Behavioural plasticity shapes population ageing patterns in a long-lived avian scavenger

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Citation: Acácio, M., Gahm, K., Anglister, N., Vaadia, G., Hatzofe, O., Harel, R., Efrat, R., Nathan, R., Pinter-Wollman, N., & Spiegel, O. (2024). Behavioral plasticity shapes population aging patterns in a long-lived avian scavenger. Proceedings of the National Academy of Sciences, 121(35), e2407298121. https://doi.org/10.1073/pnas.2407298121

Author contributions: MA, NPW, and OS conceptualized the research, MA, NA, VG, OH, RH, RE, and OS collected the data; MA, and KG analyzed the data; OS, NPW, OH, and RN secured funding; MA wrote the paper, and all authors provided critical feedback.

Keywords: behavioural ageing, behavioural plasticity, selective disappearance, movement ecology, sociality, griffon vultures

Abstract

Studying the mechanisms shaping age-related changes in behaviour ("behavioural ageing") is important for understanding population dynamics in our changing world. Yet, studies that capture within-individual behavioural changes in wild populations of long-lived animals are still scarce. Here, we used a 15-year GPS-tracking dataset of a social obligate scavenger, the griffon vulture (*Gyps fulvus*), to investigate age-related changes in movement and social behaviours, and disentangle the role of behavioural plasticity and selective disappearance in shaping such patterns. We tracked 142 individuals for up to 12 years and found a non-linear increase in site fidelity with age: a sharp increase in site fidelity before sexual maturity (<5 years old), stabilization during adulthood (6-15 years) and a further increase at old age (>15 years). This pattern resulted from individuals changing behaviour throughout their life (behavioural plasticity) and not from selective disappearance. Mature vultures increased the predictability of their movement routines and spent more nights at the most popular roosting sites compared to younger individuals. Thus, adults likely have a competitive advantage over younger conspecifics. These changes in site fidelity and movement routines were mirrored in changes to social behaviour. Older individuals interacted less with their associates (decreasing average strength with age), particularly during the breeding season. Our results reveal a variety of behavioural ageing patterns in long-lived species and underscore the importance of behavioural plasticity in shaping such patterns. Comprehensive longitudinal studies are imperative for understanding how plasticity and selection shape the persistence of wild animal populations facing human-induced environmental changes.

Significance statement

Ageing is a universal phenomenon, yet how behaviour changes with age ("behavioural ageing") and the mechanisms that shape behavioural ageing (plasticity and/or selective disappearance) are still poorly understood. We individually tracked griffon vultures for up to 12 years and tracked up to 60% of the population simultaneously. We found that older vultures display higher site fidelity, fixed movement routines, and weaker social relationships compared to younger conspecifics. Some of these patterns were driven by individuals changing their behaviour throughout their lives rather than by the selective disappearance of particular phenotypes. Our results highlight the role of individual plasticity in shaping behavioural ageing, which may have implications for our understanding of how population dynamics are impacted by a changing world.

Introduction

Ageing is ubiquitous across living organisms, leading to behavioural changes throughout life (1–4) ("behavioural ageing"). Younger, sexually immature individuals tend to differ from older, mature individuals in a number of behavioural traits, including how they move (e.g., flight performance (5)) and how they interact with conspecifics (e.g., strength of social interactions (6, 7)). Such behavioural changes may influence space use (3, 8), the spread of infectious diseases (1), and even the lifespan of individuals (9). Behavioural changes with age may also play an important role in how populations adjust to environmental change: young individuals may adopt novel behaviours and be the agents of change (10, 11), while old individuals, with their accumulated knowledge and experience, may adjust to the environment by shifting behavioural strategies over their lifetimes (12–14). Despite the importance of understanding behavioural ageing in nature, most ecological studies focus on binary comparisons between young and old animals, failing to track individuals throughout their lives (15). Specifically, longitudinal studies that follow long-lived animals throughout most of their lives are rare, mostly due to methodological constraints (15). This gap hinders the identification of gradual and non-monotonic behavioural changes in the wild or the mechanisms that underlie population-level ageing patterns.

Research on behavioural ageing reveals a spectrum of patterns at the population level (Figure 1): some behaviours remain fixed throughout life (16), while others change, either gradually (2), or drastically at specific ages (e.g., early (17, 18) or late in life (19, 20); the latter usually associated with senescence and loss of physiological or physical capacities (21, 22, 3), Figure 1A). Population-level behavioural changes with age can arise from two, non-mutually exclusive mechanisms. First, individuals may change their behaviour throughout their lifetimes (behavioural plasticity (23, 24, 6)). Second, individuals with particular behavioural phenotypes may have lower survival than others (25, 26). Across generations, the selective disappearance of these phenotypes that confer lower fitness can result in changes to the behavioural composition of the population with increasing age, without within-individual behavioural plasticity (27, 28) (Figure 1B). Ultimately, examining the patterns and mechanisms of behavioural ageing provides a foundation for understanding how populations might adjust to the environment, if through plasticity or selection, and how changes in population age-structure can influence ecological processes and the ability of a species to respond to environmental changes (19).

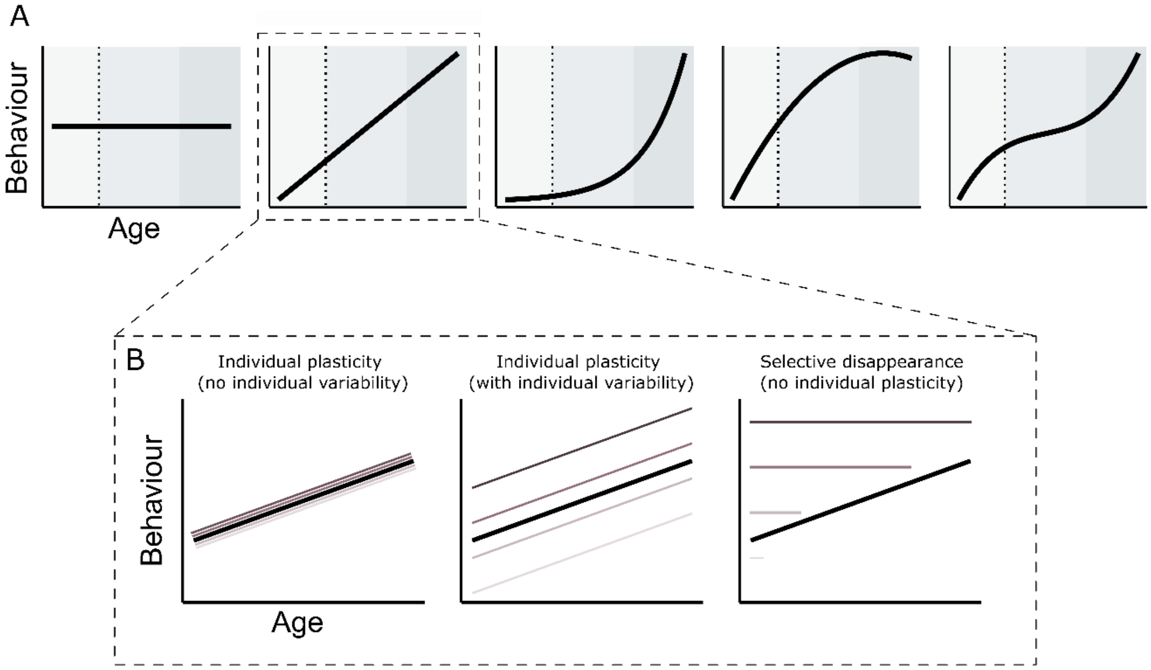

Figure 1 – Theoretical relationships and potential mechanisms of behavioural ageing. A. Five theoretical relationships between age and behaviour at the population level: no relationship; a linear relationship (monotonic change in behaviour with age); an exponential, convex, relationship (sharp change in behaviour in old individuals); a quadratic, saturating, relationship (drastic change before maturation and then a stabilization in behaviour); and a third-degree polynomial relationship (different behaviour at each life stage, for example, juveniles behaving differently from reproducing individuals, and old individuals behaving differently from the first two age groups). Note that we depict an increasing relationship between age and behaviour, but, depending on the behaviour, a decreasing relationship is possible too. The vertical dotted line indicates the age of maturation, and the different grey hues represent distinct life stages (e.g., juvenile, reproducing, old). **B.** Mechanisms that may explain population-level relationships between age and behaviour: individual plasticity without individual variability (all individuals behave and change their behaviour in the same way); individual plasticity with individual variability (individuals differ in their average behaviour but change it similarly with age); variation in behaviour among individuals with no behavioural plasticity, instead,

selective disappearance of individuals with a particular behavioural traits leads to population-level behavioural ageing. These three mechanisms can apply to any of the patterns in **A**. Thick black lines are the population-level relationship between behaviour and age and the thinner grey lines are individual-level relationships between age and behaviour.

In this study, our main goal is to examine patterns of behavioural ageing in a wild animal population. We also aim to disentangle the relative importance of individual plasticity and selective disappearance of individuals from the population in shaping observed ageing patterns in movement and social behaviours. To do so, we use a dataset of 15-year dataset of GPS-tracking of griffon vultures (*Gyps fulvus* hereafter griffons). The griffon is a long-lived obligate scavenger: in captivity, griffons live beyond the age of 40 while in the wild the survival rates decrease (actuarial senescence) after the age of 28 years (29). Griffons have a slow life cycle, reaching sexual maturity around the age of 5 and laying a single egg each year (if they breed at all). Griffons may perform seasonal long-range forays and movements (30, 31), particularly early in life (32). Griffons use social cues while flying and foraging (33) and they sleep and nest in communal roosts (34) that act as information centres, where individuals gather information about the location of resources in the landscape (35). Their large body size and longevity (which facilitate long-term GPS-tracking), as well as their high mobility and sociality, make the griffon vulture an ideal candidate for studying behavioural ageing in the wild. Furthermore, most vulture species are globally endangered or critically endangered (36). Likewise, Israeli griffons are regionally critically endangered and are the target of an intensive conservation management program, aimed at rehabilitating the population (37). Thus, understanding the patterns and mechanisms underlying behavioural ageing in this species can have potential implications for their effective conservation. For instance, uncovering different spatial requirements by age may help focus conservation efforts on areas that preserve individuals of all age cohorts.

We hypothesised that site fidelity, movement routines and social behaviours will change with age either gradually or more sharply early or late in life (Figure 1). We tested these hypotheses using a unique GPS-tracking dataset, of 319 griffons followed between 2008 and 2022. To account for the differences in the GPS transmitters' sampling rate over the 15-year sampling period (38), and to maximize the available data, we analysed different measures of roosting behaviour as a proxy for movement and social behaviour (e.g., higher roost fidelity representing higher site fidelity and higher co-roosting strength representing stronger social bonds (33)). We built seasonal co-roosting proximity-based social networks during the breeding, summer, and transient seasons (when most long-range forays occur (30)), using the full dataset of roost-locations, and for the years during which at least 25% of the griffon population was tracked (39) (2016-2022). Using a subset of 142 griffons, aged 0-24 years (Figure 2B), that remained in the main study area and that were tracked for a minimum of 30 days and maximum of over 12 years (Figure 2C), we examined how age affected the likelihood of using the same roost-site on consecutive nights ("roost fidelity"), and the predictability of roost switching sequences (i.e., if vultures switched roosts in an ordered sequence (40)- "routine"). We also evaluated how age influenced roost-site selection (i.e., selecting popular roosts – "roost popularity"), as well as griffons' social relationships, measuring the number of co-roosting partners and the average number of nights co-roosting with their social partners. Finally, we tested if these population-level behavioural changes arise from individuals changing their movement and social behaviours as they age or through the selective disappearance of individuals with particular traits. We did so by disentangling the effects of within-individual changes and of individual longevity (age at death) on behavioural ageing.

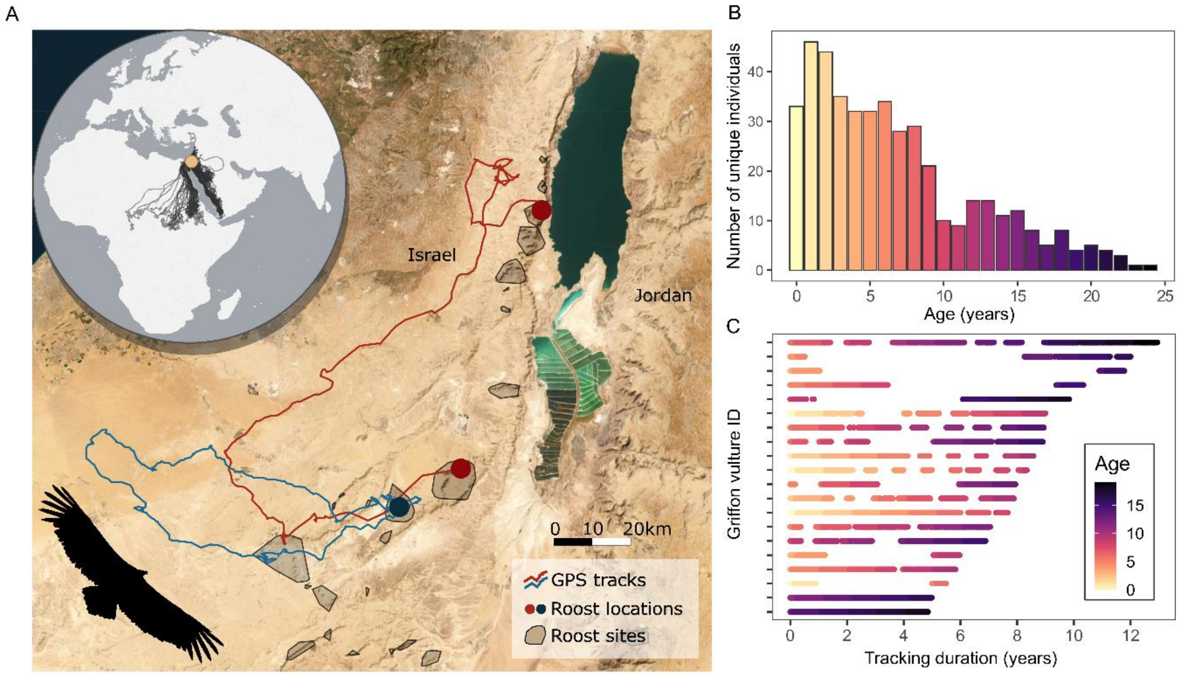

Figure 2 – Study area and GPS-tracking dataset. A. Map showing GPS-tracks of two griffon vultures in a single day: one individual remained at the same roost-site on consecutive nights (blue), and the other switched between roost-sites on consecutive nights (red). The inset shows the location of the study area, as well as the movements of griffon vultures travelling to East and Central Africa and to the Arabian Peninsula on long-range forays. **B.** Number of unique griffon vultures tracked at each age. Individuals tracked over multiple years appear in multiple age cohorts. **C.** Tracking duration (in years) of the 20 griffon vultures with longest tracking duration since the time of their first GPS deployment. Gaps indicate periods when the individual was not tracked due to the loss or failure of the GPS transmitter. For a similar figure of all individuals in the study, see Figure S7. In **B-C**, colours indicate the age of each individual, with younger individuals represented in lighter colours.

Results and discussion

Griffons increase site fidelity and movement predictability with age, shaped by individual plasticity and not by selective disappearance. We found that griffons' roost fidelity increased with age. Interestingly, this population-level relationship took the form of a third-degree polynomial. There was a rapid increase in roost fidelity until the age of 5 (griffons' age of maturation), no change between the ages of 6 and 15 years, and then another substantial increase in roost fidelity after the age of 15, indicating that old vultures tend to return to the same roost each night (Figure 3A, Table S1, Table S2). This result was not determined by the long-range forays performed predominantly by younger griffons, during which they might switch roosts more often than they would in our main study area (Figure 2, Figure S1). This population trend was mostly shaped by individual plasticity (individuals increasing roost fidelity throughout their lives, Figure S2) and not by selective disappearance, despite the slight, non-significant indication that individuals with higher roost fidelity may live shorter lives (Figure 4, Table S3).

In addition to higher roost fidelity, older griffons were also more predictable in their movement routines: when switching between roosts, older griffons were more likely to follow an ordered sequence (e.g., A-> B-> C-> A-> B -> C -> A-> …, Figure 3B, Table S4, Table S5). Furthermore, the strength of these roost switching routines (index of routine (40)) increased exponentially - changing most drastically after the age of 15 years (Figure 3C, Table S6, Table S7). Due to the smaller sample size in this analysis, we could not evaluate if this pattern emerged from individual plasticity or selective disappearance. Thus, we could not determine if behavioural predictability provides a selective advantage over the course of an individuals’ lifetime (individuals with stronger movement routines live longer), or if as individuals mature, they learn which sites they prefer and subsequently tend to frequent those selected locations.

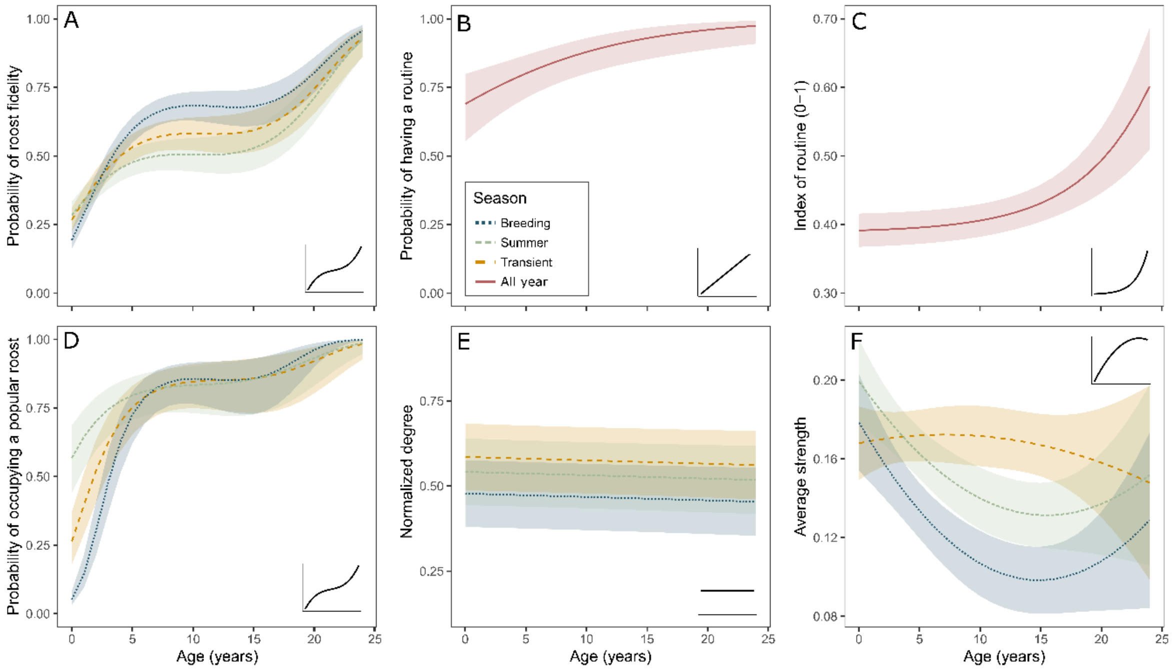

Figure 3 – Age-related changes in movement and social behaviour of griffon vultures. Each panel **A-F** represents the model predictions, back-transformed to the original data scale, and the 95% confidence intervals for the effect of age on movement (**A-C**) and social behaviours (**D-F**): **A.** probability of remaining at the same roost-site on consecutive nights (roost fidelity); **B.** probability of predictably switching between roosts in the same order (routine); **C.** strength of roost switching routines (index of routine); **D.** probability of occupying a popular roost (defined as the top 20% most used roosts in the study area); **E.** number of unique individuals a vulture interacted with over a season, normalized to the size of the GPS-tracked population (normalized degree); **F.** average number of social interactions over a season (average strength: strength divided by degree). Colours and line styles indicate the different seasons: breeding (blue, dotted), summer (green, dashed), and transient period (orange, long dashed). Red solid lines indicate analyses that did not include a seasonal effect. The inset in each panel shows the corresponding theoretical prediction described in Figure 1.

Past research, from a single population in France, found that actuarial senescence (an increase in mortality rates) in griffon vultures starts at 28 years (29). However, in the population studied here, adult griffons have lower survival than in other populations (0.86 apparent survival (41) vs 0.94 in the French population (29)), most mortality is caused by human activities (42). Consequently, griffons in this population rarely live past the age of 24. While it is unlikely that the observed increase in site fidelity and predictability starting at 15 years old results from age-related changes in cognitive or physical abilities, it is worth noting that in long-lived bird species phenotypic senescence may emerge well before actuarial senescence. For example, wild wandering albatrosses (*Diomedea exulans*) may live to the age of 50 but show a decrease in survival rates after the age of 35 (43) and signs of reproductive senescence after the age of 30 (3, 43).

It is plausible that the differences in movement behaviour of older griffons emerge from changes in their breeding duties. However, to the best of our knowledge, there is no data on how griffons' reproductive success changes after reaching old age in wild populations (either increasing due to experience or decreasing due to reproductive senescence). Future work that examines breeding status might help determine the mechanisms that underly behavioural ageing. The observed increase in roost fidelity may further result from a competitive advantage of older individuals over younger ones in occupying prime locations (44, 45). Indeed, as individuals aged, they roosted more frequently at the 20% most frequently used roost-sites within our study area ("popular roosts", Figure 3D, Table S8, Table S9), which tend to be closer to supplementary feeding stations (Figure S3). This pattern was so pronounced that griffons older than 5 (when sexual maturity is reached) spent on average 80% of their nights at only 20% of roost sites. Furthermore, griffons over the age of 20 only used the most popular roosts (Figure 3D). From a conservation standpoint, protecting effectively the 20% most used roost-sites within our study area would be sufficient to safeguard the roosting sites of adult griffons (>5 years old). Future work uncovering why these roosts are so popular may be important for guiding future conservation management actions.

Similar to roost fidelity, changes in roost selection with age were mostly determined by individual plasticity, with individuals moving into more popular roosts as they age (Figure S2), despite the slightly, non-significant, lower longevity of the individuals that occupy the most popular roosts (Figure S4, Table S3). These results suggest that while the proximity of popular roosts to feeding stations may provide short-term benefits, high fidelity to popular sites may also bear costs. For example, frequenting popular roosting sites may expose griffons to pathogens (1). Furthermore, individuals that frequent popular roost sites may be more informed about the location of resources (35). While this may be a benefit most of the time, the most common cause of mortality in this population is poisoning, thus having more information about foraging resources may be maladaptive (46) and may expose highly informed individuals to poisoned carcasses, decreasing their overall longevity. Future work may examine lifelong fitness metrics (such as breeding success) to evaluate the trade-off between the benefits of proximity to feeding stations and the costs of crowding at popular roost sites. Future analysis on individuals tracked from birth to adulthood (38) could also help to determine if older vultures tend to converge their usage on roosts they frequented when they were young, or if they become faithful to new sites as they age.

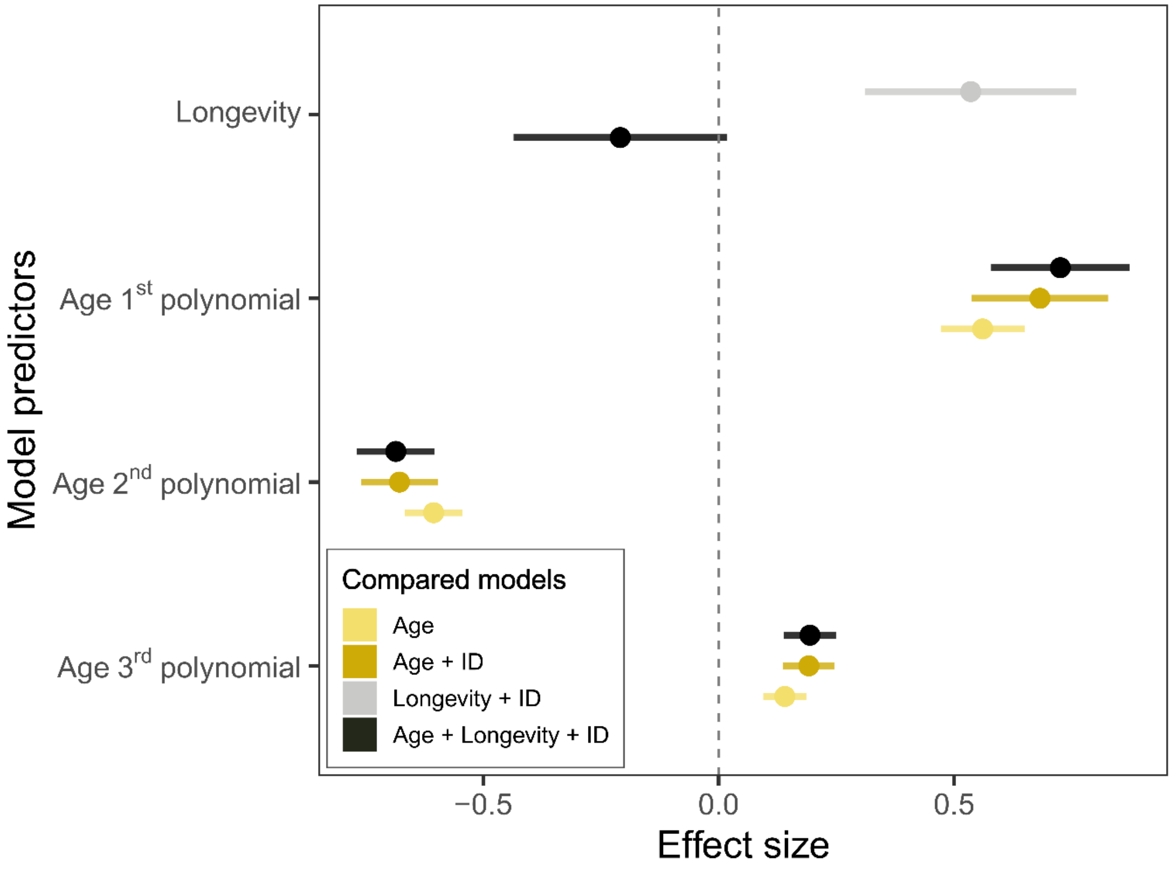

Figure 4 – Individual plasticity, rather than selective disappearance, shapes the increase in roost fidelity with age. To isolate the effect of individual plasticity (i.e., within-individual behavioural

changes) from the effect of selective disappearance (i.e., between-individual behavioural differences and selection acting on different behaviours), we compared four alternative statistical models: age only (light yellow); age and individual ID as a random intercept (dark yellow); longevity (i.e., age-at-death) and individual ID as a random intercept (grey); and age, longevity, and individual ID as a random intercept (black). All models included season as a fixed effect, and year as a random intercept. The plot shows the predicted effects and 95% confidence intervals of age (modelled as a third-degree polynomial, $y = ax^3 + bx^2 + cx + d$) and longevity on roost fidelity, for all four models. Both age and longevity are scaled. Adding longevity did not change the effect of age within the model and resulted in a non-significant negative effect size for longevity, suggesting that behavioural plasticity, and not selective disappearance, shapes the relationship between age and roost fidelity in the population. Similar plots for other response variables are included in Figure S4.

Griffons decrease the strength of social relationships with age. In addition to the changes in movement behaviour, there was also an effect of age on the social behaviour of griffons. Contrary to studies in other species (24), the proportion of the population that an individual co-roosted with (normalized degree) remained constant at all ages (Figure 3E, Table S10). This stability probably reflects a balance between juveniles having lower roost fidelity (with frequent roost switches likely increasing their degree), and adults' tendency to use more crowded roosts (exposing them to more vultures and possibly compensating for their high roost fidelity). The long temporal scales of our social networks, the small spatial scale of the study area, and the small population size also likely contributed to this result; degree is a measure that is sensitive to brief interactions, and over the course of an entire season, most griffons of all age groups were likely to have co-roosted together for at least one night, resulting in high normalized degree values.

In contrast, at the population level, the average strength of roosting relationships was lower after vultures reached the age of 10 years, during the breeding and summer seasons, but not during the transient season, suggesting that the breeding behaviour of adult individuals limits their interaction rates (Figure 3F, Table S11, Table S12). We have observed anecdotally that when one vulture tends to the eggs or chicks in the nest the other partner tends to roost at a different site. This behaviour would result in low average strength of social relationships between breeding individuals. Future studies analysing the movement and social behaviours of breeding couples would help test this hypothesis. Interestingly, older griffons have weaker co-roosting relationships despite griffons' increasing site fidelity to the most popular areas as they age. This may suggest that, similarly to primates (2, 24), older griffons may be more selective in their social relationships than their younger counterparts. Because social and spatial behaviours are intertwined (47), the changes we observe in social behaviour may also emerge from changes in spatial behaviour with age (6). The mechanisms that shape age-related patterns of social interactions remain elusive. A strong correlation between age and individual longevity rendered it impossible to test if the population-level change in average strength resulted from individuals reducing their reliance on social information with age (6), or if the pattern is due to the selective disappearance of individuals with higher average strength, for example due to higher exposure to pathogens (1) (Figure S2, Figure S4, Table S3).

Our results support our hypothesis that behaviours change differently with age, some gradually, while others change sharply early or late in life. This work adds to an increasing body of longitudinal studies analysing behavioural ageing in a multitude of vertebrate species (for example, non-human primates (2, 24), red deer *Cervus elaphus* (6), black kites *Milvus migrans* (25), amongst others (reviewed in (48)). We show that, with age, animals become more faithful to their known sites and routines, and potentially become more selective in their social relationships – interestingly, behaviours that are commonly attributed to ageing humans (49, 50). While we found that within-individual behavioural plasticity is a major driving force of behavioural ageing in a long-lived bird, selection may still act on the rate of behavioural change, for example, by favouring individuals that change more drastically earlier in life (17, 25). At the population level, the rate of behavioural change, and its timing in life, seem to differ among behaviours: griffons displayed the highest site fidelity, stronger movement routines and weakest social relationships at different stages in life. Indeed, it might be more important to be exploratory and more social earlier in life, when individuals are learning about the environment and searching for potential mates (8), and may benefit from obtaining social knowledge for a longer part of their lives (51). In contrast, remaining in the most popular locations (here defined as the most commonly used sites) may be more beneficial later in life, when older individuals can better compete for resources (44) or benefit from following others to discovered resources (35). Furthermore, long-term information gathering in old age may be less needed, making older individuals more selective in their social relationships (2, 51). From a conservation perspective, understanding what drives juvenile movements may help improve the connectivity between endangered vulture populations. Furthermore, when attempting to establish new populations, translocating breeding-aged individuals, whose site fidelity is high, may improve the success of these conservation efforts.

Similar to other species, we identified a strong effect of seasonality on behaviour (52, 53), with periods when site fidelity and social selectivity may have a greater adaptive value, like the breeding season, showing more pronounced relationships between behaviour and age. This seasonal effect is not likely driven by fluctuations in food availability, given that vultures are provisioned at several feeding stations across the study area, as a part of ongoing conservation management (54). In fact, this high predictability in food availability and distribution (55, 56) enabled us to decouple within-individual behavioural changes from changes in the environment. Nevertheless, it is plausible that the observed sharp increase in behavioural predictability in old age may be more moderate in areas with unpredictable foraging conditions (51, 57). In such challenging environments, older individuals of long-lived species may play a particularly important role in buffering the effects of poor environmental conditions, as they may act as repositories of ecological knowledge gathered throughout their lives (12, 14). As anthropogenic activities are threatening to change the age structure of populations of endangered species (20, 58), the loss of knowledge and behaviours exhibited by older individuals can hamper the ability of populations adjust to changing environmental conditions (12–14, 59).

Methods

Study system and data collection

The study was carried out in Israel, where griffon vultures are critically endangered (37). A historical population of thousands of individuals (60) declined to about 400 griffons three decades ago and to less than 200 individuals today. To prevent the local extinction of this species, there has been an intense conservation and management effort, including provisioning of food at supplementary feeding stations for vultures, release of captive-bred and translocated individuals (61), minimizing mortality caused by energy infrastructures, seasonal censuses, and monitoring through individual marking and GPS transmitters (38).

Between 2008 and 2022, we deployed GPS-Accelerometer tags (160g E-Obs GmbH) and GPS-GSM Accelerometer transmitters (50g Ornitrack from Ornitela) on 319 griffons in Israel, using Teflon harnesses in backpack (2008-2015) and leg-loop (2016 onwards) configurations. Vultures were captured in cage traps (62) and a small fraction were released from rehabilitation centres, captive-breeding and translocation programs (61). During tagging, all griffons were ringed with metal and colour rings and marked with patagial tags for field identification. During capture, they were aged based on their morphological characteristics, including feather shape and moulting patterns (flight feathers, great coverts, and neck ruff feathers), and the bill and eye colours (63, 64). Every year, about 100 griffons are trapped or re-trapped; therefore, almost all individuals are aged when they are still younger than 4 years old. We designated individuals as age 0 in their first year of life, changing to age of 1 on the 15th of December of the same year (the approximate start of the breeding season). Nine griffons were initially captured when they were already adults (>5 years old) and therefore it was not possible to reliably age them in the field. To estimate their age, we compared their roost fidelity with individuals of known age, starting when they were at least 15 years old. On average, their roost fidelity was not different from the cohort of 18 years old, and therefore we assumed this was their average age (Figure S5). To ensure that the addition of these individuals did not shape our results, we performed all statistical analysis with and without the individuals of unknown age and the results remained the same (Figure S6).

Considering our high recapture rate, we were able to replace the GPS devices that had either stopped working or that had fallen off the griffons. The average duration of a single deployment was of 457 days (min = 1, max = 2962, including only terminated deployments, Figure S7), and the median number of deployments per bird was 1 (mean = 1.5). Yet, one individual was re-deployed with new GPS devices 6 times during its life. Overall, the gap between deployments was of 543 days (min = 0 days, max = 3622 days).

The GPS transmitters typically recorded location and ground speed every 10 minutes during the day (average 13min, SD = 68min), and provided one or two additional locations during the night, when vultures are inactive. Yet, the sampling rates vary according to the battery charge, specific research questions (e.g., periods of high-resolution tracking at 1Hz (5)), and the GPS transmitter's longevity; at the end of the battery's lives, transmitters often fail to charge and provide only 1 point per day, usually at night, when vultures are in the roosts (see Acácio et al (38) for an example). We initially filtered the data to remove the first date of GPS deployment, as well as any dates when the individuals were captured or, on rare occasions, at the wildlife hospital. We also filtered outlier positions; an observation was considered an outlier if the speed between two consecutive locations was over 50m/s, or if two consecutive nighttime locations were over 10km apart. We then manually identified vultures that spent most of their time in the southern region of Israel during the study period (n = 210), excluding griffons that spent most of their time in the northern region of Israel or in other countries (Türkiye, Greece, Bulgaria), as their movement patterns might differ from the ones in the south of Israel. All distance metrics were calculated as the shortest distance between the two points on an ellipsoid (WGS84), using the R package "geosphere" (65).

We then divided each year into three distinct seasons: breeding, summer, and the transient period. We considered the "breeding" season to last from December 15th of the previous year (when griffons start to select their nest site and partner) to May 14th of the current year (when griffons are either still caring for an old chick or, considering the low breeding success in our studied population, have already failed their breeding attempt). We defined the "summer" season between May 15th and September 14th (post-breeding for some individuals, and late breeding for others), and the "transient" period (when long-range forays typically occur (31)) between September 15th and December 14th. All data processing, analyses, and mapping were conducted in R (66). All code and data are available at https://github.com/msa2015/Ageing_Vultures.

Roost-location and roost-site identification

Vultures roost in deep canyons with poor GPS coverage, resulting in frequent GPS failures within the roost. Thus, to determine where vultures roosted, we identified, for each individual, the last GPS position of the day that was recorded 60min before sunset or later (including nighttime locations, if available). If there was no GPS position during that time frame, we used the first GPS position of the following day that was obtained within 60min after sunrise or earlier. If none of the GPS positions met one of these two criteria, we calculated the geodesic distance between the last GPS position of the day (if this position was obtained during the afternoon) and the first GPS position of the next day (if this position was obtained in the morning). If the distance between these two locations was 2km or less, we considered the last position of the day to be the roosting location.

To define roost-sites, we grouped the identified roost-locations (N = 145,270) using the DBSCAN clustering algorithm (Density-Based Spatial Clustering of Applications with Noise). We used 1km as the epsilon distance (the maximum distance between two points for one to be considered close to the other), and a minimum of 50 locations to identify the core points. We identified a total of 10,720 different roost-sites. The most popular roost-site included 25,834 roost-locations. Roost-locations that were not clustered into a roost-site (for example, for griffons that were performing long-range forays and roosting in unusual locations) were identified as their own unique roost-site

(N=10,666). To visualize the roost-sites, we built convex hulls based on the roost-locations of each site (as shown in Figure 2A). This analysis was performed using R package “fpc” (67).

Roost fidelity and routine behaviours

We computed a daily metric of “roost fidelity”: if a vulture remained in the same roost-site on two consecutive nights, we considered the vulture to have used the same roost. To ensure our results were not sensitive to the clustering method, we repeated all analyses using a threshold of 1km and 20km for considering two consecutive nights as using the same roost-site (Figure S1). In addition, to guarantee that our results were not influenced by the younger griffons’ long-range forays (during which they might switch roosts more often than they would in our main study area), we repeated the models with these long-distance travels removed, resulting in the same patterns (Figure S1).

We then investigated movement routine for griffons that switched roosts within our main study area (Israel and surrounding areas: longitude 34.2-36.5, latitude 29.3-33.2), as most of the griffons remained in this area throughout the study period. We quantified movement routine as the degree of predictability in a sequence of roost-sites when griffons switched roosts (40, 56). To do so, for each griffon, we considered the order of the roost-sites they used within a year as a roost sequence (removing consecutive nights at the same roost-site), and for each sequence we computed a routine index using an algorithm developed by Riotte-Lambert et al (40). This routine index ranges from 0 (complete unpredictability of roost switching sequence) to 1 (complete predictability of roost switching sequence). Because longer sequences are more reliable for routine identification, we performed this analysis at the yearly level rather than breaking sequences by season, thus maximizing the length of the roost switching sequences (average sequence length = 46 roost-switches, range = 10-243).

Identifying popular roosts

We hypothesized that age may affect the intensity of use of popular roosts. We started by identifying the “popular roosts” by examining the number of roost-locations at each roost-site. We then considered “popular roosts” to be the top 20% of roost-sites with the highest number of locations (out of all roost-sites with at least 2 roost-locations) (Figure S8). In total, we identified 6 popular roost-sites out of 31 available roost-sites within our main study area.

We controlled for three possible biases that could influence our results: the threshold for defining roost popularity, the tendency of younger individuals to leave the main study area, and the high roost fidelity of older individuals. To examine if the results were influenced by the popularity threshold, we repeated our analyses using 25% and 30% thresholds for roost popularity. We also investigated if our results could be explained by younger individuals being more likely to leave the main study area (to peripheral regions where there are no “popular roosts”). To do so, we repeated the analyses without the long-range forays. We found that the results were not affected by the chosen popularity threshold or by the elimination of the long-range forays (Figure S9). Finally, we also note that our popularity index was not driven by the roost usage of old individuals: first, older individuals are uncommon in the dataset (Figure 2B) and thus do not drive roost-site popularity estimate. Second, when calculating the top 20% of roost-sites using a random and balanced design (in terms of the ages of the individuals), our results remained the same (Figure S10).

Social behaviour

To quantify the social behaviour of griffon vultures, we examined co-occurrence at roosting sites. For this analysis we only considered years when at least 25% of the total Israeli griffon population was continuously GPS tracked (39) (2016-2022, Figure S11). A conservative estimate of the minimum percentage of the tracked population ranged between 26% and over 60%. We excluded any nights that the griffons roosted outside the main study area, because we could not be sure if they were roosting alone or with non-GPS tracked griffons from other populations. We then constructed a series of seasonal social networks (N=20 year-season combinations), in which vultures that roosted within 1km of each other were considered to be co-roosting. The weight of the interactions between two individuals was calculated as a simple ratio index, based on their seasonal interaction frequency, divided by the total number of nights within a season when both individuals were tracked and could have roosted together (68–70). From these networks, we derived three individual-level network centrality measures: normalized degree, strength, and average strength. Normalized degree is the number of unique individuals a griffon co-roosted with within a season, divided by the number of individuals in the seasonal network minus 1 (average network size = 87, range = 30-133). Strength is a measure of how many interactions an individual had at roosts and is calculated as the sum of the weights of all interactions (edges) of an individual. Average strength is the ratio between strength and degree (i.e., strength divided by degree), representing how strongly connected a griffon is on average to each of the individuals it shared a roost with.

Changes in movement behaviour with age

To evaluate the influence of age on the movement behaviour of griffon vultures, we fitted a series of generalised linear mixed models (GLMMs), using the R package “glmmTMB” (71). We considered three response variables to describe the movement behaviour of griffons: "roost fidelity” (binomial distribution with a logit link function, 1 = remained at the same roost; 0 = switched between roosts), “probability of having a routine” (binomial distribution with a logit link function, 1 = index of routine is larger than 0, 0 = index of routine is 0), and “routine index” (beta distribution with a logit link function, values ranging between >0 and 1, with higher values indicating higher predictability in roost switching sequence). For these analyses, we considered only individuals with at least 30 identified roosts in a season (roost fidelity), or at least 30 roosts in a sequence within a year (routine). On average, we identified 607 roosts for each individual (min = 36, max = 3120). To ensure that tracking duration did not impact our results, we performed a sensitivity analysis and repeated our data analysis twice: using individuals that were tracked for at least 182 days (6 months) and again, only with individuals that were tracked for 365 days (1 year) or more (Figure S12). The results of both analyses did not differ from results of the full dataset (Figure S13, Figure S14). Overall, using the 30-days' threshold, we identified the roost fidelity for 142 griffons (86,192 roost-locations); we modelled the probability of routine for 135 griffons (627 roost switching sequences); and we modelled the influence of age on the routine index for 115 griffons (312 roost switching sequences, with routine index >0).

The structure of each model was as follows: roost fidelity as a function of age, season, and their interaction; probability of routine as a function of age and length of the roost sequence (log transformed); routine index as a function of age (because length of the roost sequence was not statistically significant and was therefore dropped from the model). All models had year and individual as random intercepts. For each response variable, we fitted four models, each with a different functional relationship between behaviour and age: linear ($y = ax + b$), quadratic ($y = ax^2 + bx + c$), exponential ($y = a^x$), and third-degree polynomial ($y = ax^3 + bx^2 + cx + d$) (Figure 1). Depending on the behaviour, these models may represent an increasing or decreasing relationship between behaviour and age. We also fitted a null model with only random effects. We analysed the model residuals using R package "DHARMa" (72). For each response variable, we ranked models according to their AIC and selected the model with the lowest AIC. If the top models had delta AIC < 2, we selected the simplest model.

Changes in sociality with age

To analyse how age affects griffon vultures' social behaviour, we fitted a series of GLMMs considering four response variables: "probability of occupying a popular roost" (binomial distribution with a logit link function, 1 = spent the night in a popular roost, 0 = spent the night in a non-popular roost), "normalized degree" (beta distribution with a logit link function, values ranging between 0 and 1), "strength" and "average strength" (both with gaussian distributions and identity link functions, continuous variables >0). To ensure that our indices were not biased by an incomplete representation of the population's social network in particular seasons, for these analyses we only considered individuals that were tracked for at least 30 nights within a season, and seasons that had at least 30 tracked individuals. We were left with 16 unique networks and 108 griffons (total of 510 data points).

Models for each of the social behaviour measures included age, season, and their interaction as explanatory variables. For normalized degree, the interaction was not statistically significant and was dropped from the model. All models had year and individual as random intercepts. The model with strength as a response variable did not fit our data correctly (high heteroscedasticity), and therefore this variable was removed from further analysis. For roost popularity, normalized degree, and average strength, we tested the four functional relationships of age (linear, quadratic, exponential, third-degree polynomial), as detailed above, and chose the best model according to the AIC.

Mechanisms shaping age-dependent movement and social behaviours

To assess the relative importance of selective disappearance and/or individual plasticity for shaping behavioural ageing in movement and social behaviour of griffons, we considered the subset of individuals with known death year (and consequently their age at death, i.e. longevity). Because the Israeli griffon population is heavily monitored, if a GPS tag shows no movement a ranger is sent to the field to investigate a possible mortality event (38). Furthermore, almost all individuals are observed in the field during their lifetime, either during the seasonal census or at their nest or at feeding stations (average number of yearly observations per GPS-tracked individual = 3, range = 0-67). As a result, we considered a vulture to be dead if it was found dead in the field, or if it was not seen in the field for at least 5 times its usual visual observation rate. This rate was calculated from all the observations for each individual during their lifetime, with or without a GPS transmitter (e.g., if individual A was seen every 2 months, then it would be considered dead if it was not seen for 10 months; if individual B was seen every 36 months, then it would be considered dead if it was not seen for 180 months). The age-of-death was the age the individual was last seen alive plus its usual observation rate (as an individual could have died at any point during that period). Individuals that were never observed in the field (e.g. if they were mainly active outside Israel due to natal or breeding dispersal) were not considered dead unless their body was found (n = 3 individuals). To ensure our results were robust to the used 5-fold threshold, we repeated all analyses with a 10-fold rate threshold, as well as with an alternative approach of a uniform 2 year-gap since the last observation (for all individuals). All three age-at-death estimates provided similar results for the relative importance of longevity and behavioural plasticity (Figure S15, Figure S16). For the analysis of the mechanism of behavioural ageing we had 59 individuals for the "roost fidelity" and "probability of occupying a popular roost" analyses, 55 individuals for the "probability of routine" analysis, 41 individuals for the "routine index" analysis, and 29 individuals for the "average strength" analysis. With this reduced dataset for the effect of age on the probability or index of routine (due to the absence of older individuals in this subset of data), we could not evaluate the role of selective disappearance or individual plasticity for these variables.

We then performed a test for selective disappearance as described by Van de Pol & Verhulst (6, 27). We fitted the best model of each of our response variables ("roost fidelity", "probability of routine", "routine index", "probability of occupying a popular roost", and "average strength") using four different models: age only, without any other variables ("Age" model); age and individual ID as a random intercept, to account for individual variation ("Age + ID" model); longevity (i.e., age at death) and individual ID as a random intercept ("Longevity + ID" model); and age, longevity as fixed effects and Individual ID as a random intercept ("Age + Longevity + ID" model). All models had season as a fixed effect and year as a random intercept. The model residuals were analysed, as well as the collinearity between variables (variance inflation factor, VIF). These four models allowed us to isolate the effect of individual plasticity (i.e., within-individual changes) from the effect of selective disappearance (i.e., between-individual changes). If adding longevity changes the effect of age within the model, it implies that selective disappearance (and not individual plasticity) shapes the age-dependent pattern found at the population level (more details in Van de Pol & Verhulst (6, 27)). After building the four models (“Age”, “Age + ID”, “Longevity + ID” and “Age + Longevity + ID”) for each response variable, we selected the model with highest predictive power based on AIC. For the “average strength”, the VIF between age and longevity in the “Age + Longevity + ID” model was over 10 implying these two variables were collinear; thus, we could not assess if plasticity or selection drives the changes in average strength. To ensure that our results were not driven by the complex relationship between behaviour and age, or by a non-linear relationship between behaviour and longevity, we fitted all models with age as a linear effect, second-degree and third-degree polynomials. We also fitted longevity as a quadratic term. Doing so did not affect our conclusions regarding the mechanisms of behavioural ageing in griffons (Table S13, Figure S17, Figure S18). In the main text, present the models with the lowest AIC (third-degree polynomials and longevity with a linear effect) while the remaining model outputs can be found in Table S13.

Data and code accessibility

Analysis code is available at https://github.com/msa2015/Ageing_Vultures. The data are available in Zenodo, under the DOI: 10.5281/zenodo.10651582. The GPS-coordinates were shifted a few kilometres from the original location to ensure species safety, while maintaining all geometric attributes needed for reconstructing the analyses.

Funding statement

Funding for this work was provided by the NSF-BSF grant: NSF IOS division 2015662/BSF 2019822 to NPW and OS, as well as BSF grant 255/2008 to RN. MA was supported by the George S. Wise Postdoctoral Fellowship (Tel Aviv University).

Acknowledgments

We want to sincerely acknowledge all individuals who have contributed to the conservation of griffon vultures in Israel, and without whom this work would not have been possible. In particular, we thank the workers and rangers of the INPA for their hard work and dedication, specially Ygal Miller, Asher Perez, Avishai Bar-On, Yaniv Levy-Paz, Dvora Shilo, Lior lev, Sappir Simchi, Elad Zisso, Elya Maatuf (Elika) and Arye Rosenberg. We also acknowledge the members of the Movement Ecology Laboratory at the Hebrew University of Jerusalem. Finally, we thank all members of the Movement Ecology and Individual Behavior Laboratory at Tel Aviv University, in particular Assaf Uzan for all support, and thank Elvira D'Bastiani for helpful discussions on earlier versions of this work.

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Supplementary Material

Behavioural plasticity shapes population ageing patterns

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The supplementary file includes:

Figs. S1 to S18

Tables S1 to S13

Table of contents

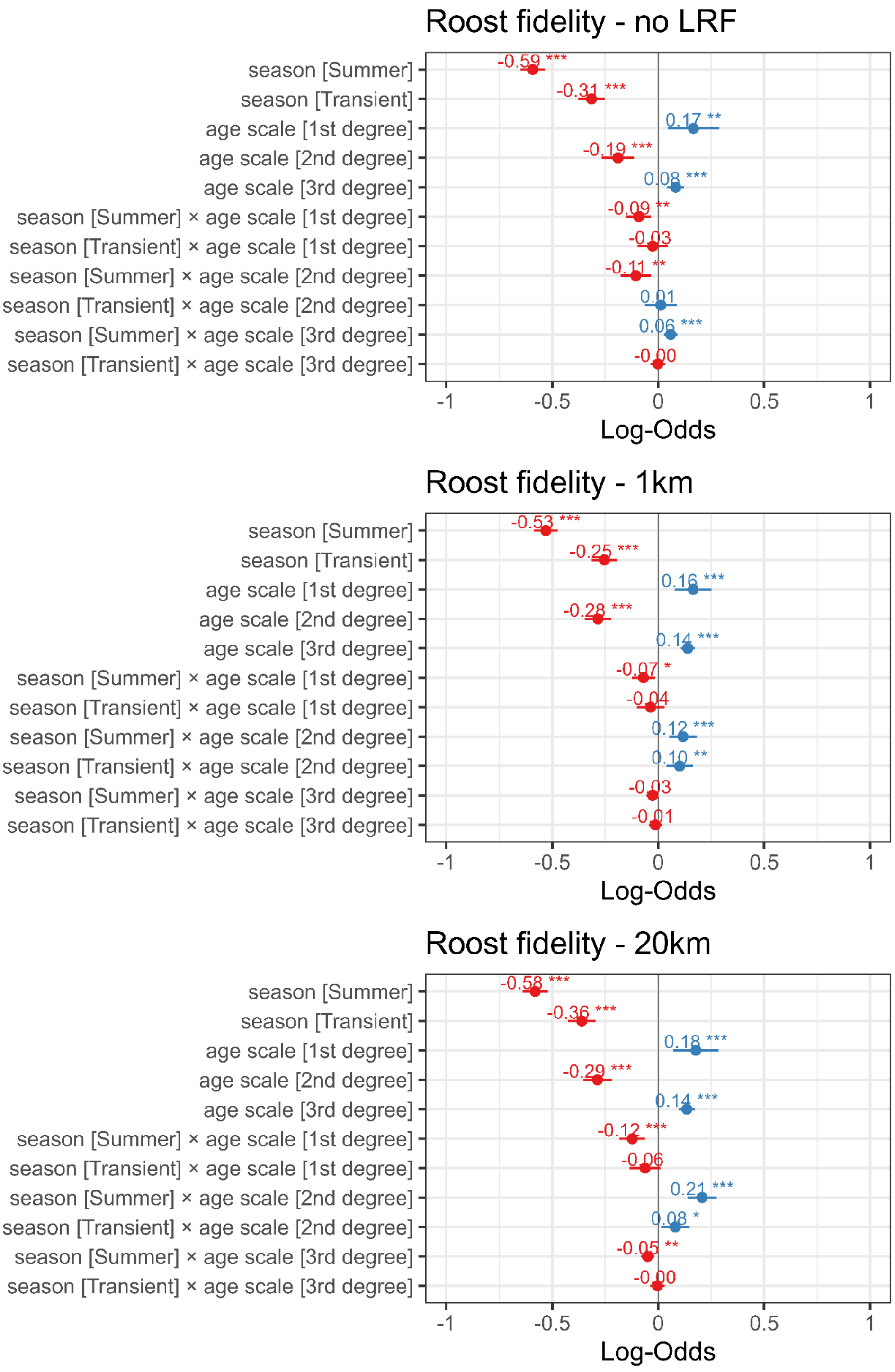


Figure S1 – Effect of age on roost fidelity, excluding the long-range forays (LRF) and using different distance thresholds for roost fidelity (1km and 20 km). Effect estimates (log-odds) of the GLMMs, testing the relationship between age and the probability of roost fidelity, **a.** without the periods of the long-range forays, **b.** considering a threshold of 1km for an individual to change roosts, and **c.** considering a threshold of 20km for an individual to change roosts. All models had year and individual as random effects. The vertical line shows the vertical intercept that indicates no effect, and the p-value is indicated on top of the error bars. Note that in all three cases, the third-degree polynomial relationship between age and roost fidelity was maintained, as well as the interaction with season.

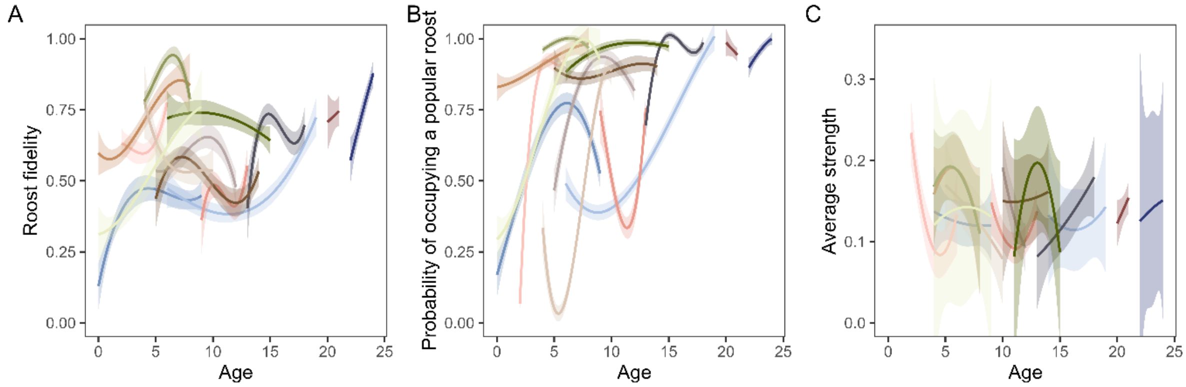


Figure S2 - Long-term tracking of 15 individuals, highlighting the changes in movement and social behaviour as individuals age. Individual changes with age in **A.** roost fidelity, **B.** probability of occupying a popular roost, and **C.** average strength of co-roosting relationships. Each line represents an individual and the shaded area the 95% confidence interval. Same individual is represented with the same colour in all three plots. Individual lines were built using the mathematical functional relationship of each variable, 3rd-degree polynomial for roost fidelity and roost popularity, and quadratic for average strength.

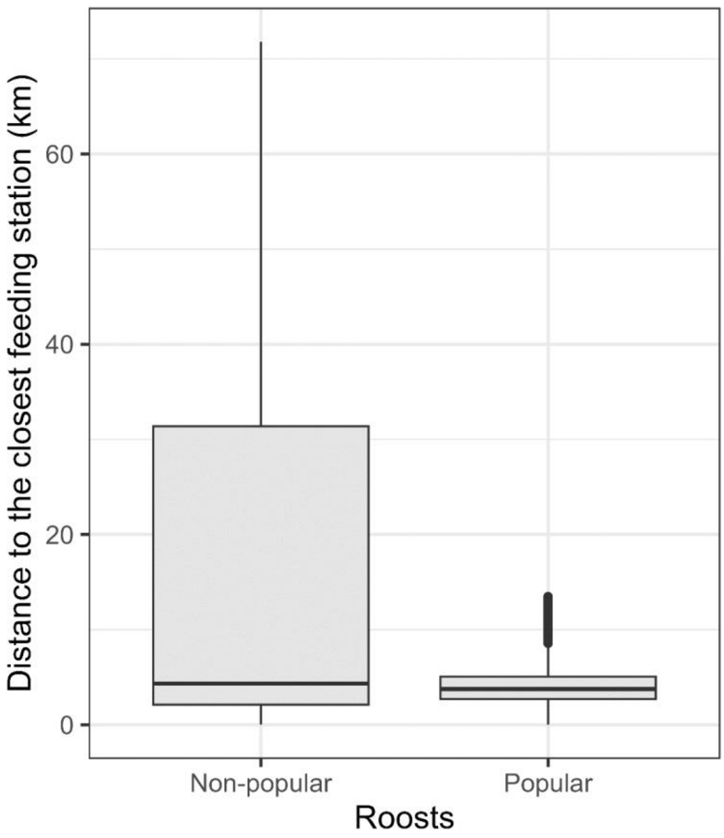


Figure S3 – Distance of popular roosts (top 20% used roosts) and all other roosts in the South of Israel to the closest supplementary feeding station (in km). The distance was calculated as the geodesic distance of each roost location to the closest feeding station.

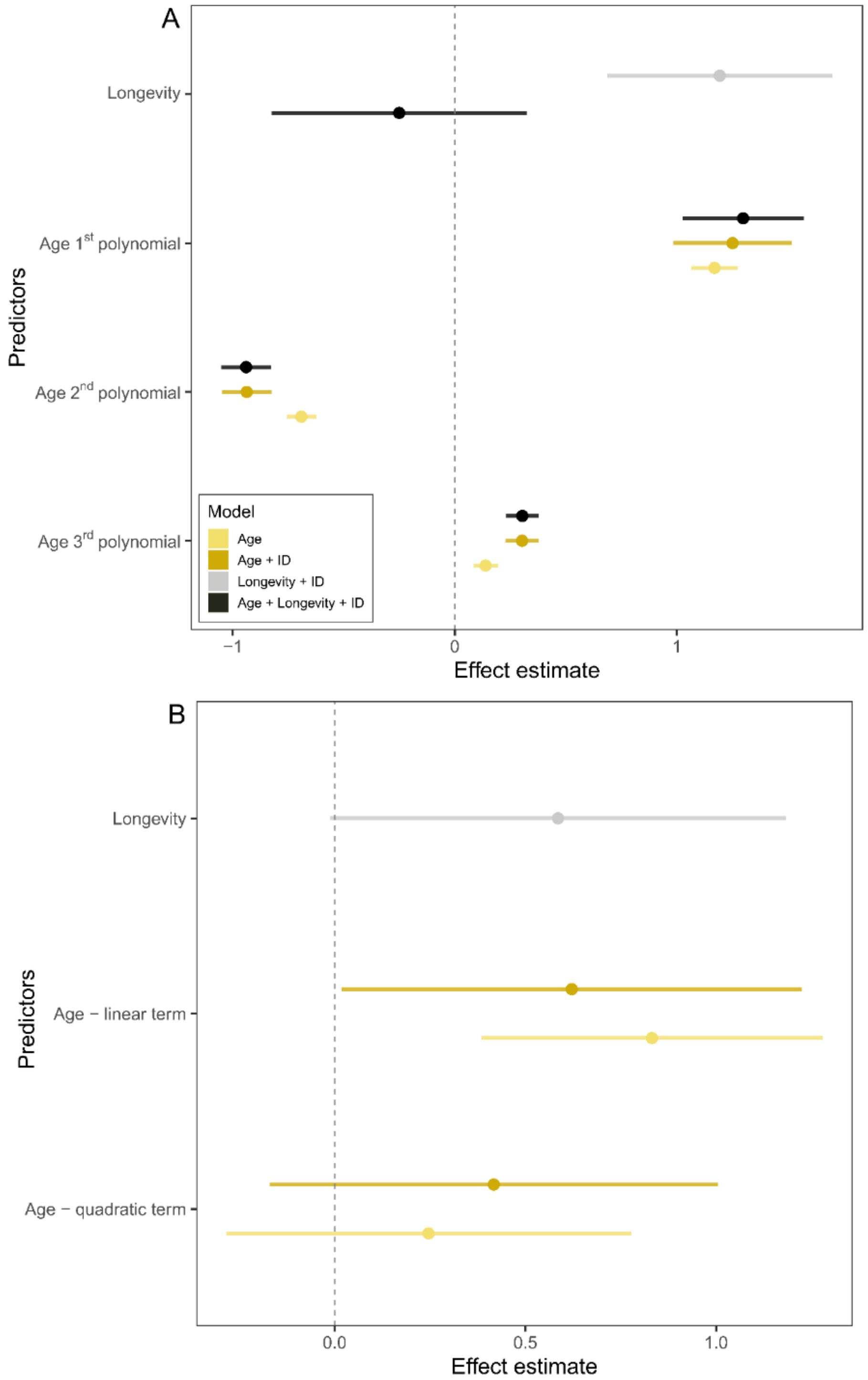


Figure S4 – Mechanisms shaping the changes in the probability of occupying a popular roost and changes of average strength with age. Effect of age and longevity (i.e., age at death) on **A.** probability of occupying a popular roost, and **B.** average strength, in four different statistical models: age only (light yellow); age and individual ID as a random effect (dark yellow); longevity and individual ID as a random effect (grey); and age, longevity, and individual ID as a random effect (black). All models included season as a fixed effect, and year as a random effect. Both age and longevity are scaled. These models allow us to isolate the effect of individual plasticity (i.e., within-individual behavioural changes) from the effect of selective disappearance (i.e., between-individual behavioural differences and selection acting on certain behaviours). Adding longevity did not change the effect of age within the model for roost popularity, suggesting that behavioural plasticity (and not selective disappearance) shapes the age-dependent behavioural pattern found in the population. Due to a high collinearity between age and longevity, it was not possible to disentangle the role of plasticity and selection in shaping changes in average strength with age.

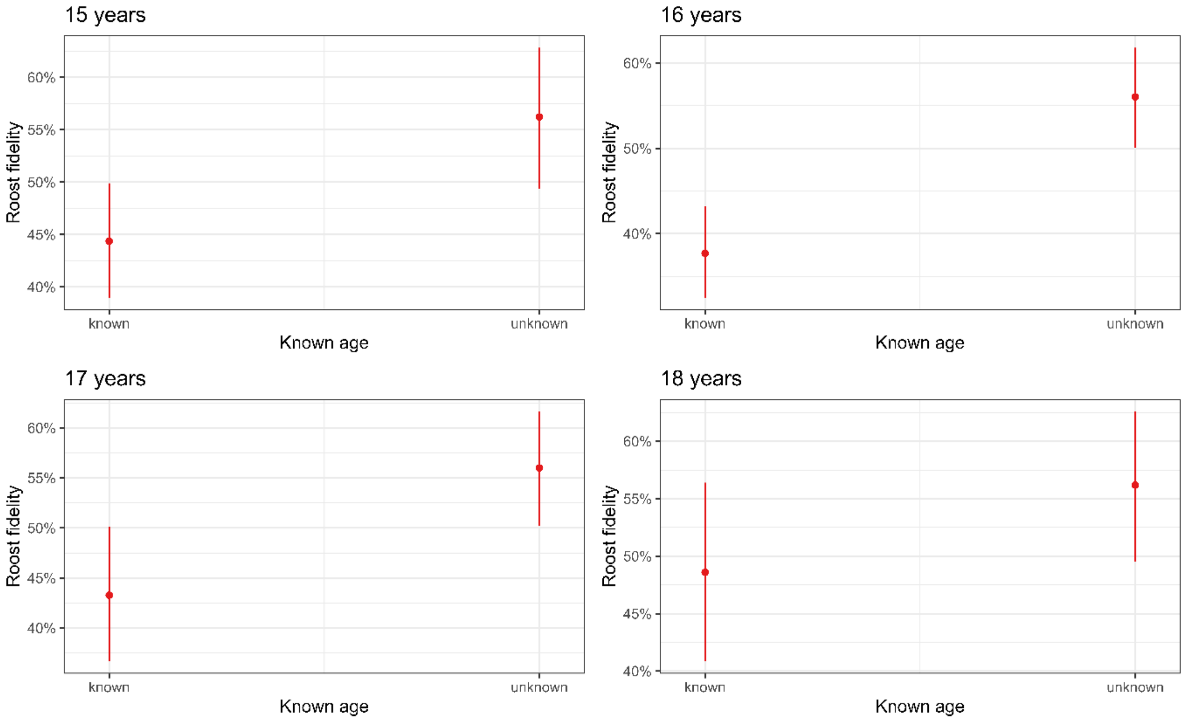
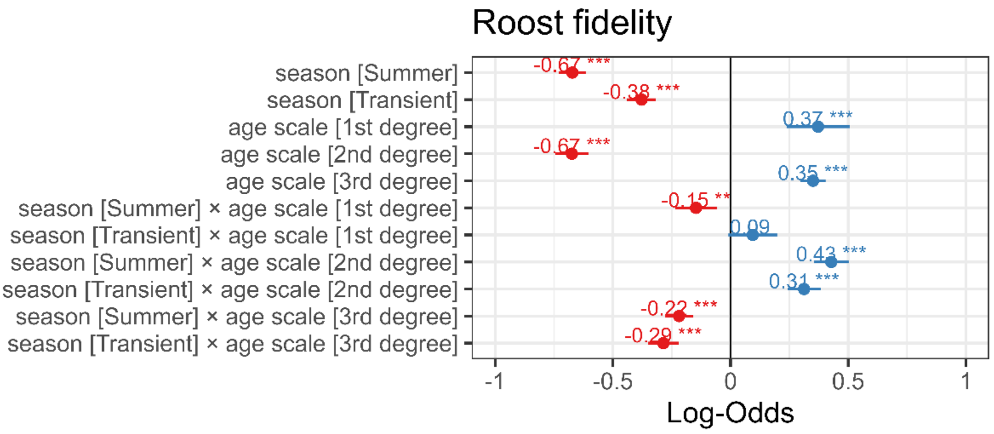
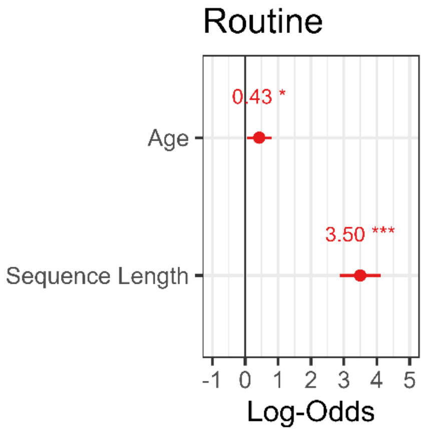
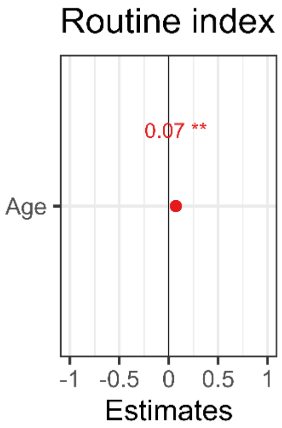
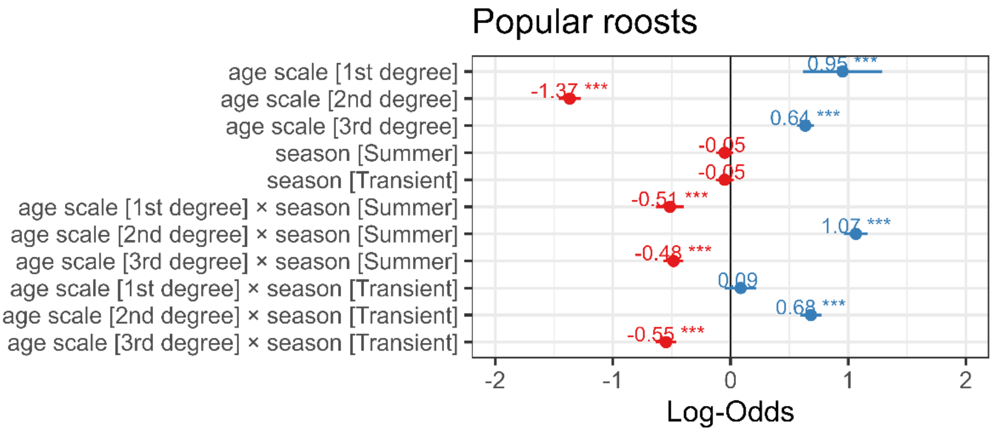


Figure S5 – Estimated age of the 9 individuals of unknown age, based on their roost fidelity behaviour. Nine griffon vultures (out of 142) were initially ringed when they were already adults (>5 years old), rendering impossible to know their real age based on their physical appearance. To estimate their age, we ran 4 GLMMs (binomial family and individual as a random effect), comparing the roost fidelity behaviour (binomial, 1/0) of individuals of known age and unknown age. We started the comparison when the griffons of unknown age were at least 15 years old and compared them to known 15-year-old individuals. Since there were significant differences between the two groups, we compared the individuals of unknown age with 16-, 17-, and 18-year-olds, until we could not find significant differences in roost fidelity between the individuals of known age and the individuals of unknown age (at the age of 18). Thus, we assumed the old individuals of unknown age were at least 18 years old.


Roost fidelity


Routine


Routine index


Popular roosts

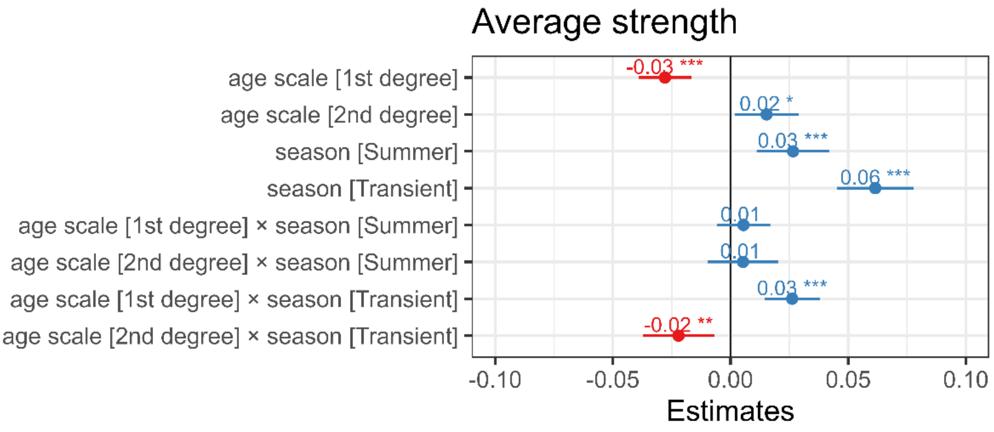

Average strength

Figure S6 – Behavioural ageing (roost fidelity, routine, roost popularity and average strength) without the griffons of unknown age. Estimates of the generalized linear mixed models, testing the relationship between age and **a.** roost fidelity, **b.** probability of having a routine, **c.** index of routine, **d.** probability of occupying a popular roost, **e.** average strength. The model with degree did not converge, and the results are not shown. The vertical line shows the vertical intercept that indicates no effect, and the p-value is indicated on top of error bars. This sensitivity analyses show that including the old individuals whose age was not known did not influence our conclusions.

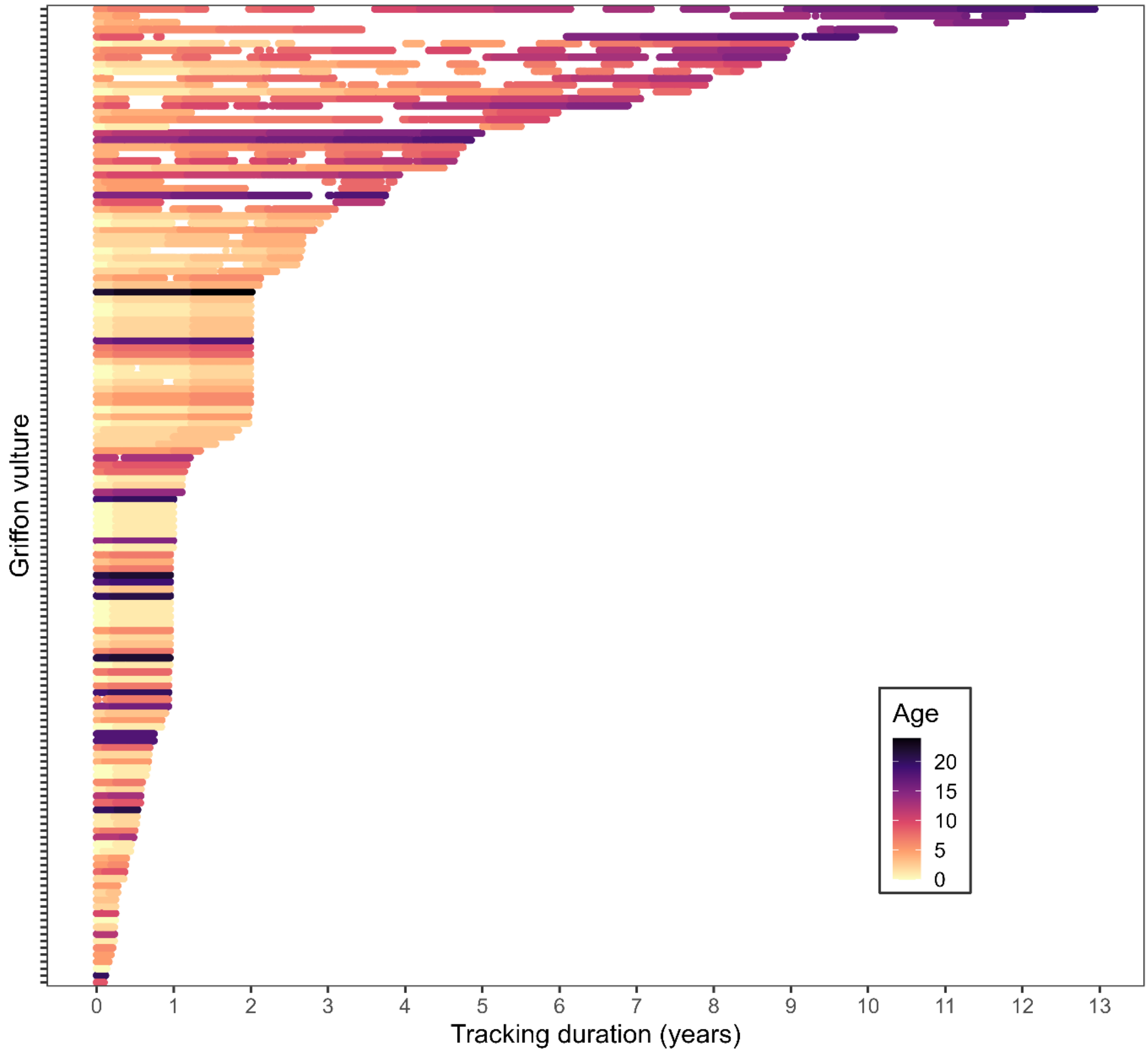


Figure S7 - Tracking duration (in years) of the griffon vultures included in this study. Gaps indicate periods when the individual was not tracked due to the loss or failure of the GPS transmitter. Colours indicate the age of each individual, with younger individuals represented in lighter colours.

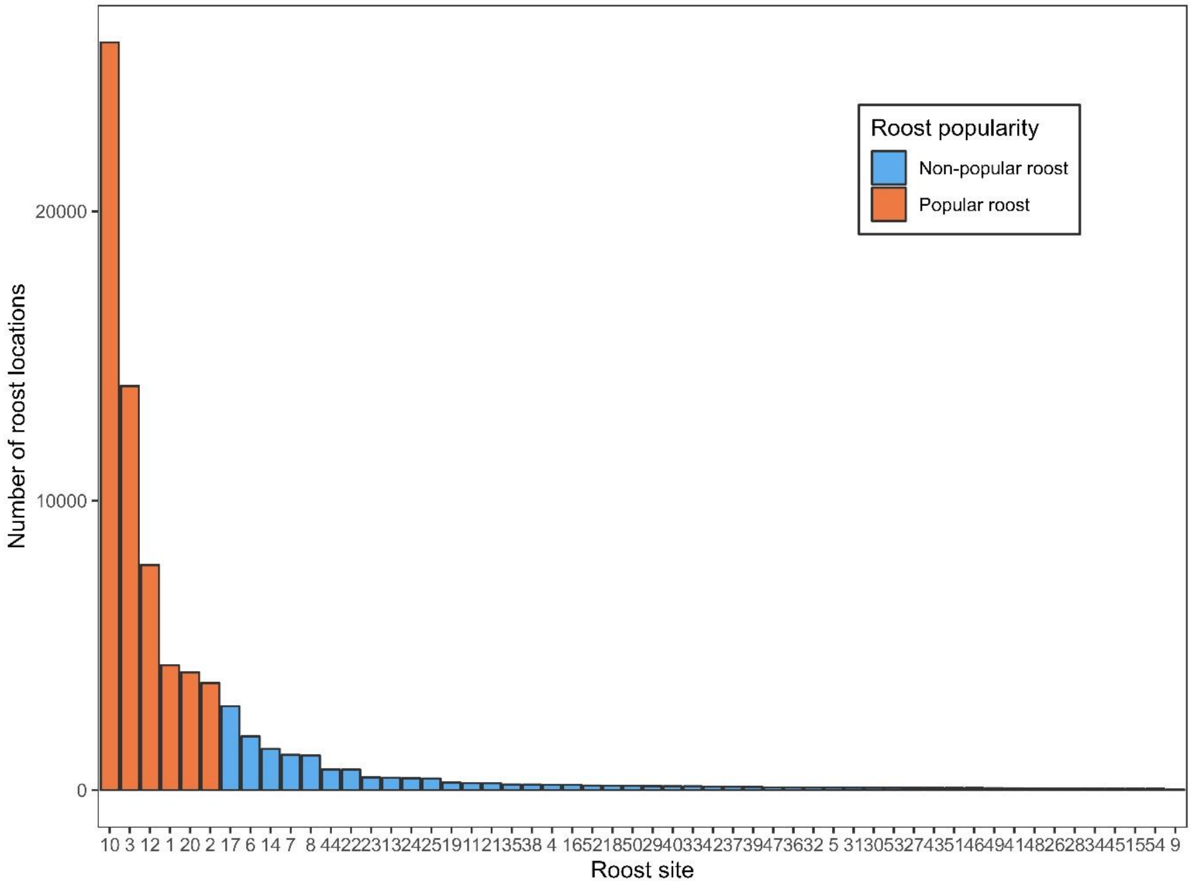
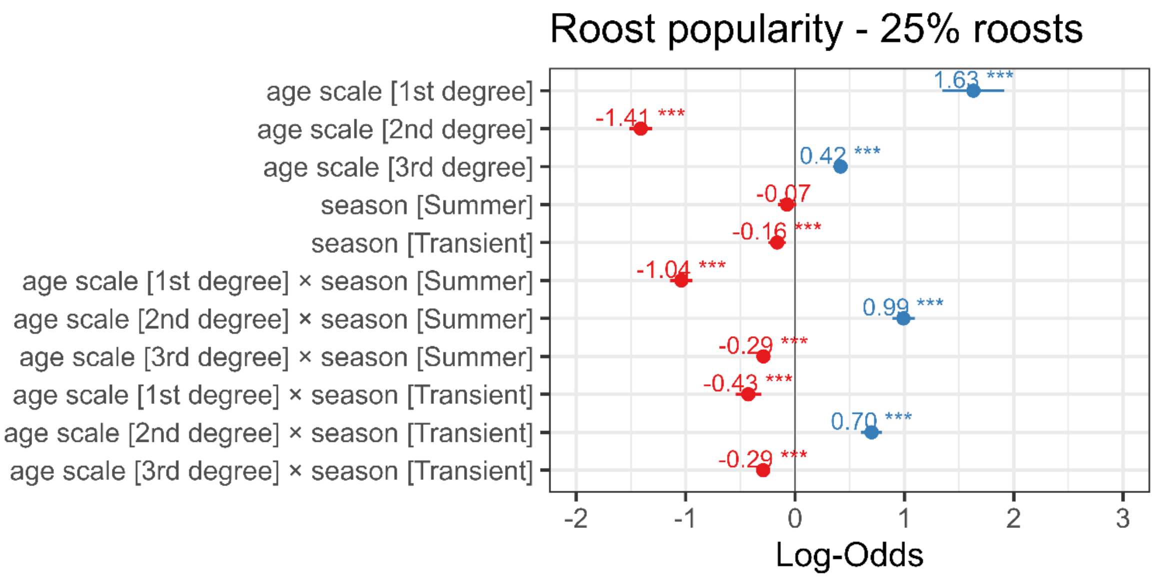
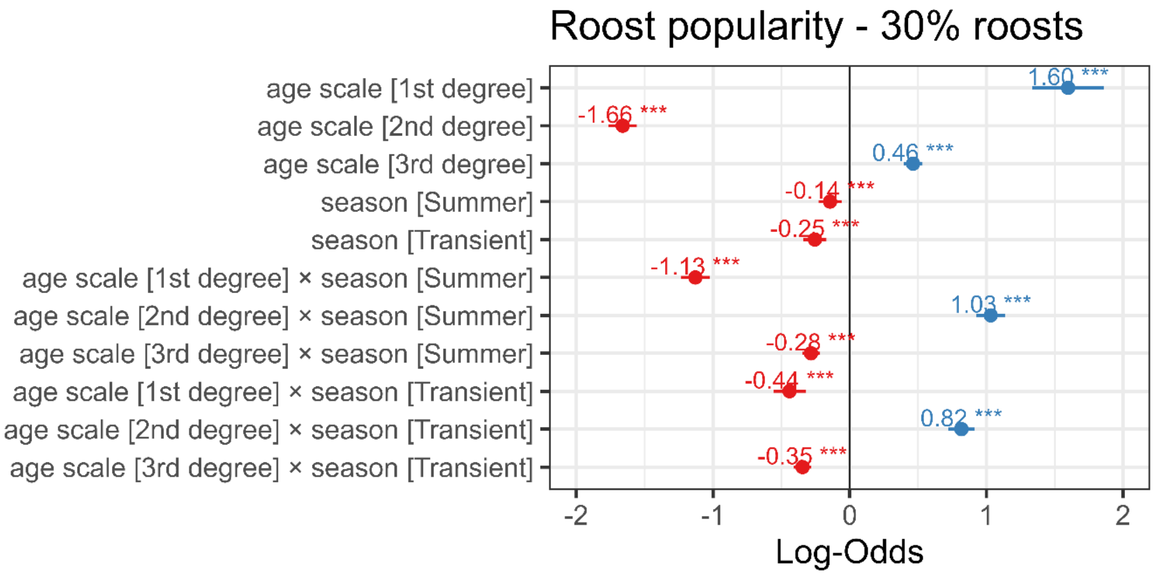


Figure S8 – Number of roost locations in each roost site. The “popular roosts” (in orange) were defined as the top 20% most used roost sites in the study area (mostly Israel); the remaining were classified as “non-popular roosts” (in blue).


Roost popularity - 25% roosts


Roost popularity - 30% roosts

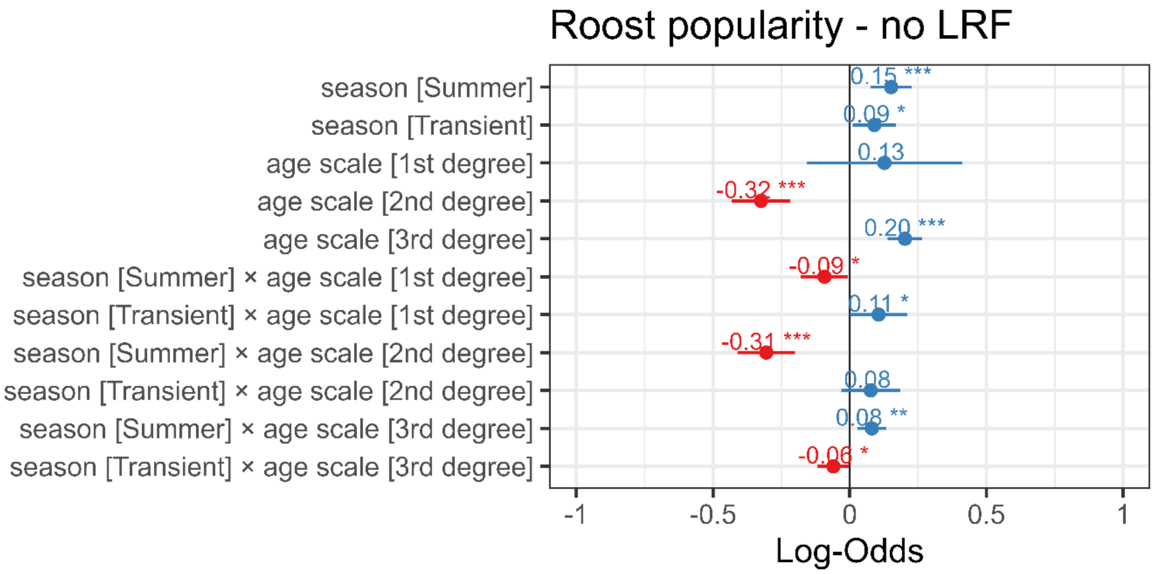

Roost popularity - no LRF

Figure S9 – Effect of age on the probability of occupying a popular roost, using different thresholds for "popular roosts" (25% and 30%) and excluding the long-range forays (LRF). Odds ratios of the same mixed models, testing the relationship between age and the probability of using a popular roosts **a.** where a popular roost was defined as the top 25% of the most used roosts, **b.** where a popular roost was defined as the top 30% of the most used roosts, and **c.** excluding any data during the long-range forays (LRF). The vertical line shows the vertical intercept that indicates no effect. Note that in all three cases, the third-degree polynomial relationship between age and roost fidelity was maintained, as well as the interaction with season.

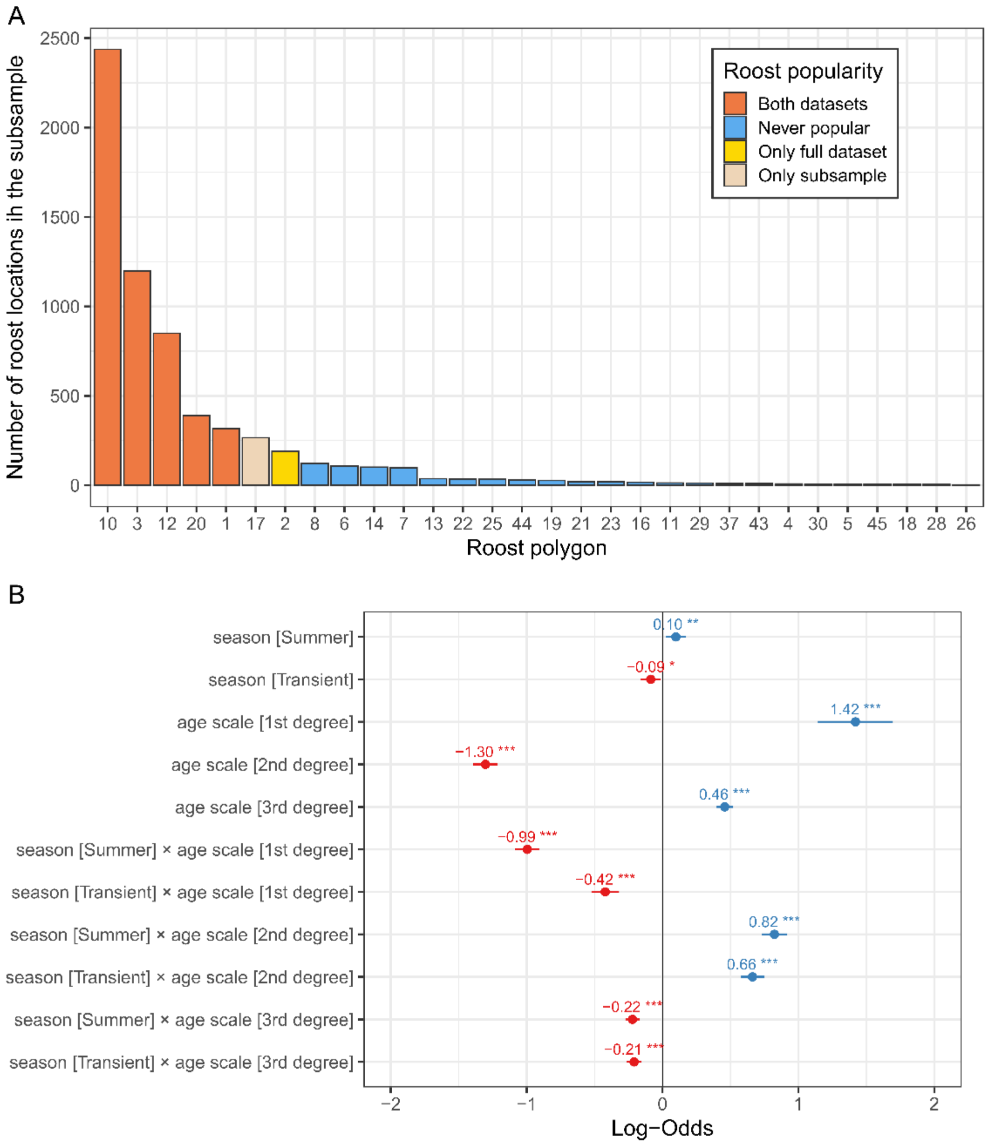


Figure S10 – Effect of age on the probability of occupying the popular roosts, using a balanced designed, in terms of the ages of the individuals. A. Popular roosts, classified as the top 20% of most used roosts in a random subsample of the full dataset, containing the same number of roost-locations per age (100 roost-locations per season, 300 per year). The colours show the roosts-sites that were classified as "popular" when using the full dataset and the subsampled dataset (orange); that was only classified as popular when using the full dataset (yellow); that was only classified as popular when using the subsampled dataset (beige); and that were always classified as "non-popular" (blue). **B.** Estimates and significance value of the generalized linear mixed model, analysing the effect of age and season (and their interaction) on the probability of using a popular roost (classified using the subsampled dataset: roost-sites 10, 3, 12, 20, 1 and 17). Note that the results are the same as using a classification based on the full dataset.

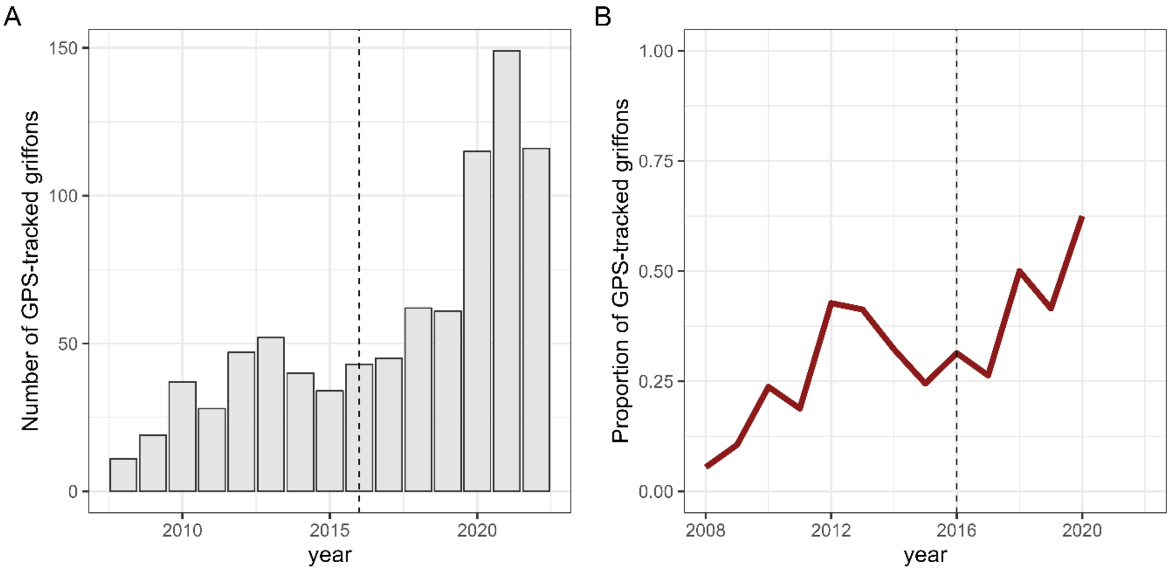


Figure S11 – Number and proportion of GPS-tracked vultures in Israel. A. Total number of griffons GPS-tracked in Israel between 2008 and 2022. **B.** Proportion of GPS-tracked vultures, in relation to the total griffon vulture population size in Israel. For the sociality analyses, we only considered when at least 25% of the population was continuously tracked (since 2016 – dashed line). The data for the vulture census was not available for the years of 2021 and 2022, and therefore it was not possible to calculate the proportion of GPS-tracked griffons. However, given the declining trend of the population, we estimate that in 2022 about 70% of the whole population was being tracked.

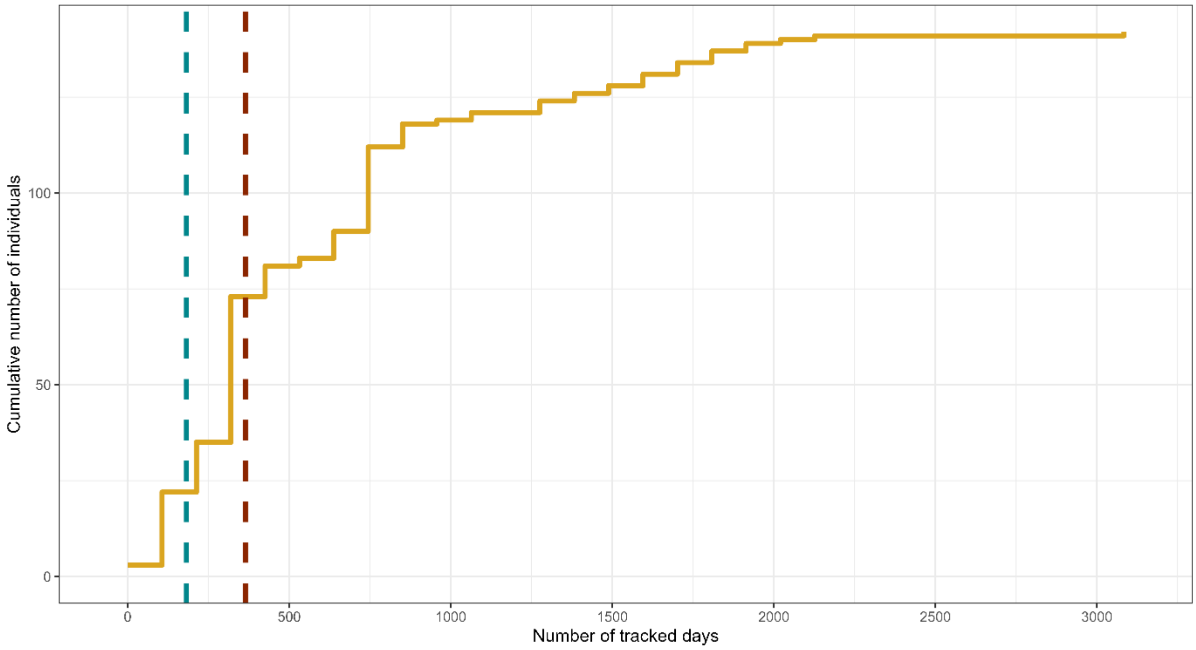


Figure S12 – Total number of days each griffon was GPS-tracked. To ensure our results were not influenced by the difference in tracking duration of different individuals, we re-ran all models using only individuals that were tracked for 182 days (6 months, to the right of the green dashed line) and individuals that were tracked for at least 365 days (1 year, to the right of the red dashed line).

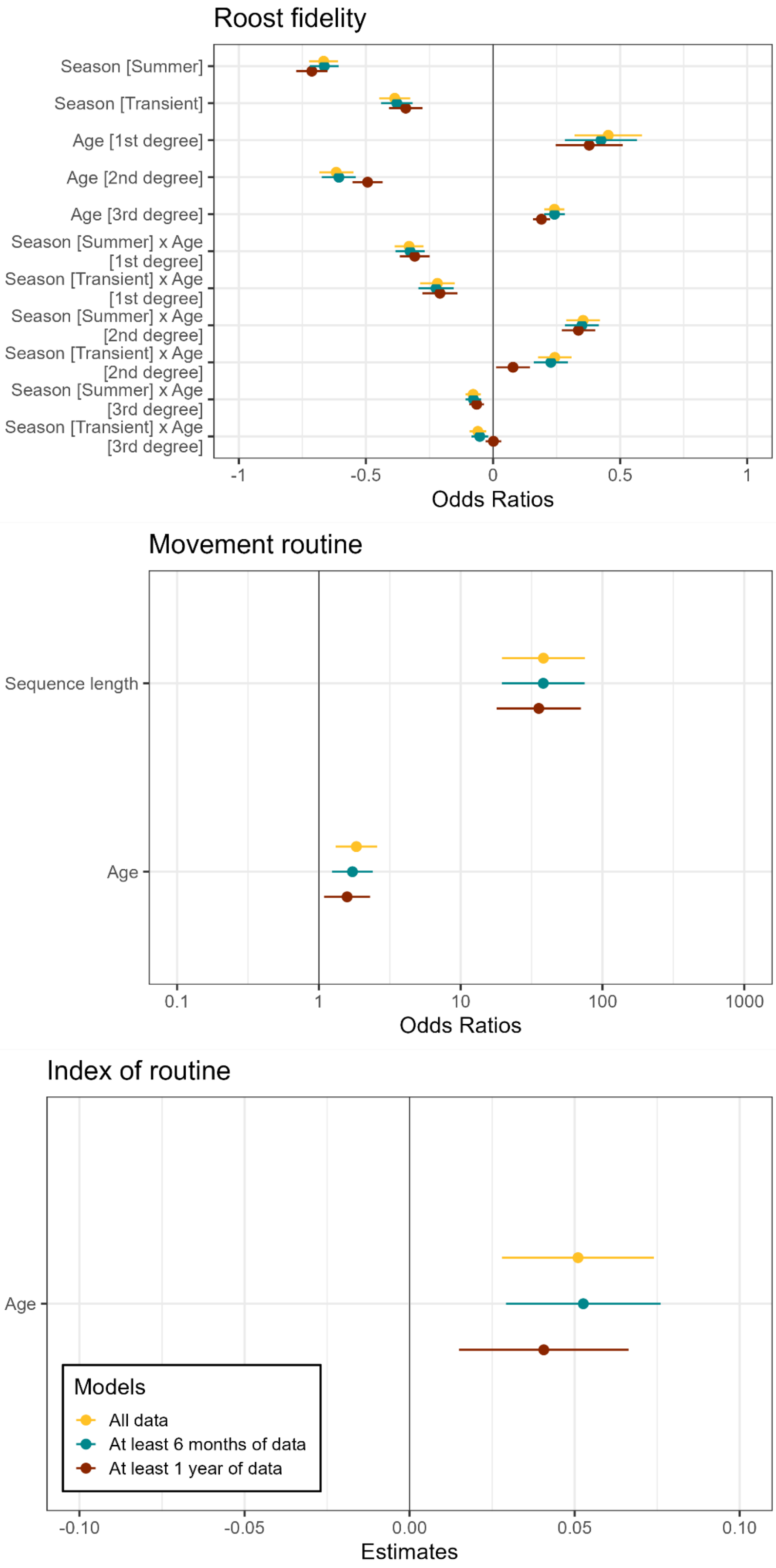


Figure S13 – Effect of age on roost fidelity, movement routine and index of routine, including individuals that were GPS-tracked for at least 30 days (yellow), 6 months (turquoise) or 1 year (red). Including a more conservative threshold of tracking duration did not change the effect of age on movement behaviour, apart from the interaction between age and season (transient) on roost fidelity.

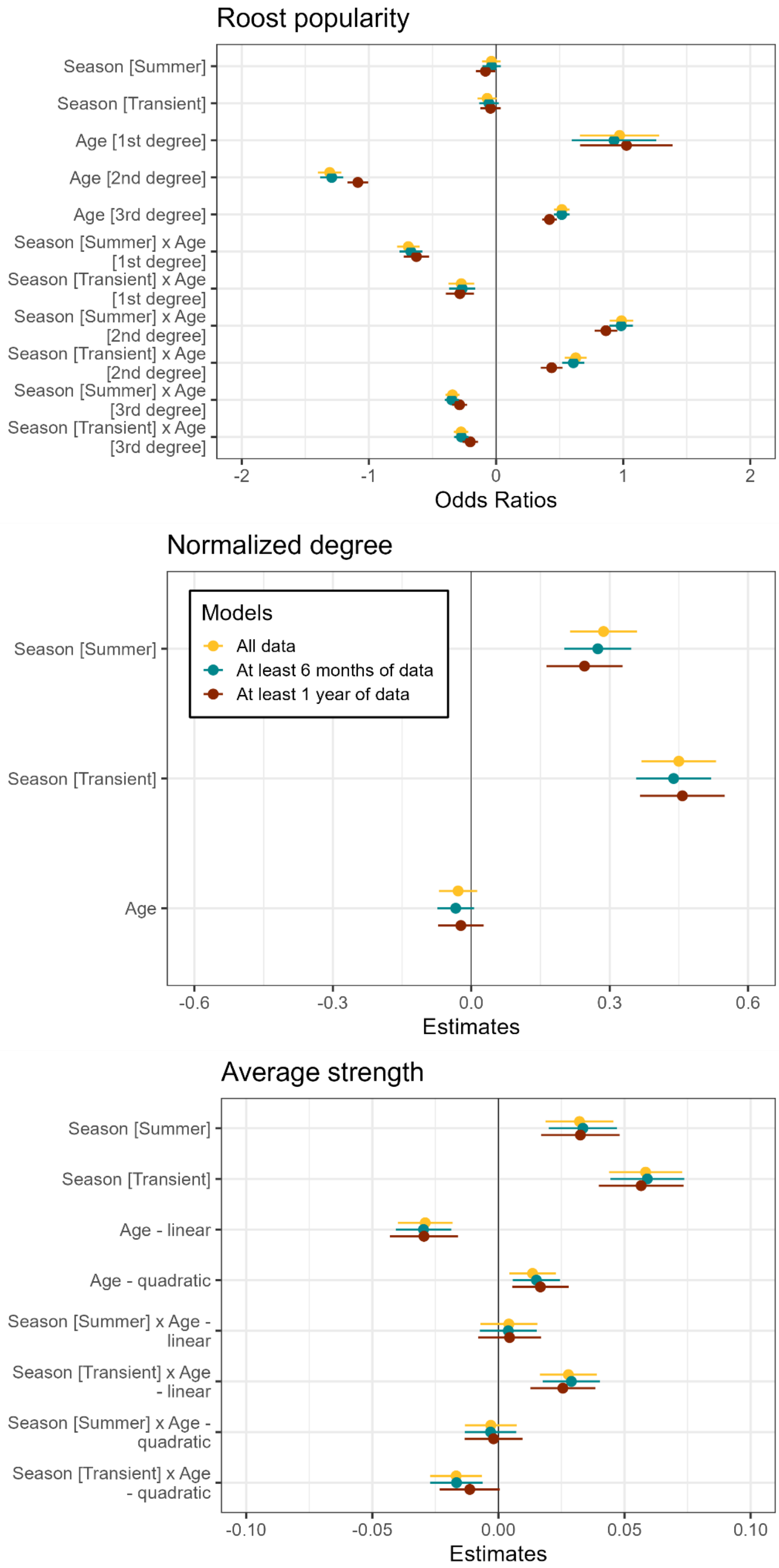


Figure S14 – Effect of age on the probability of selecting a popular roost, on degree (normalized) and on average strength of social relationships, including individuals that were GPS-tracked for at least 30 days (yellow), 6 months (turquoise), or 1 year (red). Including a more conservative threshold of tracking duration did not change the effect of age on social behaviours.

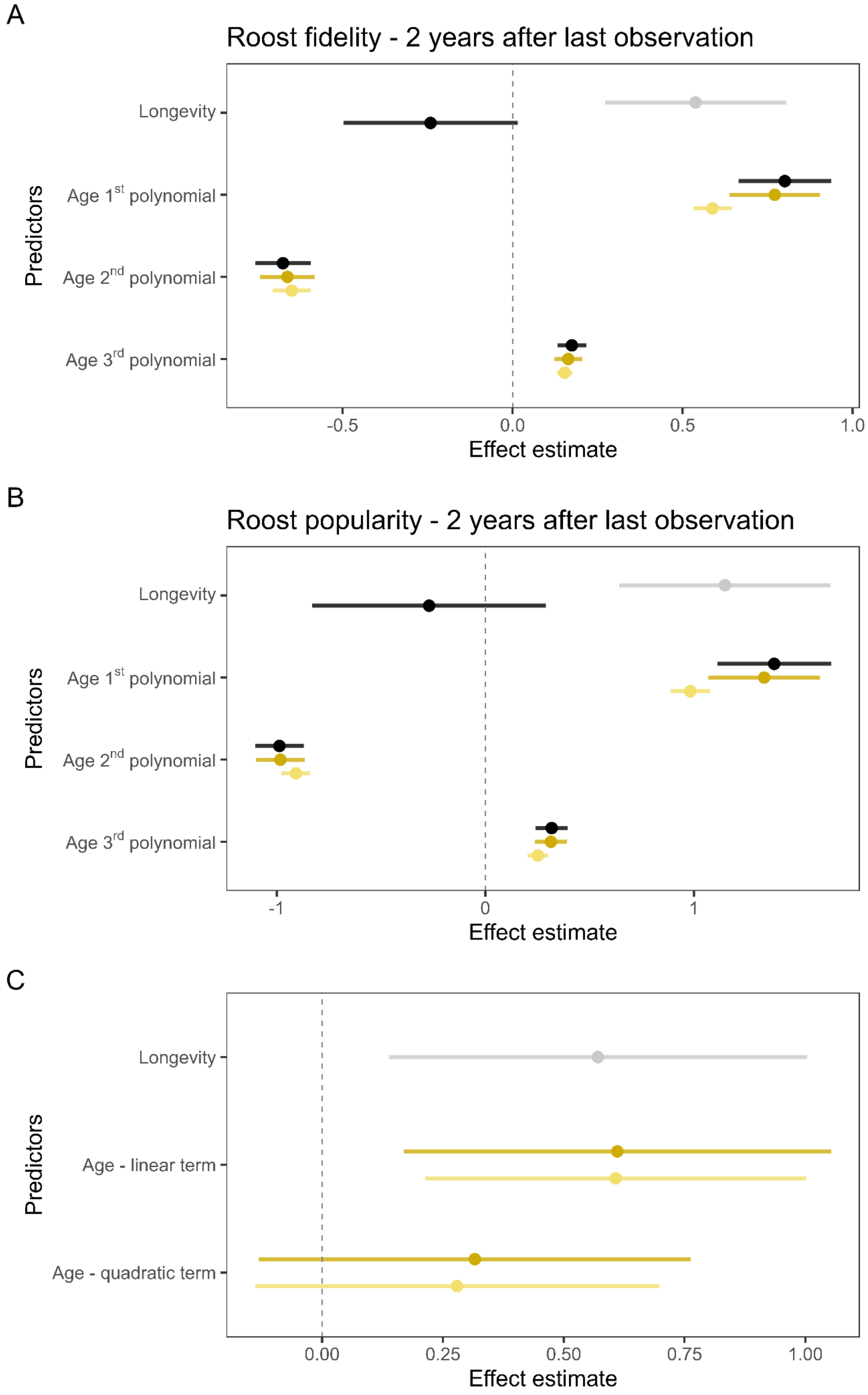


Figure S15 – Mechanisms shaping behavioural ageing, using a different threshold to estimate longevity (2 years since the last observation). Effect estimates of age and longevity (i.e., age at death) on roost fidelity (**A**), probability of occupying a popular roost (**B**), and average strength (**C**) in four statistical models: age only (light yellow); age and individual ID as a random effect (dark yellow); longevity and individual ID as a random effect (grey); and age, longevity, and individual ID as a random effect (black). All models included season as a fixed effect, and year as a random effect. Both age and longevity are scaled. Adding longevity did not change the effect of age within the model of roost fidelity and roost popularity, suggesting that behavioural plasticity (and not selective disappearance) shapes these age-dependent behavioural patterns found in the population. Note that for average strength, the high collinearity between age and longevity did not allow us to test the effect of individual plasticity and selective removal on this parameter.

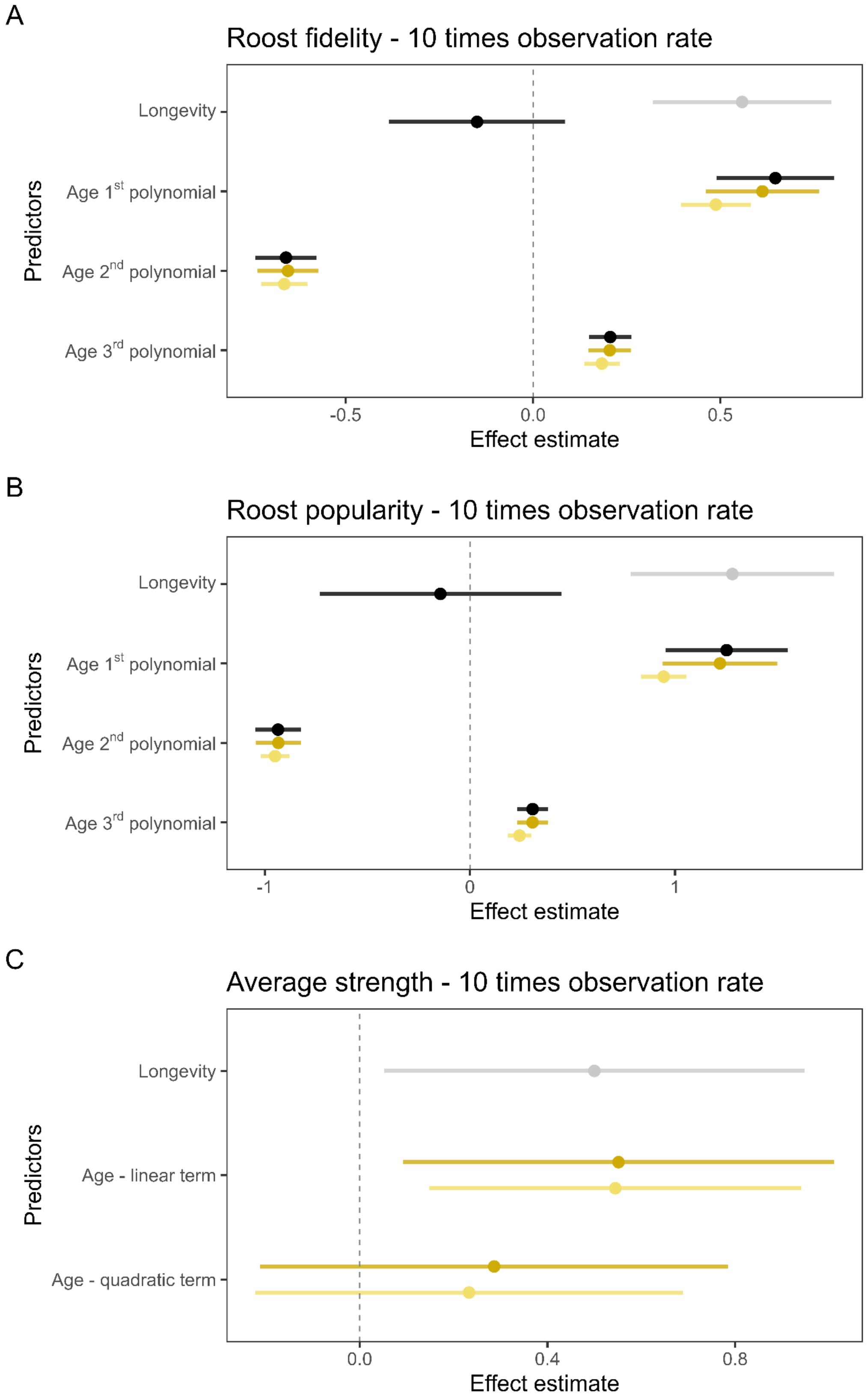


Figure S16 – Mechanisms shaping behavioural ageing, using a different threshold to estimate longevity (10 times the usual observation rate). Effect estimates of age and longevity (i.e., age at death) on roost fidelity (**A**), probability of occupying a popular roost (**B**), and average strength (**C**) in four statistical models: age only (light yellow); age and individual ID as a random effect (dark yellow); longevity and individual ID as a random effect (grey); and age, longevity, and individual ID as a random effect (black). All models included season as a fixed effect, and year as a random effect. Both age and longevity are scaled. Adding longevity did not change the effect of age within the model of roost fidelity and roost popularity, suggesting that behavioural plasticity (and not selective disappearance) shapes these age-dependent behavioural patterns found in the population. Note that for average strength, the high collinearity between age and longevity did not allow us to test the effect of individual plasticity and selective removal on this parameter.

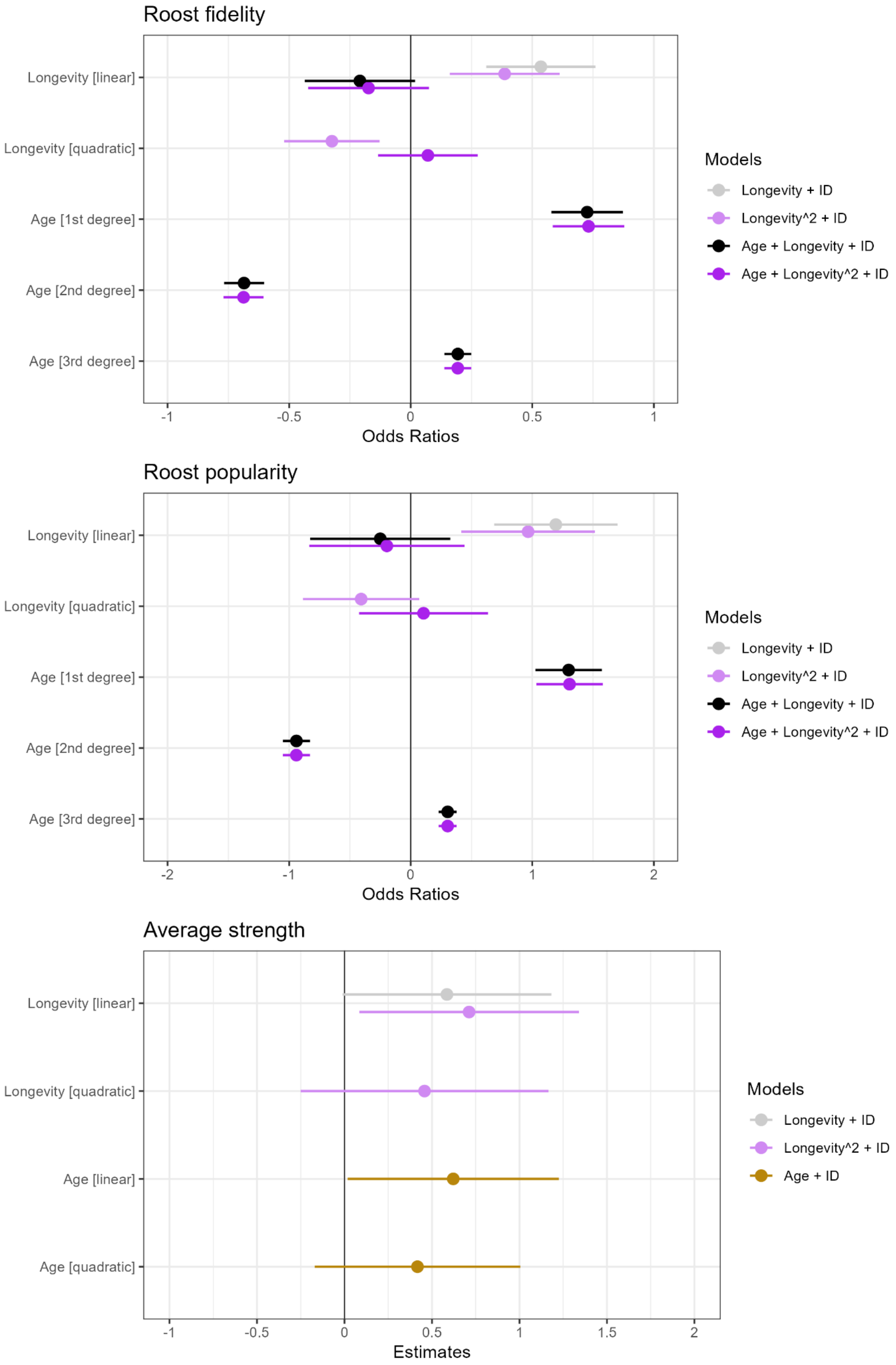


Figure S17 – Mechanisms shaping behavioural ageing in griffon vultures, allowing for a non-linear effect of longevity. Fitting the models including longevity as a quadratic term did not change our conclusions: roost fidelity and selection were shaped by behavioural plasticity, but it was still not possible to conclude the mechanisms underlying the changes in co-roosting average strength with age.

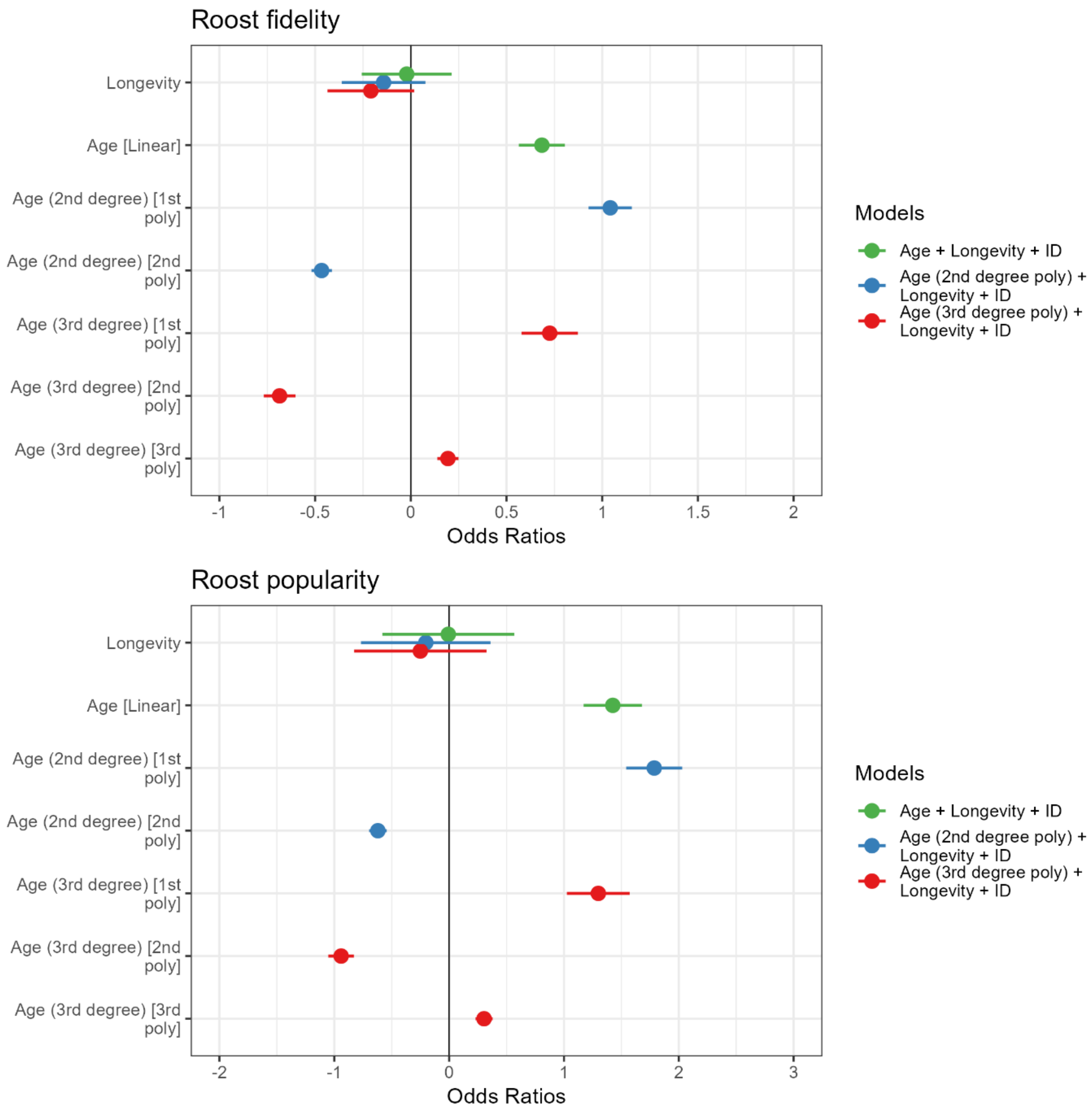


Figure S18 – Effect of longevity across the increasingly complex age polynomial formulations. The effect of longevity did not change despite fitting age as a linear effect, second-degree, or third-degree polynomial.

Table S1 – Functional relationships between age and roost fidelity. Comparison of the GLMM binomial models, with roost fidelity (1/0) as response variable, and season and age (with a linear, quadratic, exponential, or third-degree polynomial transformations), and their interaction as predictors. All models had individual and year as random effects. The models are ordered based on their performance: models with lower AIC were preferred if the difference in AIC was >2. If the difference in AIC was <2, the simplest model was selected as the best model.

Model	AIC (weight)	BIC (weight)	R2 conditional	R2 marginal
Third degree polynomial	103005 (>0.999)	103136 (>0.999)	0.245	0.082
Quadratic	103147 (<0.001)	103250 (<0.001)	0.235	0.072
Linear	103418 (<0.001)	103492 (<0.001)	0.241	0.063
Exponential	103618 (<0.001)	103692 (<0.001)	0.295	0.009

Table S2 – Effect of age on roost fidelity. Results of the GLMM binomial model, with roost fidelity (1/0) as response variable, and season and age (with a third-degree polynomial transformation), and their interaction as predictors. The model had individual and year as random effects. Age was scaled and centered around the standard deviation and mean.

Predictor	Estimate	Std. Error	z-value	p-value
Intercept	0.669	0.108	6.173	<0.001
Season – Transient	-0.387	0.031	-12.41	<0.001
Season – Summer	-0.667	0.029	-23.04	<0.001
Age – 1st polynomial	0.453	0.068	6.708	<0.001
Age – 2nd polynomial	-0.617	0.034	-18.02	<0.001
Age – 3rd polynomial	0.241	0.020	11.96	<0.001
Season – Transient x Age – 1st polynomial	-0.219	0.035	-6.280	<0.001
Season – Summer x Age – 1st polynomial	-0.330	0.029	-11.38	<0.001
Season – Transient x Age – 2nd polynomial	0.243	0.034	7.204	<0.001
Season – Summer x Age – 2nd polynomial	0.354	0.034	10.46	<0.001
Season – Transient x Age – 3rd polynomial	-0.060	0.017	-3.616	<0.001
Season – Summer x Age – 3rd polynomial	-0.079	0.015	-5.093	<0.001

Random effects	Variance	Std. Deviation
Individual	0.644	0.802
Year	0.063	0.252

Table S3 – Mechanisms shaping the patterns of behavioural ageing (roost fidelity, roost popularity, and average strength). Comparison of the models to determine the mechanism underlying behavioural ageing (individual variability and/or selective disappearance) in three different behaviours: roost fidelity, occupying a popular roost, and average strength. All models had year as random effects. The models are ordered based on their performance: models with lower AIC were preferred if the difference in AIC was >2. If the difference in AIC was <2, the simplest model was selected as the best model.

Analysis	Model	AIC	AIC weight	BIC weight
Roost fidelity	Age	39410.0	<0.001	<0.001
	Age + ID	37525.4	0.352	0.972
	Longevity + ID	38096.6	<0.001	<0.001
	Age + Longevity + ID	37524.2	0.648	0.028
Roost popularity	Age	33730.7	<0.001	<0.001
	Age + ID	26474.1	0.655	0.992
	Longevity + ID	27262.2	<0.001	<0.001
	Age + Longevity + ID	26475.4	0.345	0.008
Average strength	Age	-317.1	<0.001	<0.001
	Age + ID	-337.1	0.527	0.221
	Longevity + ID	-336.9	0.473	0.779

Table S4 – Functional relationships between age and movement routine. Comparison of the GLMM binomial models, with routine (1/0) as response variable, and sequence length (with a logarithmic transformation) and age (with a linear, quadratic, exponential, or third-degree polynomial transformations) as predictors. All models had individual and year as random effects. The models are ordered based on their performance: models with lower AIC were preferred if the difference in AIC was >2. If the difference in AIC was <2, the simplest model was selected as the best model.

Model	AIC (weight)	BIC (weight)	R2 conditional	R2 marginal
Linear	432.7 (0.214)	454.9 (0.305)	0.764	0.713
Exponential	431.2 (0.462)	453.4 (0.657)	0.756	0.717
Quadratic	432.5 (0.236)	459.2 (0.037)	0.761	0.717
Third-degree polynomial	434.5 (0.087)	465.6 (0.001)	0.761	0.718

Table S5 – Effect of age on the probability of having a movement routine. Results of the GLMM binomial model, with routine (1/0) as response variable, and sequence length (with a logarithmic transformation) and age as predictors. All models had individual and year as random effects. Age was scaled and centered around the standard deviation and mean.

Predictor	Estimate	Std. Error	z value	p-value
Intercept	2.744	0.340	8.079	<0.001
Age	0.609	0.171	3.565	<0.001
Sequence length	3.646	0.342	10.66	<0.001

Random effects	Variance	Std. Deviation
Individual	0.596	0.772
Year	0.117	0.342

Table S6 – Functional relationships between age and the index of routine. Comparison of the GLMM beta distribution models, with index of routine (0-1) as response variable, and age (with a linear, quadratic, exponential, or third-degree polynomial transformations) as predictor. All models had individual and year as random effects. The models are ordered based on their performance: models with lower AIC were preferred if the difference in AIC was >2. If the difference in AIC was <2, the simplest model was selected as the best model.

Model	AIC (weight)	BIC (weight)	R2 conditional	R2 marginal
Exponential	-482.7 (0.578)	-464.0 (0.797)	0.698	0.216
Linear	-479.4 (0.115)	-460.7 (0.159)	0.699	0.185
Quadratic	-480.4 (0.187)	-458.0 (0.040)	0.690	0.227
Third-degree polynomial	-479.5 (0.119)	-453.3 (0.004)	0.706	0.216

Table S7 – Effect of age on the index of routine. Results of the GLMM beta distribution model, with index of routine (0-1) as response variable, and age (with an exponential growth transformation) as predictor. The model had individual and year as random effects. Age was scaled and centered around the standard deviation and mean.

Predictor	Estimate	Std. Error	z value	p-value
Intercept	-0.403	0.051	-7.966	<0.001
Age	0.051	0.011	4.349	<0.001

Random effects	Variance	Std. Deviation
Individual	0.016	0.125
Year	0.018	0.135

Table S8 – Functional relationships between age and the probability of occupying a popular roost. Comparison of the GLMM binomial distribution models, with roost popularity (1/0) as response variable, and age (with a linear, quadratic, exponential, or third-degree polynomial transformations), season, and their interactions as predictors. All models had individual and year as random effects. The models are ordered based on their performance: models with lower AIC were preferred if the difference in AIC was >2. If the difference in AIC was <2, the simplest model was selected as the best model.

Model	AIC (weight)	BIC (weight)	R2 conditional	R2 marginal
Third-degree polynomial	69731 (>.999)	69862 (>.999)	0.626	0.152
Quadratic	70061 (<.001)	70164 (<.001)	0.629	0.154
Linear	70773 (<.001)	70848 (<.001)	0.628	0.151
Exponential – did not fit the data	--	--	--	--

Table S9 – Effect of age on the probability of occupying a popular roost. Results of the GLMM with a binomial distribution model, with roost popularity (1/0) as response variable, and age (with a third-degree polynomial transformation), season, and their interaction as predictors. The model had individual and year as random effects. Age was scaled and centered around the standard deviation and mean.

Predictor	Estimate	Std. Error	z value	p-value
Intercept	1.563	0.266	5.882	<0.001
Age – 1st polynomial	0.971	0.158	6.133	<0.001
Age – 2nd polynomial	-1.309	0.047	-28.05	<0.001
Age – 3rd polynomial	0.517	0.031	16.56	<0.001
Season – Transient	-0.070	0.039	-1.812	0.070
Season – Summer	-0.037	0.037	-0.991	0.322
Season – Transient x Age – 1st polynomial	-0.274	0.052	-5.281	<0.001
Season – Transient x Age – 2nd polynomial	0.626	0.044	14.15	<0.001
Season – Transient x Age – 3rd polynomial	-0.275	0.029	-9.618	<0.001
Season – Summer x Age – 1st polynomial	-0.690	0.045	-15.22	<0.001
Season – Summer x Age – 2nd polynomial	0.986	0.047	20.91	<0.001
Season – Summer x Age – 3rd polynomial	-0.343	0.028	-12.19	<0.001

Random effects	Variance	Std. Deviation
Individual	3.742	1.934
Year	0.422	0.650

Table S10 – Effect of age on normalized degree. Results of the LMM model, with normalized degree as response variable, and season and age as predictors, and individual and year as random effects. Age was scaled and centered around the standard deviation and mean.

Predictor	**Estimate**	**Std. Error**	**t value**	**p-value**
Intercept	0.480	0.049	9.863	<0.001
Age	-0.006	0.004	-1.300	0.196
Season – Transient	0.107	0.010	11.10	<0.001
Season – Summer	0.064	0.008	7.555	<0.001

Random effects	**Variance**	**Std. Deviation**
Individual	0.001	0.032
Year	0.014	0.117

Table S11 – Functional relationships between age and average strength. Comparison of the LMM models, with average strength as response variable, and season and age (with a linear, quadratic, exponential, or third-degree polynomial transformations), and their interaction, as predictors. All models had individual and year as random effects. The models are ordered based on their performance: models with lower AIC were preferred if the difference in AIC was >2. If the difference in AIC was <2, the simplest model was selected as the best model.

Model	**AIC (weight)**	**BIC (weight)**	**R2 conditional**	**R2 marginal**
Quadratic	-1639.3 (0.445)	-1588.5 (0.145)	0.474	0.202
Third-degree polynomial	-1639.8 (0.550)	-1576.2 (<.001)	0.485	0.214
Linear	-1630.2 (0.005)	-1592.1 (0.855)	0.465	0.184
Exponential – did not fit the data	--	--	--	--

Table S12 – Effect of age on average strength. Results of the LMM model, with average strength as response variable, and season and age as predictors, and individual and year as random effects. Age was scaled and centered around the standard deviation and mean.

Predictor	Estimate	Std. Error	z value	p-value
Intercept	0.114	0.008	14.19	<0.001
Age – linear	-0.029	0.006	-5.246	<0.001
Age – quadratic	0.014	0.005	2.865	0.004
Season - Transient	0.058	0.007	7.902	<0.001
Season – Summer	0.032	0.007	4.682	<0.001
Season – Transient x Age - linear	0.028	0.006	4.840	<0.001
Season – Transient x Age - quadratic	-0.167	0.005	-3.192	0.001
Season – Summer x Age - linear	0.004	0.006	0.722	0.470
Season – Summer x Age - quadratic	-0.003	0.005	-0.577	0.564

Random effects	Variance	Std. Deviation
Individual	0.001	0.029
Year	<0.001	0.008

Table S13 – Comparison of the roost fidelity, popular roosts and average strength models fitting longevity (linear and a quadratic effect), and age and longevity (also linear and quadratic). The best model (in bold) was selected according to the AIC difference. For models with ΔAIC < 2, the simplest model was selected. For the average strength, longevity and age were highly collinear (VIF > 10) and therefore it was not possible to include both terms in the model. Overall, including "longevity" as a quadratic term did not change our main conclusions.

Response variable	Model	AIC (weight)	BIC (weight)
Roost fidelity	Longevity	38096.6 (<0.01)	38146.5 (<0.01)
	Longevity^2	38088.9 (<0.01)	38147.1 (0.01)
	Age^3 + Longevity	**37524.2 (0.68)**	**37648.8 (0.99)**
	Age^3 + Longevity^2	37525.7 (0.32)	37658.7 (0.01)
Roost popularity	Longevity	27262.2 (<0.01)	27312.5 (<0.01)
	Longevity^2	27261.6 (<0.01)	27320.2 (<0.01)
	Age^3 + Longevity	**26475.4 (0.72)**	**26601.0 (0.99)**
	Age^3 + Longevity^2	26477.3 (0.28)	26611.3 (0.01)
Average strength	Longevity	-336.9 (0.34)	-317.7 (0.67)
	Longevity^2	-336.5 (0.28)	-314.6 (0.14)
	Age^2	-337.1 (0.38)	-315.2 (0.19)