this circle (mainly in Paris city). Each year of the study period was divided into 4 capture-recapture sessions: a winter session (from January to March), a spring session (April-June), a summer session (July-September) and an fall session (October-December). This structure enabled to introduce a season parameter, with an annual periodicity. The first session was summer 2015, and the last was fall 2021, which corresponded to a total of 26 sessions. We considered two age classes: young individuals in their first calendar year (1y), from ringing as juvenile in the hatching year to the 31st of December of the same year, and older birds named adults (Ad). In CMR models, the age class was modelled with a combination of group (implemented in the dataset) and age-effect (as modelled in Mark): each bird was assigned to a group depending on its age determined at marking (either 1y or Ad). Birds of Ad age at marking remained in the Ad age class over their capture-recapture history. Birds of the 1y age at marking were initially in the 1y age class but moved to the Ad age class when transition from their first fall session to their first winter session.

Using this dataset, we performed capture-mark-recapture analyses using the program MARK 6.2[22], to compare various models for survival, recapture and transition (the later as movements between JDP and Paris) probabilities (Φ, p and Ψ respectively[23]), using a logit-link function. We used the Akaike's Information Criterion corrected for small sample size and data overdispersion (QAICc) in model selection[24]. We considered a low QAICc as revealing a good compromise between the fit to the data (likelihood of the model) and the number of parameters used by the model. We set the threshold for a significant difference between two models at two QAICc points. We considered that the Φ, p and Ψ parameters could potentially vary according to the following variables: time (i.e., the focal parameter varies between all sessions); Season (i.e., the focal parameter varies between seasons only); Age class (1y vs. Ad); Location (JDP vs. Paris); and Lockdown, defined as the period running from April 2020 to December 2020 and implemented as a temporal covariate. When more than one variable was tested for a given parameter, we tested models with full interaction between variables (*) and those with only additive effects between variables (+). In order to limit the number of models tested, we considered a step-by-step approach to explore the various effects and parameters.

The initial model included the effects of time and location and their interaction for all parameters (model 15 in Table S1 in supplementary materials). We simplified the model and first selected the best parameter structure for p, then simplified the model for Φ while keeping the best structure for p. Finally, we simplified Ψ while keeping the best structure for p and Φ. We then included an age effect on Φ, p and Ψ. Finally, the lockdown effect was tested only on a set of final models on the Φ and then Ψ parameters, using "Season" as null models (the lockdown effect was not tested on p since p was already time dependent in the final models).

CMR models, and in particular multi-state models, are associated with several assumptions concerning parameter homogeneity and the independence of survival, transition and recapture events[25,26]. To verify these assumptions, we used the program u-care[27] prior to model selection in Mark. With u-care, we assessed the fit of the data to a Jolly MoVe (JMV) model for multistate models. The JMV model is a general model which allows detection parameters to depend on the previous state occupied. Statistical violations of the JMV model include transience (when individuals captured for the first time have a lower probability of being recaptured in the future, as compared to individuals of the same sample that had been captured previously), trap-dependence (when there is a statistical link for an animal between the fact of having been captured at one time step and its probability of being recaptured at the next time step) and memory (when animals belonging to the same sample behave differently depending on which sites they had visited previously).

Data availability

The datasets used and analyzed during the current study can be freely viewed on the web-site www.corneilles-paris.fr, while data downloads are available from the corresponding author on request.

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Author contributions
FJ and AR were involved in study conception and design. FJ ringed all birds, PLC and FJ participated to further recapture data. AR and PLC analyzed the data. All authors contributed to writing the manuscript, reviewed and approved the final version.

Declarations

Competing interests
The authors declare no competing interests.

Additional information
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