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Apparent survival rates of wild and captive-bred-released Corvus corax in an anthropogenic alpine environment

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Abstract

Anthropogenic landscapes continue to grow, and so does our human impact. While most wildlife species avoid anthropogenic landscapes, some – specifically diet and habitat generalists – can even thrive in them. Commons ravens *(Corvus corax) are* such generalists, whereby large foraging groups can be subsidized by anthropogenic food sources. But living in close human presence entail risks, stemming from collisions with infrastructure and direct persecution. Furthermore, large numbers of ravens have potential to cause human-wildlife conflicts, that might also impact their population dynamics. To gain wider knowledge on the ecology of ravens in anthropogenic landscapes, insights in their survival rates might be beneficial for future population management strategies. Long-term resighting-data from individually colour-marked ravens (n=504), generated over 15 years at a predictable wild boar feeding site in the Cumberland Game Park, Upper Austria, was used to run a series of capture-mark-recapture analyses (Cormack-Jolly-Seber models), to compare annual apparent survival rates between ravens of different age classes, sexes, and origins. The latter refers to a captive-bred-release research project, where raven hatched in captivity are parent raised and after a family and a peer group phase, released to integrate into a wild population of non-breeding ravens. Additionally, mortality data from GPS-tagged ravens (n=166) was summarized, to quantify typical causes of death in relation to age, sex, origin, and season. Our results show no significant differences in apparent survival rates of neither captive-bred ($\Phi=0.65$) and wild-caught ($\Phi=0.72$), nor male ($\Phi=0.73$) or female ($\Phi=0.71$) raven. Age had the only significant impact on survival probability, with juveniles having significantly lower annual survival rates ($\Phi=0.53$) than subadults ($\Phi=0.73$) and adults($\Phi=0.72$). The analysis of the GPS data on true mortality stated a strong effect of age on survival, but also showed significantly higher ($\chi^2 = 5.77$, $p = 0.02$) origin-specific mortality numbers in captive-bred-released individuals, especially in autumn, i.e. the time of release. Taken together, these results suggest that experience, expressed via age and partly via origin, is the key factor for survival in ravens foraging at anthropogenic food sources in the Austrian Alpes.

Überlebensraten von Kolkraben in anthropogenen Lebensräumen der österreichischen Alpen

Zusammenfassug

Mit wachsendem anthropogenen Einfluss gehen viele Naturräume für Wildtiere verloren. Während die meisten Wildtierarten solche anthropogen veränderten Landschaften meiden, können einige - insbesondere Nahrungs- und Lebensraumgeneralisten – sogar vom Menschen und assoziierten Ressourcen profitieren. Kolkraben *(Corvus corax)* sind Generalisten, die zusätzliche anthropogene Nahrungsquellen nutzen. Das Leben in unmittelbarer Nähe des Menschen ist jedoch auch mit Risiken verbunden (z.B Kollisionen mit Infrastruktur, direkte Verfolgung, etc.). Große Rabenpopulationen in anthropogenen Gebieten können zu Konflikten zwischen Menschen und Wildtieren führen, die wiederum negative Auswirkungen auf die Populationsdynamiken haben. Um den Wissenstand zur Ökologie von Rabenvögeln in anthropogenen Landschaften zu erweitern, sind Langezeitdaten die zur Ermittlung von Überlebensraten entscheidend sind, wertvoll um zukunftsorientierte Managementstrategien die eine Koexistenz ermöglichen, zu entwickeln Hier verwenden wir Anwesenheitsdaten von individuell markierten Raben (n=504), welche über 15 Jahre an einer regelmäßig stattfindenden Wildschweinfütterung im Cumberland Wildpark, Oberösterreich, generiert wurden, um eine Reihe von Fang-Widerfang- Analysen (sogenannte „Mark-Recapture Cormack-Jolly-Seber-Modelle") durchzuführen. Diese Modelle ermöglichen einen Vergleich der jährliche Überlebensraten von Raben im Alpenraum, in Hinblick auf verschiedene Altersklassen, Geschlechter und auch ihrer Herkunft. Letzteres bezieht sich auf verschiedene Kohorten: in freier Wildbahn geboren, oder in menschlicher Obhut von Kolkraben aufgezogen und anschließend ausgewildert und in die freifliegende Population integriert. Zusätzlich wurden Mortalitätsdaten von GPS-besenderten Raben (n=166) analysiert, um typische Todesursachen in Abhängigkeit von Alter, Geschlecht, Herkunft und auch Jahreszeit zu quantifizieren. Die Ergebnisse zeigen keine signifikanten Unterschiede in den modellierten Überlebensraten von in Gefangenschaft geschlüpften (Φ=0,65) und wild gefangenen (Φ=0,72), männlichen (Φ=0,73) oder weiblichen (Φ=0,71) Raben. Nur das Alter der Tiere zeigte einen signifikanten Einfluss auf die Überlebenswahrscheinlichkeit, wobei juvenile Raben im ersten Lebensjahr eine signifikant niedrigere jährliche Überlebensrate (Φ=0,53) aufwiesen, als subadulte (Φ=0,73) und adulte (Φ=0,72) Artgenossen. Die Analyse der GPS-Daten zur tatsächlichen Sterblichkeit, ergab ebenfalls einen starken Einfluss des Alters auf die Überlebensraten, aber auch eine signifikant höhere (χ^2 = 5,77, p = 0,02) herkunftsspezifische Sterblichkeitsrate bei in Gefangenschaft geschlüpften und freigelassenen Individuen, insbesondere im Herbst, d. h. zum

Zeitpunkt der Freilassung. Zusammengefasst deuten diese Ergebnisse darauf hin, dass Erfahrung, hier in der Variable Alter reflektiert, und auch die Herkunft, den größten Einfluss auf Überlebensraten aufweisen. Prädation, illegale Verfolgung sowie Verkehrskollisionen waren die am häufigsten festgestellten Todesursachen der Raben, welche anthropogene Nahrungsquellen in den österreichischen Alpen nutzen.

Introduction

Human activity in anthropogenic landscapes has direct and indirect effects on wildlife and natural habitats (Van Dyck, 2012). While the increasing fragmentation of habitats through human activity has negative impacts on biodiversity, life in anthropogenic landscapes presents risks and opportunities for wildlife (Fehlmann et al., 2021). Additional foraging possibilities as well as direct (e.g. persecution) and indirect (e.g. habitat loss) threats, coming with the anthropogenic context, create challenging and dynamic conditions for all kind of species. Ecological generalists, species with broad niches which can adapt to changing environmental conditions and varying food sources (Devictor et al., 2008) , and synanthropic species - wild species cohabiting with humans and depending on anthropized areas to varying degrees, are favoured by these conditions and represented in various taxa (Devictor et al., 2008; Johnston, 2001; Klegarth, 2017; Shochat et al., 2010; West et al., 2016)

Common ravens (*Corvus corax*) are such a generalist species, found across all over the northern hemisphere in all kinds of natural and anthropogenic habitats (J. Marzluff et al., 2001). These large-brained birds do not only benefit from the additional and diverse food supply available in areas influenced by humans but also from nesting possibilities provided by anthropogenic infrastructure(Webb et al., 2004). Although they provide key ecosystem services such as scavenging and seed dispersal (Nogales et al. 1999; Whelan et al. 2008), there has been a history of conflicts between raven and humans due to their bad reputation in western/agricultural mythology for being ill-omens as well as the danger they can pose to newborn livestock (Peebles & Spencer Jr, 2020). That is why raven faced nearly extinction in wide parts of Europe in the mid-1900s due to legal and illegal persecution (Amar et al., 2010; Jokimäki et al. 2022).

Since the middle of the 20th century, raven populations are increasing again (Birdlife International, 2004; Amar et al., 2010). However, human food sources (Jain et al., 2022), provided deliberate or unintentionally, continued illegal persecution and collisions with traffic infrastructure are factors influencing raven survival in anthropogenic habitats (Webb et al. 2004; Marzluff et al., 2006; Robb et al., 2008; Rodewald et al., 2011). The ravens opportunistic use of anthropogenic food sources can often happen in large numbers(Beck et al., 2020; Jain et al., 2022; Loretto, Schuster, et al., 2016a). Which also harbours potential for human-wildlife conflicts, for example, at hunting infrastructure like feeding sites or at composting facilities.

Survival rates are key indicators for the health status and trends in numbers of bird populations and allow conclusions on drivers influencing them. Although there is research on anthropogenic factors and their impact on raven demography and survival (Restani et al., 2001, Webb et al., 2004, Marzluff et al., 2006, Jain et al., 2022), little is known about cohort- specific (sex, age, origin) differences in survival rates, which might allow further understanding of population viability and causes of mortality.

Ravens in the Austrian Alpes

The raven population in the Northern Austrian Alpes has been intensively studied over the past decades, with the focus on behavioral and cognitive research (Bugnyar, 2023). Notably, a monitoring program has been launched in 2007, during which individually marked ravens are sampled in a systematic way at the birds' main foraging sites in the Cumberland Wildpark, Grünau im Almtal. Most of those birds are non-breeders (i.e., immatures or adults without a breeding territory) with different degrees of fission-fusion dynamics (i.e., some birds can be observed almost daily whereas others pass by only occasionally; (Braun & Bugnyar, 2012). They are accompanied during foraging by territorial breeding pairs from the vicinity of the park. While most marked ravens are of wild origin (with known sex and age-class), a subset (about 30%) originate from a scientific breeding program in captivity (with a known pedigree), following the procedure of the re-introduction program for ravens in the 80ies and 90ies (Koch et al. 1986). The captive-bred released ravens and a subset of the wild ravens are GPS tagged to track their movements. Taken together, the long-term data derived from this well-known population of free-ranging ravens offers an ideal opportunity to investigate possible factors affecting the birds' survival.

Factors affecting survival

Season:

Season-specific survival can be influenced by anthropogenic context due to differing availability of food over the year, caused by fluctuation in, for example, touristic activities or agriculture (Jain et al., 2022). The seasonal cohort-specific survival probabilities may also be influenced by changing predation and hunting pressures, which we expect to be highest during breeding season, when energy demands might increase predation pressure, but also during the (human) hunting season, when opportunities for persecution are highest.

Age:

As typical corvids, ravens are long-lived and large-brained species; hence experience plays important role in how they deal with their environment(FRITZ & KOTRSCHAL, 1999; Miller et al., 2023). Indeed, juvenile birds readily acquire information about foraging sites as well as predators via individual and social learning. Notably group foraging and -roosting provides opportunities for info exchange regarding the spatial and temporal distribution of food and might reduce predator exposure of an individual (Chapman & Valenta, 2015; MARZLUFF et al., 1996; Wright et al., 2003) in raven populations. Juvenile, unexperienced ravens that are not yet integrated into social groups might therefore encounter food scarcity and increased predation pressure compared to adult, well integrated, experienced raven. (Wiens et al. 2006). Especially in the survival rates of those individuals, relying the most on the benefits of group foraging, like information exchange and antipredator mechanisms, I expect strong seasonal effects in the first year of life.

Sex:

Ravens are slightly size dimorphic between sexes, (Boarman et al., 1999). Apart from physiological and social advantages for bigger and heavier males (Boucherie et al., 2022) inequalities in parental care for male and female fledglings, may influence survival rates in later live (Ersoy et al., 2021a). More explorative males might face higher risk of mortality during dispersal (Stöwe et al., 2006; Yoder et al., 2004) or might take more risk when foraging together with predators, which might also lead to injury or death (Stahler et al., 2002).

Origin:

Although the social environments captive-bred and wild ravens are similar (parent-raised), captive-bred birds don't have any direct experience with predators pre-release and don't experience food scarcity because of continuous availability of human-provided food in their first months of life in captivity. These captive-bred birds, reared by their raven parents, spend the last 3 months before their release in autumn within a peer-group of other birds of the same age and life experience. They are not yet integrated into the wild population after release – which happens stepwise with wild juveniles that are following their free-ranging parents and are exposed to these foraging groups earlier than the captive-bred-release cohort, released in autumn. The presence of their parents might also help wild juveniles with social integration into the local population. The different skillsets, in terms of antipredator behaviour and foraging skills, juvenile captive-bred and wild-caught raven get early-life and start into the wild with, might influence survival chances post release.

Research questions

I here use data on individually marked free-ranging ravens collected at the birds' main foraging sites in the Cumberland Wildpark. Resighting-data generated over the past 15 years allows me to run capture-mark-recapture survival estimation models and to test possible effects of the above-mentioned factors on the survival estimates. Additionally, movement/mortality data generated from a subset of 150 GPS-tagged ravens allows me to identify causes of mortality and seasonal patterns.

Specifically, I address the following research questions. 1) Are there differing survival rates over the seasons? (Spring, Summer, Autumn, Winter) 2) Are there differences in survival rates between age classes (juvenile, subadult, adult)? 3) Do sexes differ in their survival? 4) Are there differences in survival between captive-bred-released and wild-caught birds? 5) What are the main causes of mortality, and are there cohort- or season related pattern.

Material and Methods

Study system

Corvus corax is a large generalist species found all over the norther hemisphere, known for its cognitive complexity and their complex social structures (Bugnyar, 2023). Their intelligence and behavioural flexibility enable them to adapt to a wide range of habitats and to thrive in anthropogenic landscapes, benefiting from additional food sources and leftovers provided by humans.

The Konrad Lorenz Research Centre for Behaviour and Cognition (KLF) is a core facility of the University of Vienna, located in the northern Austrian Alps. The landscape surrounding the study site, the Alm valley, is characterized by transformed and natural habitat with small villages, agricultural and wild meadows, and mixed forests up to altitudes of 700m. Coniferous forests are found between 700m and 1,500m, above which alpine vegetation occurs up to the highest peaks at around 2,500m above sea level. Land-use practices of the region include forestry, agriculture, hunting and fishing, mining, and various summer (e.g., hiking, mountainbiking) and winter (e.g., skiing) tourist activities. The core study area, the Alm valley (Grünau im Almtal), covers approx. 230 km^2 (https://www.statistik.at, 2023).

The Cumberland Wildpark, is a game park displaying European wildlife species in enclosures, located in the valley (47°48′19.08″ N, 13°56′55.32″ E) and open for visitors all year round (Summer: 9am-5pm / Winter: 10am-4pm). These animal enclosures present popular foraging opportunities for the local non-breeding raven population, and several other scavenging passerine bird species. Ravens scrounge food from inside these game parks animals’ enclosure. Some of these impose a risk for injuries or even death to the scrounging ravens. Popular sites are the wild boar, fallow deer, Przewalski's horse and the combined wolf-bear enclosure (Braun & Bugnyar, 2012). The food opportunities at the park attract ravens all year round, with raven numbers ranging from 30 in summer to 150 in winter (Loretto, Schuster, et al., 2016b).

Individual marking

The ravens’ frequent use of the resources within the park, makes the site very suitable for trapping, individual-marking and long-term monitoring of the local population. Ravens are neophobic and require a long period of time before they habituate to a trapping structure, which requires long trapping periods over several months at the time and a continuous trapping effort (Heinrich, 1988; Miller et al., 2015). The drop-in traps are baited with meat and checked (if set) at least twice per day.

Since 2007, captive-bred released (n=159) and wild-caught (n=345) common ravens (n=504) are individually marked for behavioural and cognitive studies (Bugnyar, 2023). These markings allow for clear and easy identification of the individuals from a distance with binoculars once individuals are released.

The patagial wing tags are made of PVC truck canvas material, unique in colour and shape, and mounted on one wing on the elastic and nerveless skin between the bird’s shoulder and elbow joint. Each bird receives a metal identification ring (supplied by the Austrian Ornithological Centre [AOC]) with a unique registered number and identified with the ringing site code of Austria. Birds also receive a combination of coloured rings, with one ring providing information about the origin of the bird (the original family the raven was raised in) and another containing a short 3 alpha-numeric identification code which is unique within the study population.

Presence data

The presence data we used to run capture-mark-recapture modelling analysis were generated at the game park´s regular wild boar feeding, where individually marked birds are identified based on their unique colour tagging features (rings and wing tags). It started in 2007 and takes place at least 4 times a week (on average on 242 days per year) from the same observational position, with continuous data collection for about 20-40 minutes, starting at 8 am. In addition to the presence of the marked individuals, an estimated total number of ravens on site, the type and amount of food offered as well as weather data are recorded to address questions about the foraging or environmental context. Low variation in resighting efforts, in regularity as well as spatially, are conducive to model analysis of long-term data (Abadi et al., 2013). Therefore, just sightings of marked individuals at this regular boar feeding in the game park were accounted for the modelling analysis. Sightings submitted via the AOC the Austrian Ornithological Centre are very rare (a handful per year), and to prevent spatial distribution of resighting areas and efforts, not accounted for in the modelling approach.

Variables/Data Wrangling

To prepare the presence data for the model analysis, it had to be converted into detailed encounter histories (per annum). For this purpose, the attendance numbers of each year were summed up, if a year’s sum was higher than 0, the individual was present in this year and thus received a “1” for this particular year, and if the bird was not recorded at least once in a given year, it received an absence as “0”. After that, a 15-digit, one-digit-per-year, binary code was created (1=present/0=absence). This code, the encounter history (ch) was then combined with the individual’s categorical covariates of interest (e.g. sex, age, origin) for further analyses.

Demographic data

Sex

In collaboration with the University of Veterinary Medicine Vienna the sex of the bird was determined using blood samples collected during the marking and measuring process. Blood samples were taken from the brachial vein on the underside of the wings and are used to determine the sex as well as the health status (disease; parasites) of the birds.

Age

The age of wild-caught birds was estimated using a combination of indicators such as inner-beak colour (pink for juveniles, with a transition from red - brown for subadult to black for adults)(Heinrich & Marzluff, 1992), plumage expression (slightly brown for juveniles, black for sub/adults) and body weight. For survival rate estimation, age classes were established, with birds up to their first year of life considered as juveniles, from 1 to 3 years of age as subadults, and from 3 years onwards as adults.

These thresholds capture the minimum age estimations of the individuals and distinguish among the most critical first year of life as juveniles, the biological non-breeding age as sub-adults, and the adult phase of sexual maturity where breeding is biologically possible but socially limited to a few breeding pairs that hold territories(W. C. Webb et al., 2009, 2012) while the non-breeder groups display a strong fission-fusion dynamic (Loretto et al., 2017) and consist of all age classes. We calculated the actual age, needed for the modelling approach, at the time the individuals were seen at the wild boar feeding site by subtracting the estimated age at the time of tagging from the year of sighting.

Origin

At the Konrad Lorenz Research Center, captive-bred ravens have been allowed into free-flight occasionally since the mid 90ies (FRITZ & KOTRSCHAL, 1999) and regularly since 2013 (Loretto, Reimann, et al., 2016). Notably, those captive-bred birds are raised by their biological parents. After fledging, they stay with their parents in aviaries for 10 weeks. They are then separated from their parents and housed together with same aged peers in two non-breeder aviaries (80m^2) consisting of ~10 birds each, for 6 weeks until they are released into the wild, typically in the first week of September. We apply a “soft release” whereby the aviaries are opened, and the ravens are free to leave, and return, as they like. Most individuals leave the aviary within the first few days, but some take up to several weeks. As long as ravens return to their release aviary, they are provided with supplementary food to ease the way into independence. After release, these ravens are likely to join the local non-breeder population. Of all the ravens marked, 60% of the individuals were observed at the game parks wild boar feeding at least once (unpublished data). They benefit from social foraging opportunities and the resources provided (to other animals) at the nearby game park. They also start exploring additional foraging opportunities created by predictable anthropogenic food sources such as restaurants, ski resorts and waste facilities in the Alm valley area (Jain et al., 2022; Loretto, Reimann, et al., 2016).

Descriptive mortality data

The data used for the additional analysis of mortality causes in relation to cohort and seasonal variation originate from a GPS tagging program which started in 2017 to gain insights into the early life experiences of ravens, their resource- and space-use, as well as social structures non-breeding ravens. Both, wild-caught (n = 68) and captive-bred-released (n = 97) ravens have been GPS tagged with Ornitela units (OrniTrack-25 with elevated solar panels, Ornitela UAB, Lithuania; https://www.ornitela.com/25g-transmitter) that weigh ~ 28g including the Teflon straps and Aluminium crimps and are mounted with a backpack harness. The solar powered GPS transmitters send location-time-series movement data via the GSM (cell phone) network in intervals determined by the solar re-charge of the transmitter (on average, we receive 1 GPS fix/15 min in summer and 4 GPS fixes per day in winter). To minimize potential negative impact of tagging on the birds, logger weight never exceeds 3% of the individual's bodyweight (see Loretto, Schuster, et al., 2016b), (Millspaugh & Marzluff, 2001) The average weight of tagged females (n=213) was 1025±70 g SD and 1150 g±120 g SD of males (n=256), based on all individuals measured when ringed and colour-marked over the years.

Their movement data allow for conclusions to be drawn about the circumstances before and at time of death in combination with other information (e.g., weather, season, location). In the event of a successful logger search and retrieval (n= 64), the condition of the carcass and the logger allow for inferences to be made about the possible causes of death. Predator information at the death site can also be deduced from the logger and carcass. For instance, torn out feather pins centred around a plucking site are typical for avian predators and the time of death might point towards a diurnal raptor (e.g. goshawk) or nocturnal raptor (e.g., eagle owl), while broken feathers would indicate death by a mammalian predator (e.g., fox/marten). Ravens that died from illegal persecution were identified based on gunshot wounds and were exclusively found in close proximity to hunting related infrastructure (see appendix for examples).

Long or abrupt periods of bad weather at critical times of the year may indicate starvation or fatalities caused by extreme environmental conditions. A specially trained conservation dog and metal detectors are used to support the search for the loggers of deceased individuals in all kinds of terrain.

Besides mortality of the individual, equipment failure is a common reason (n=13) for tracking to terminate. These equipment failures can be identified on the tag panel, as they can occur despite the battery status appearing as charged, or when there is no apparent GPS cluster (i.e., several GPS fixes at one single location that indicate immobility of the tag and/or bird). To date, 2 birds have lost their GPS tags something that is easy to identify in the accelerometer (ACC) data that record the tag position on the bird and alert any abnormalities.

To distinguish between the causes of ended tracking, every case was analysed based on the individual combination of GPS, ACC and the temperature sensor on the tag, provided right before the time when tracking ended.

For season-specific analysis of the mortalities, the year was divided into four seasons of 3 month, while beginnings and ends of the months were used as boundaries (Spring: March - May; Summer: June-August; Autumn: September- November; Winter: December - February).

To compare the proportion of deaths between the sexes and captive-bred and wild-caught birds two-sample tests for the equality of proportions using the prop.test() function (R Core Team, 2023) were performed.

Modelling Approach/Analysis

We used capture-mark-recapture (CMR) (Cormack, 1964; Jolly, 1965; Seber, 1962)methods to model the apparent annual survival rate of ravens from 2007 to 2022 (t=15 years) using the processed long-term resighting data, generated from the presence list at the wild boar feeding site. To avoid any heterogeneity in resighting efforts, only resighting data from this wild boar feeding (and not from the GPS data) were accounted for the CMR modelling approach, meaning the derived apparent survival rates are inferred by the encounter history of each individual and do not include information on true survival based on, on-board biologging units.

Cormack-Jolly-Seber models (CJS) were run in Rstudio with the package Rmark (Laake, 2013)using individuals encounter history at the wild boar feeding to estimate apparent yearly survival probability (Φ) and recapture probabilities (q). As we were primarily interested in survival, recapture probability values were mainly used to check for irregularities in data structure.

Table 1: List of all candidate model formulas for the survival analysis of colour-marked ravens (n=504) in the Austrian Alps. Each model consisted of a survival probability (Φ) and a recapture probability (q) component. The candidate model list consisted of each possible combination of candidate model formulas for the two components.

Mod.1=list(formula=~1)
Mod.2=list(formula=~ageclass)
Mod.3=list(formula=~origin)
Mod.4=list(formula=~ageclass+origin)
Mod.5=list(formula=~sex)
Mod.6=list(formula=~ageclass+sex)
Mod.7=list(formula=~origin+sex)
Mod.8=list(formula=~ageclass+origin+sex)
Mod.9=list(formula=~time)
Mod.10=list(formula=~origin+time)
Mod.11=list(formula=~sex+time)
Mod.12=list(formula=~origin+sex+time)
Mod.13=list(formula=~ageclass+origin+ageclass:origin)
Mod.14=list(formula=~ageclass+origin+sex+ageclass:origin)
Mod.15=list(formula=~ageclass+sex+ageclass:sex)
Mod.16=list(formula=~ageclass+origin+sex+ageclass:sex)
Mod.17=list(formula=~ageclass+origin+sex+ageclass:origin+ageclass:sex)
Mod.18=list(formula=~origin+sex+origin:sex)
Mod.19=list(formula=~ageclass+origin+sex+origin:sex)
Mod.20=list(formula=~origin+sex+time+origin:sex)
Mod.21=list(formula=~ageclass+origin+sex+ageclass:origin+origin:sex)
Mod.22=list(formula=~ageclass+origin+sex+ageclass:sex+origin:sex)
Mod.23=list(formula=~ageclass+origin+sex+ageclass:origin+ageclass:sex+origin:sex)
Mod.24=list(formula=~origin+time+origin:time)
Mod.25=list(formula=~origin+sex+time+origin:time)
Mod.26=list(formula=~origin+sex+time+origin:sex+origin:time)
Mod.27=list(formula=~sex+time+sex:time)
Mod.28=list(formula=~origin+sex+time+sex:time)
Mod.29=list(formula=~origin+sex+time+origin:sex+sex:time)
Mod.30=list(formula=~origin+sex+time+origin:time+sex:time)
Mod.31=list(formula=~origin+sex+time+origin:sex+origin:time+sex:time)

A candidate model list, containing combinations of the 3 covariates (sex, age class, origin) was created and run. To limit model complexity, we decided to only include two-way interactions in our explanatory analysis. The best fitting models were ranked according to their AICc (Akaike's information criterion corrected for small sample size) (AICc; Akaike 1974) and model weight **xi** (Burnham & Anderson 2002). After testing for overdispersal in the data using goodness-of-fit test (GOF) and degrees of freedom) (overdispersion=3,44), We applied QAICc (Quasi AICc; as opposed to AICc) for model selection and used adjust.chat(3,44) to corrects for overdispersion in the data. As there were no clearly better models in the top model (QAICc value <2) selection, model averaging was carried out with all models in the top model list with QAICc values less than 4, to get estimates from all covariates of interest even if they are not in the top models (Δ**DQAICc<2).** Estimates were plotted with the package ggplot2 (Wickham, 2016).

Results

For modelling apparent annual survival rates and encounter probabilities, re-sighting data at the wild boar enclosure (hereafter ‘presence data’) from 504 ravens of different origin (captive-bred-released n=159; wild-caught-released n=345) and sex (male n=226; female n=273), with known age were used. These individuals were ringed and colour-marked between 2007 and 2022.

Top Model selection list

The list of best fitting models (Delta QAICc<2) ranked according to the QAICc selection criterion, corrected for small sample size and overdispersal shows that the predictor variable age class occurs in all the top models. The best-ranked model (Delta QAICc=0) (see Table 2) had a model weight of 0.11 and is suggesting an age effect on survival probabilities (Φ), and constant recapture probability over time (q).

Table 2: Selection of Top Models for survival analysis of individually colour-marked raven (n=504) from 2007 to 2022 in the Autrian Alps - (presented up to DeltaQAICc <2) ranked after QAICc ([Akaike’s information criterion corrected for small sample size and overdispersal]

Modell[a]	**npar**	**QAICc**	**DeltaQAICc**	**weight**	**Qdeviance**
Phi(~ageclass)p(~1)	4	593.81	0	0.11	301.38
Phi(~ageclass)p(~ageclass)	5	594.39	0.58	0.08	299.95
Phi(~ageclass + origin)p(~1)	5	594.60	0.79	0.07	300.16
Phi(~ageclass + sex)p(~1)	5	595.03	1.23	0.06	300.59
Phi(~ageclass + origin)p(~ageclass)	6	595.18	1.37	0.06	298.72
Phi(~ageclass)p(~sex)	5	595.28	1.48	0.05	300.84
Phi(~ageclass + sex)p(~ageclass)	6	595.61	1.81	0.04	299.16
Phi(~ageclass + origin + sex)p(~1)	6	595.66	1.85	0.04	299.20
Phi(~ageclass)p(~origin)	5	595.78	1.98	0.04	301.35

*[a]The models consist of two parts: **Phi(Φ)**, Survival probability and **p()** recapture probability. The brackets show which factors (age;sex;origin) were accounted for each of those two values in the specific model. **npar** counts the number of parameters included in the models, which were ranked after **QAICc** ([Akaike’s information criterion corrected for small sample size and overdispersal] where the lowest **QAICc** value indicate the best fitting model for the given data. **Weight** shows the support of a model in comparison to the other models.*

Apparent annual survival probabilities

Apparent annual survival rates were constant between years 2011 and 2021; p=0.72, and slightly below between 0.68 and 0.71 from 2007 to 2010). Apparent annual survival rates for 2022 are not included yet due to missing estimates, needed for their modelling (from resighting data 2023).

Age

As indicated by model averaging, the age class effect was the strongest of all investigated predictor variables (Figure 1). Adults (Φ =0.72) and subadults (Φ =0.74) showed no significant differences in their estimated annual survival rates whereas juveniles, in their first year of life, had significantly lower annual survival rates (p=0.53) than adults and subadults.

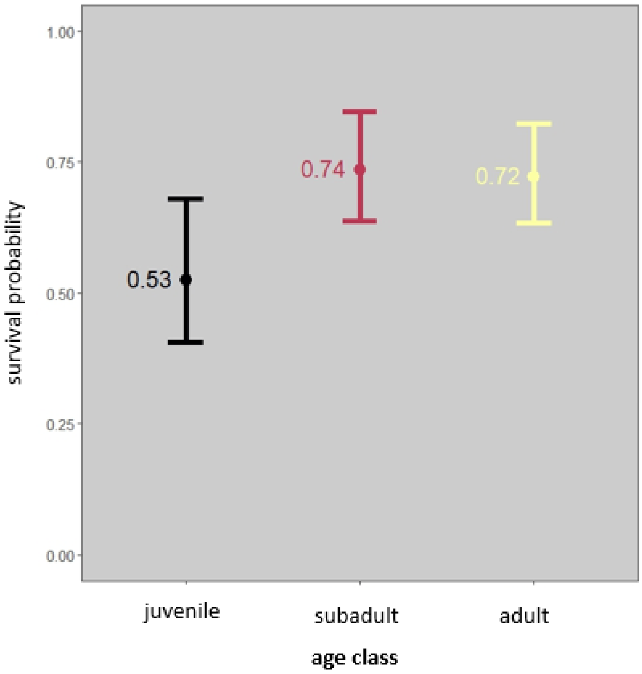

Figure 1: Age-specific apparent annual survival rates of juvenile(age<1year) (Φ =0.53), subadult (age=1-2 years) (Φ =0.74) and adult ravens (age3+ years) (Φ =0.72) of a free-ranging non-breeding group in the Austrian Alps, colour-marked between 2007 and 2022.

Origin

Origin-specific analysis on the annual survival rates of captive-bred-released (n=159) and wild-caught (n=345) raven showed no statistically significant differences (Figure 2). Wild-caught individuals had slightly higher Φ -values (Φ =0.73) in their estimated annual survival rates than captive-bred-released (Φ =0.7) ones.

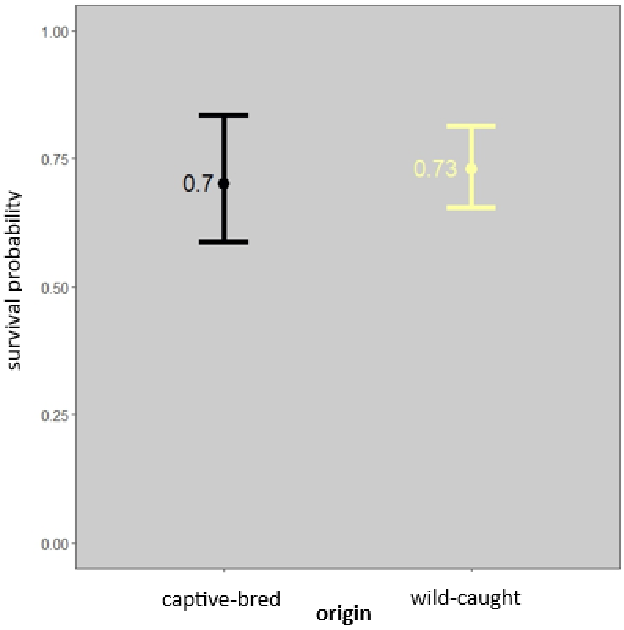

Figure 2: Origin-specific apparent annual survival probabilities of captive-bred-released(Φ =0.7) and wild-caught(Φ =0.73) raven in the Austrian Alps, colour-marked between 2007 and 2022.

Sex

Regarding sex-specific survival probabilities, no significant differences were found in the annual survival rates of male (n=226; Φ =0.73) and female (n=273; Φ =0.71) raven (figure 3).

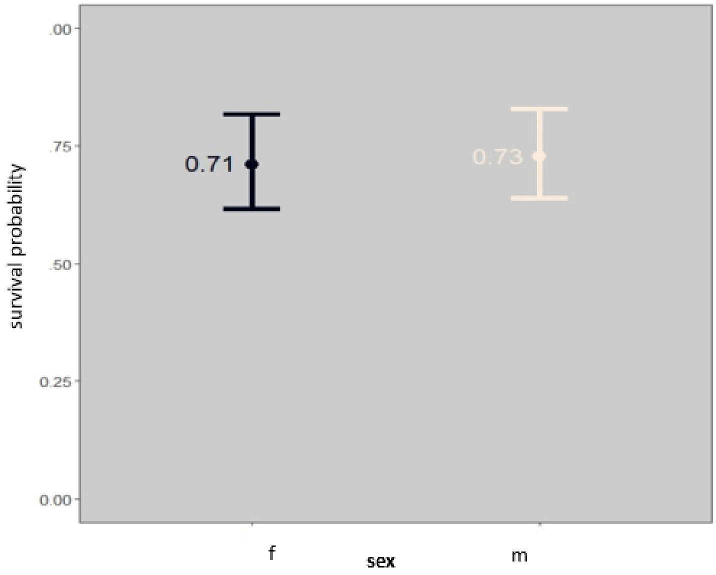

Figure 3. Sex-specific apparent annual survival probabilities of female (n=274; p=0.71) and male(n=226; p=0.73) raven.

Encounter Probabilities

The encounter or recapture probabilities (**q**) in all three predictor variables showed no significant differences between the cohorts grouped by age, origin, and sex (Figure 4). In other words, if a bird was recorded at the wild boar feeding, the chances of it belonging to one of the subgroups studied, were the same.

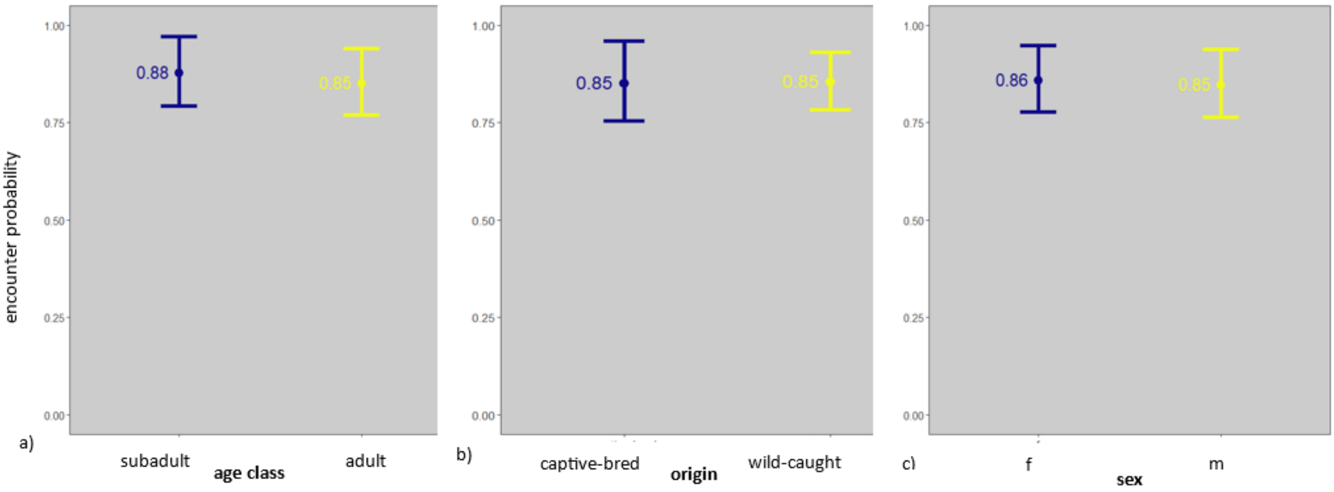

Figure 4: Encounter probabilities of 504 colour-marked raven in the Austrian Alps dependent on age (subadult p=0.88; adult p=0.85), origin (captive-bred p=0.85; wild-caught p=0.85) and sex (male p=0.85; female p=0.86)

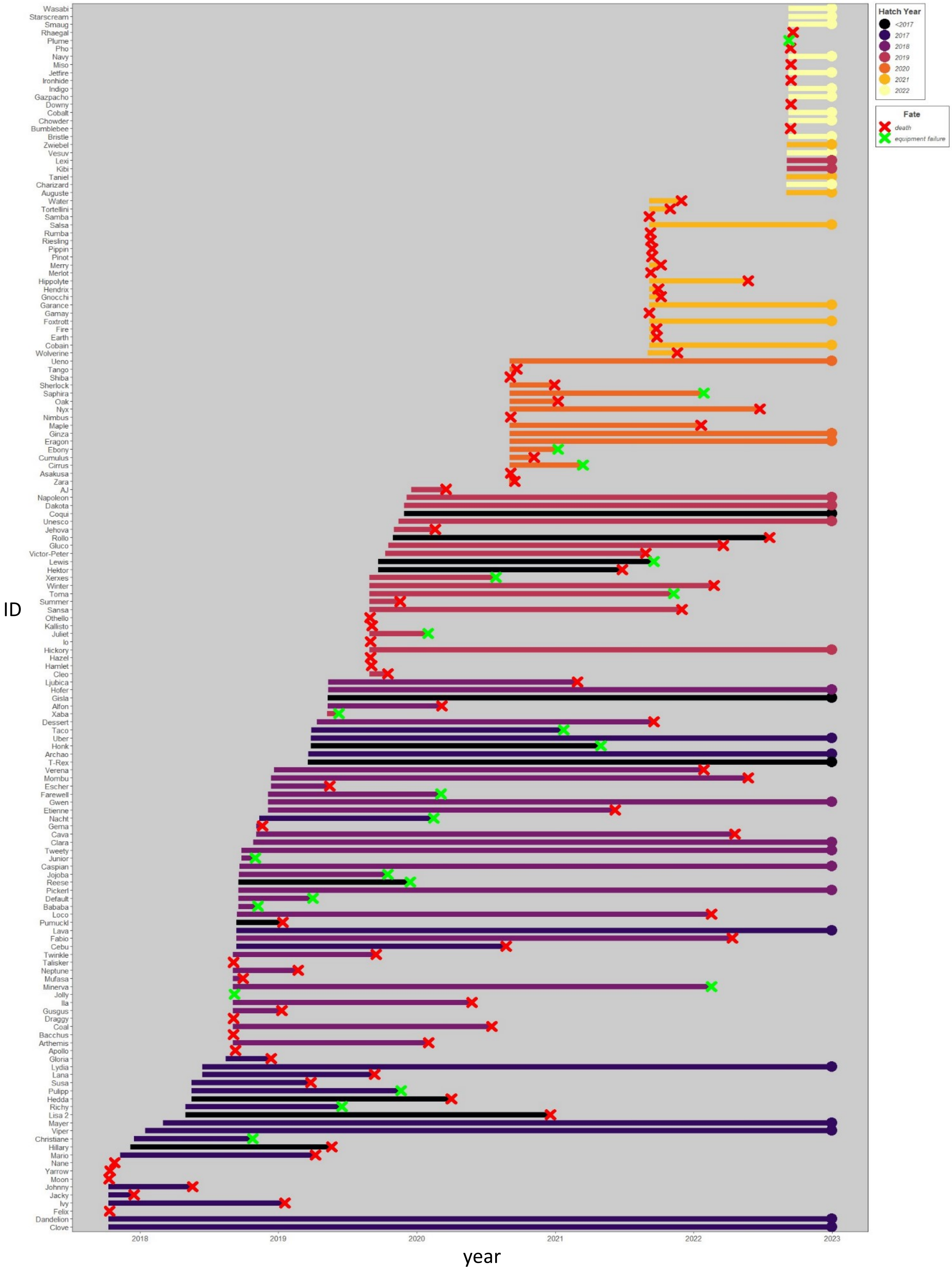

Figure 5: GPS-tagged raven (n=166) with known (red ‘x’) and unknow fate (green ‘x’; likely due to equipment failure), their year of release or capture and the year they hatched in (colour gradient; estimated as minimum for wild-caught ravens).

Causes of mortality

Of the 165 ravens that were equipped with a GPS tag from 2017-2021 (captive-bred n=98; wild-caught n=68) (see Figure 5), 97 have died, and in 64 of these, the cause of death could be estimated (red ‘x’) based on movement data and mortality clusters, environmental conditions at the time of death, habitat type the carcass was found in, time of death (day, night or dawn/dusk) and the condition of the logger and the carcass of the deceased individual. Among the deaths with unknown cause of mortality, no significant differences or patterns were discernible within the studied groups (sex; age; origin) (See Table 3). Average deployment times of GPS-transmitters of dead individuals (mortality signal) and the ones with equipment failures (green \`x\`) were calculated to check whether the suggested life span of GPS-tags could be a possible cause for the end of data-transmissions on individuals with loggers indicating equipment failure. Average logger deployment time for individuals with mortality signal (n=64) was 287 days, loggers assigned to equipment failure (n=26) ended transmitting after 388 days. Out of 26 equipment failures, 19 of them happened in the month from September to February (Autumn and Winter).

In all 64 known mortality cases, 31% of them were predation by eagle owls (n=33), followed by predation by mammalian predators (n=9) (See table 3). The location the logger was last active (see figure 6), allows conclusions on possible predators. Inaccessible terrain near rock walls for example is a typical eagle owl territory and in combination with typical predation signs on the raven’s carcass or/and logger would emphasize strong evidence for predation by this big owl species.

In addition to predation by wild animals, there was predation by animals from the adjacent game park (Wolf=4; Wild boar=1; Lynx=1), where the ravens scrounge food from the captive animals. There was one case of predation by companion animals, in which a hunting dog caught a naive freshly released juvenile in a backyard that functioned as the dog enclosure.

Mortality cases in the category “environmental factors”, were caused by hailstorm (n=1) and starvation likely together with a high endo-parasite infestation (n=3). Challenging environmental conditions occurring in critical times during the year can be fatal for unexperienced juveniles.

Two types of mortality causes could be assigned to the category "human-caused" (n=10), 7 of them were illegally shot, 3 of them died in collisions with traffic; 8 of them were juvenile captive-bred birds, released in autumn.

Prop-test indicated no significant sex-specific difference in the proportions of release numbers to mortality numbers of male (56%, n=43 out of 77) and female (61%, n=54 out of 88) GPS tagged ravens (χ^2=0.313, p=0.57).

There were significant differences in the proportion of deaths among captive-bred (67%, n = 65 out of 97) and wild-bred (47%, n = 32 out of 68) individuals ($\chi^2 = 5.77$, $p = 0.02$). Particularly striking is the high number of captive-bred (n=27) individuals that were predated on by eagle owls.

According to these GPS-based mortality data, out of all known cases of ended GPS transmission (known and unknown; n=97) 67% were juvenile birds in their first year of life, while subadults (14%) and adults (18%), on the other hand, show only minor differences in mortality numbers. Out of 50 known cases of predation (wild and captive-bred animals combined) 35 of them were juvenile birds. It also became obvious that all the illegally shot individuals were male juveniles in autumn.

When looking at the seasonal occurrences of confirmed mortalities, autumn (n=38), the time when captive bred birds are released into the wild, is the season with significantly more cases of mortality than the other three seasons combined (winter=14; spring=9; summer=3).

The fact that all the captive-bred-released birds are juveniles makes a clear trend for eagle owl predation on juveniles in autumn obvious. Out of 19 eagle owl predations, 17 were on captive-bred birds. Out of 7 cases of predation by captive animals (wolf, lynx, wild boar, dog), 6 happened on captive-bred-released birds. When analysing for sex-specific differences in the numbers of mortalities, no significant differences between male and female ravens could be found, but out of 7 shot ravens, 6 were males.

Table 3: Mortality causes of the GPS-tagged ravens (n=97) assigned to the predictor variables, sex, age, origin, and season.

GPS-inferred mortality causes	**Sum within Mortality cause**	**Categories**										
		Age class			**Sex**		**Origin**		**Season**			
		juvenile	subadult	adult	m	f	captive-bred	wild-caught	Spring	Summer	Autumn	Winter
Eagle Owl	33	23	7	3	14	19	26	7	4	1	19	9
Fox/Marten	9	6	1	2	4	5	7	2	3	0	3	3
Golden Eagle	1	1	0	0	1	0	1	0	0	0	1	0
Lynx	1	0	1	0	0	1	0	1	1	0	0	0
Wolf	4	3	1	0	1	3	4	0	1	0	2	1
Wild Boar	1	1	0	0	0	1	1	0	0	0	1	0
Dog	1	1	0	0	0	1	1	0	0	0	1	0
Starvation	3	2	0	1	1	2	1	2	0	1	2	0
Hailstorm	1	0	0	1	0	1	0	1	0	1	0	0
Shot	7	5	2	0	6	1	5	2	0	0	6	1
Traffic Collision	3	3	0	0	2	1	3	0	0	0	3	0
Unknown	33	10	12	11	14	19	16	17	8	3	13	9
Total	97	49	30	18	43	54	65	32	17	6	51	23

Figure 6 shows the spatial distribution of the last GPS fix of every deceased GPS-tagged raven over the time of the GPS-tagging program and their probable cause of death in the core study area. Mortality causes were grouped by colour into human-induced (=yellow symbols), environmental factors (=grey) and predation, subdivided into mammalian/ground- (=green) and avian (=red) predation. The Game Park and the surrounding area is the place where most ravens die, but this is also the area where they spent most time at. As Predation was grouped by colours, it became obvious that predation by mammals is concentrated in and around the game park, whereas the last GPS points of ravens killed by avian predators (red symbols) are widely distributed across the surrounding mountains. Illegal shootings are also concentrated around settlements and hunting infrastructure in the valley.

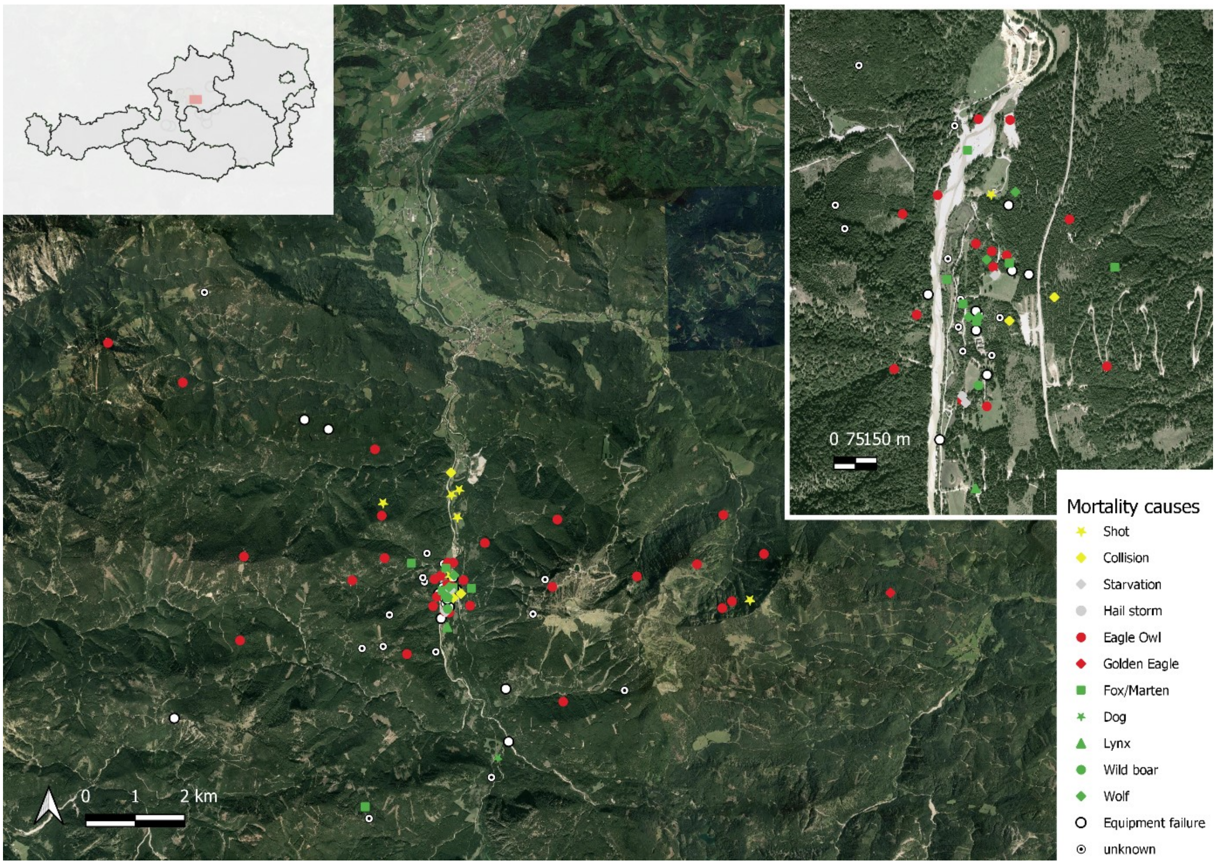

Figure 6: Spatial distribution and mortality cause of GPS-tagged raven where known (n= 64) and unknown (n=33) in the Alm valley in Austria (Human-induced=yellow; environmental factors=grey; avian predation =red; ground predation=green; equipment failure/cause unknown=white).

Discussion

When modelling apparent survival rates of colour-marked raven, we revealed significantly lower survival probabilities in juveniles (Φ =0.53) compared to subadults (Φ =0.74) and adults (Φ =0.72). No differences were obvious between males (Φ =0.71) and females (Φ =0.73), or between captive-bred-released (Φ =0.7) and wild-caught (Φ =0.73) ravens. The quantitative analysis based on true mortality of GPS-tagged ravens revealed similar results regarding age- and sex-specific survival, with no noticeable difference between males and females and high mortalities in juveniles. However, origin determined earlier mortality in captive-bred-released birds during their first year of life (Table 2) compared to wild caught ravens in the same age class. When assessing seasonal differences in mortality numbers, we found most deaths occurred in autumn (n=38), whereby numbers were 1.5 times higher than in winter n=14, spring n=9, and summer n=3 combined.

Factors affecting survival

There were no apparent yearly variations in survival and resighting probabilities over the course of the studied period (2007-2022). This low variance was to be expected, given the systematic nature of our presence data, where data had been collected in standardized manner at one location (wild boar enclosure) and under consistent effort (almost daily observations during morning feeding between 8am and 9am).

Both analyses on sex-specific mortality (survival modelling approach and true mortalities based on GPS data) showed no differences in survival probabilities between male and female ravens. Ravens are size-dimorphic (average weight $m_{(n=75)}$ = 1135.3 g; $f_{(n=66)}$ = 998.93 g; based on weights at GPS tagging in our population), with breeding pairs investing equally in parental care (Ersoy et al., 2021b) and no pronounced differences in seasonal space use (Roth et al., 2004) between males and females (Jain et al., 2022). Although annual survival probabilities of the sexes seem to be similar, there may be age-specific differences within the sexes as male and female fledglings experience parental care differently, with fathers preferring male offspring when provisioning food (Ersoy et al., 2021b). Furthermore, as space-use and dominance differ between breeding, which is possible after 3 years of age, and non-breeding ravens (W. C. Webb et al., 2012), one might expect sex-specific differences to become apparent in breeders only. However, our population mainly consists of non-breeders.

A strong effect of age on raven survival was obvious in both analyses, with juveniles indicating significantly lower survival probabilities and more confirmed mortalities than the other studied age classes (subadult; adult). Similar results were published by Webb et al. in 2004 on juvenile raven survival and the positive influences of additional food sources provided by humans.

Although the Game Park represents the ravens’ most important foraging site (Loretto, Schuster, et al., 2016a), there are various human subsidies, which raven of the alm valley also take advantage of (Jain et al., 2022).

Juveniles might furthermore not yet have enough experience with predator avoidance compared to older ravens and are more often subject to predation in their first autumn and winter. This was also confirmed by our mortality analysis based on GPS data, with 78% of all confirmed deaths due to predation, 70% within these affecting juvenile birds and 81% within these occurring in autumn and winter.

When we retrieve intact carcasses (i.e., no pieces missing) we measure the body mass and can infer on death by starvation – sometimes linked to severe endoparasite infestation – if the ravens are heavily underweight. These cases are rare and might be due to the study located within the game park, where supplementary food provided to animals in enclosures is available all-year round. This could mean that our native birds are less affected by seasonal fluctuations in the natural food supply compared to ravens, which travel outside the valley and might have only limited access to anthropogenic food sources. To find out whether this is the case, however, further studies on survival rates of wild populations without or limited access to anthropogenic food sources need to be carried out in order to be able to make comparisons. This consistent foraging opportunity might especially benefit juveniles, particularly captive-bred-released individuals that tend to show less fear towards humans due to their positive early-life experience with animal care takers and visitors in the zoo enclosures. Juveniles usually rank low within the dominance hierarchy of non-breeding groups (P. Boucherie et al., 2022; Braun & Bugnyar, 2012; W. Webb et al., 2004) and are largely depending on social foraging groups due to their lack of experience in finding their own food in early life (Braun& Bugnyar, 2012). In being low-ranking, they can be excluded from smaller or ephemeral food sources that are usually monopolized by high ranked individuals (Jain et al., 2022). These foraging groups provide safe access to food, as the group also profits from dilution effects towards predators and the presence of experienced ravens who might be more vigilant and alarm against predation (Gallego-Abenza et al., 2021; W. Webb et al., 2004).

Advantages of social integration and alliances might not only apply to diurnal foraging groups, but also to nocturnal roost sites. Most predation events could be assigned to eagle owls (n=33 out of 64 confirmed mortalities), which happens during dawn, dusk or at night (Penteriani et al., 2008), when ravens form these communal roosts (Loretto, Reimann, et al., 2016; Wright et al., 2003). Individuals that are not yet socially integrated (i.e., juveniles in their first winter) or are not integrated any more (older individuals or those that have lost their partner (Boucherie et al., 2019)), might sleep solitary and are easy targets for predators.

Although the modelled survival probabilities of captive-bred versus wild-caught individuals did not reveal differences, true mortalities differed substantially between the two cohorts in the first fall. The high number of captive-bred individuals that were depredated by eagle owls might be explained by the lack of experience in anti-predator behaviour of freshly released captive-bred individuals and the absence of their parents. These juveniles are naïve against predators and might be easy prey for both avian and mammalian predators in the weeks after release. Furthermore, these predators have territories themselves why predation events might cluster in certain areas or peak in single years (Hadad et al., 2022). In 2022 for example, 10 out of 26 mortalities were predations by eagle owls. However, this disadvantage for captive bred birds due to lack of experience with predators is only recognizable for a few months until they are fully integrated into the wild non-breeding population.

The frequent and intense all year-round use of the game parks' foraging opportunities (Jain et al. 2022) might support the large local non-breeder population. Under such human subsidized conditions, ravens are known to shift their diets from food provided by the natural habitat (e.g arthropods, plant material, carcasses) towards anthropogenic food sources. This might reduce daily travel distances (i.e., distances between nesting/roosting site to the anthropogenic food source; (Kristan et al., 2004; W. Webb et al., 2004), might allow for the establishment of micro-territories in close proximity (Segura & Acevedo, 2021) and might reduce predation pressure on natural prey populations(Madden et al., 2015). While ravens are scavengers and not known to actively kill larger numbers of individual prey, high raven populations can still have negative impacts on other species' diversity and abundance (Brussee & Coates, 2018; O'Neil et al., 2018).

The map on the spatial distribution of the last GPS-fixes of the tagged ravens shows a high concentration of mortalities and equipment failures in and around the game park, which underlines the intensive use of the game park by the ravens (Jain et al. 2022). It is also known that the largest night roosts are also located in close proximity (~500m) to the game park (Braun et al., 2012 and unpublished data).

The average deployment time (388days) of loggers (OrniTrack-25, Ornitela UAB, Lithuania; https://www.ornitela.com/25g-transmitter) with equipment failures did not exceed producers recommended life span (xx) of the devices. 19 out of 26 of these equipment failures occurred in autumn. Thus, it is likely that the logger of these individuals stops functioning in first winter due to low solar radiation and cold temperature which does not sustain battery recharge. If the (juvenile) bird then does not survive its first winter (which is quite likely, given the low survival rates of 53%) the solar panel does not have a chance to recover the battery in spring. In such cases we do not receive a mortality cluster and have no chance of retrieving the logger as the last location was still recorded on a living (moving) individual. If we factor this into our quantifications, the real mortality of juvenile raven could be even higher.

Other possible causes for an abrupt ending of data transmission without a typical mortality cluster where GPS fixes accumulate within a radius of ~20 m (reflecting the GPS uncertainty) could be illegal shootings/targeted persecutions. Several transmissions ended near compost sites, where ravens and other scavenging birds are generally not welcome, and close to hunting towers or farmhouses. One way of hiding any traces of illegal activity is to remove the carcass and destroy the GPS tag.

The fact that out of 10 cases of mortality in the category ´human-induced´, eight were captive-bred-released birds and all of these mortalities occurred in autumn might furthermore be explained by their upbringing without any fear from humans. They might even seek close proximity in hope to receive food. While captive-bred birds are not hand-fed (they are fully parent raised), they still associate human care with food provisioning. Most of these human-induced mortalities are close to anthropogenic infrastructures. These birds might be more likely to die in traffic collisions and through illegal persecution, for example, when being around hunting infrastructure. For a more detailed understanding of the influence of physical conditions on the survival of different origin groups, the integration of body measures into future survival analyses could be considered. Furthermore, through education and awareness-raising in the local hunting community, deaths due to persecution could be reduced in the future.

After the tagging, captive-bred-released and wild-caught raven start out into the wilderness with very different prerequisites, captive-bred birds lack experiences with predators, while wild-caught individuals might already be more integrated into the local non-breeder group in autumn. Thus, captive-bred-released birds might be subject to increased predation risk to them yet to be developed antipredator behaviour due to their low integration into the social foraging group and potential peripheral location at roost sites.

On the other hand, the body condition of captive-bred-released birds might be higher than of wild-caught birds as they receive regular high-value food and are medicated against parasites. Wild-caught birds might have already battled times of starvation in times of critical environmental conditions on the nest and post-fledging(W. Webb et al., 2004) and might have developed a stronger immune system due to the exposure to parasites (and the lack of medication). Those that have succumbed to these conditions would not be part of the population from where we draw our GPS-tagged birds.

The acquired information on apparent annual and seasonal survival rates and cohort-specific differences (sex, age, captive-bred vs. wild-caught) this study provides, can advise reintroduction projects as well as population management strategies in the future.

Study limitations

Comparing captive-bred released ravens with wild-caught juveniles is not without limitations, as the best raven trapping time is autumn when juveniles become independent of their parents. Hence, mortalities that occur pre-trapping cannot be quantified. Actual mortality rates of wild juveniles might be higher than we see in our data, as these GPS-tagged juveniles already survived critical months in autumn already (Stiehl, 1985), while captive-bred-released ravens have not yet been subject to natural selection.

Conclusion

The survival rates of the raven population in the alm valley (that is heavily dependent on anthropogenic food sources) proved to be similar to other studies carried out on the survival of ravens and the influence of anthropogenic food sources in various ecological conditions. Juvenile birds, individuals with the least life experience, showed the lowest survival rates, suggesting the importance of social information, which is facilitated by group formation and integration, for survival.

The diverse and intensive use of the wildlife park, which has also been identified in other studies on raven movement and resource use (Jain et al., 2022; Loretto, Reimann, et al., 2016; Loretto, Schuster, et al., 2016a), might reduce the possible impact of increased raven populations, due to the introduction of captive-bred individuals in the study area, on other species and natural habitats. However, for a deeper insight into the impact of ravens foraging habits on local biodiversity and the role of artificial food sources in the alm valley, more specific research is needed.

A study on an American raven population showed that survival and the influences of human presented food sources may result in a diet shift, from natural to human-presented food (Webb et al., 2004). Possibly, a shift from natural to human induced causes of mortality with decreasing distance from natal territory to anthropogenic areas may also be expected. More years of the GPS programme with more data on actual causes of death and numbers will be helpful to investigate this hypothesis.

Ethics clearance:

This study complies with all current Austrian laws and regulations concerning the work with wildlife and adheres to the ASAB/ABS Guidelines for the Use of Animals in Research. Ravens were trapped, blood sampled and marked according to the procedure described in(Braun & Bugnyar, 2012) and the Corvid Lab, Department of Behavioural and Cognitive Biology, University of Vienna, obtained the licence for GPS-tagging of ravens from the commission for animal experimentation of the Austrian government under the approval number ‘BMBWF-66.006/0015-V/3B/2018’ and is valid until 30/06/2022. Further, the study was approved by the Internal Ethics Committee (Permit Number 2014–018) of the Faculty of Life Sciences, University of Vienna.

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Appendix/supplementary material

Retrieved carcasses and tagging equipment of deceased raven in the Alm Valley and their estimated cause of mortality.

Starvation

Figure 1: Retrieved carcass of a starved raven (carcass weight 840g)(source: Archive Corvid Lab).

Shot/Persecution

Figure 2: Carcass of a shot raven found under a tree next to a settlement – no visible predation marks (source: Archive Corvid Lab).

Traffic collision

Figure 3: Raven that most likely died from the consequences of a traffic collision. The carcass was found in close proximity to the valley's main road, there were no predation signs but blood swelling on the neck, indicating a possible fracture caused by the collision (source: Archive Corvid Lab).

Fox/Marten

Figure 4: Broken and bitten off feathers and GPS-logger with bite marks of a raven predated on by mammal predators, most likely fox or marten (source: Archive Corvid Lab).

Eagle owl

Figure 5: Plucked feathers at mortality site, most likely predation by an eagle owl (source: Archive Corvid Lab).