



Behavioral plasticity shapes population aging patterns in a long-lived avian scavenger

Marta Acácio^{a,1} , Kaija Gahm^b, Nili Anglister^a , Gideon Vaadia^a, Ohad Hatzofe^c, Roi Harel^d , Ron Efrat^e , Ran Nathan^f , Noa Pinter-Wollman^b , and Orr Spiegel^{a,1}

Affiliations are included on p. 8.

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Studying the mechanisms shaping age-related changes in behavior (“behavioral aging”) is important for understanding population dynamics in our changing world. Yet, studies that capture within-individual behavioral changes in wild populations of long-lived animals are still scarce. Here, we used a 15-y GPS-tracking dataset of a social obligate scavenger, the griffon vulture (*Gyps fulvus*), to investigate age-related changes in movement and social behaviors, and disentangle the role of behavioral plasticity and selective disappearance in shaping such patterns. We tracked 142 individuals for up to 12 y and found a nonlinear increase in site fidelity with age: a sharp increase in site fidelity before sexual maturity (<5 y old), stabilization during adulthood (6 to 15 y), and a further increase at old age (>15 y). This pattern resulted from individuals changing behavior throughout their life (behavioral 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 behavior. Older individuals interacted less with their associates (decreasing average strength with age), particularly during the breeding season. Our results reveal a variety of behavioral aging patterns in long-lived species and underscore the importance of behavioral 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.

behavioral aging | behavioral plasticity | selective disappearance | movement ecology | sociality

Aging is ubiquitous across living organisms, leading to behavioral changes throughout life (1–4) (“behavioral aging”). Younger, sexually immature individuals tend to differ from older, mature individuals in a number of behavioral 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 behavioral changes may influence space use (3, 8), the spread of infectious diseases (1), and even the lifespan of individuals (9). Behavioral changes with age may also play an important role in how populations adjust to environmental change: Young individuals may adopt novel behaviors and be the agents of change (10, 11), while old individuals, with their accumulated knowledge and experience, may adjust to the environment by shifting behavioral strategies over their lifetimes (12–14). Despite the importance of understanding behavioral aging 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 nonmonotonic behavioral changes in the wild or the mechanisms that underlie population-level aging patterns.

Research on behavioral aging reveals a spectrum of patterns at the population level (Fig. 1): Some behaviors 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 (3, 21, 22), Fig. 1A]. Population-level behavioral changes with age can arise from two, nonmutually exclusive mechanisms. First, individuals may change their behavior throughout their lifetimes [behavioral plasticity (6, 23, 24)]. Second, individuals with particular behavioral 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 behavioral composition of the population with increasing age, without within-individual behavioral plasticity (27, 28) (Fig. 1B). Ultimately, examining the patterns and mechanisms of behavioral aging provides a foundation for understanding how

Significance

Aging is a universal phenomenon, yet how behavior changes with age (“behavioral aging”) and the mechanisms that shape behavioral aging (plasticity and/or selective disappearance) are still poorly understood. We individually tracked griffon vultures for up to 12 y 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 behavior throughout their lives rather than by the selective disappearance of particular phenotypes. Our results highlight the role of individual plasticity in shaping behavioral aging, which may have implications for our understanding of how population dynamics are impacted by a changing world.

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¹To whom correspondence may be addressed. Email: martaoc@tauex.tau.ac.il or orrspiegel@tauex.tau.ac.il.

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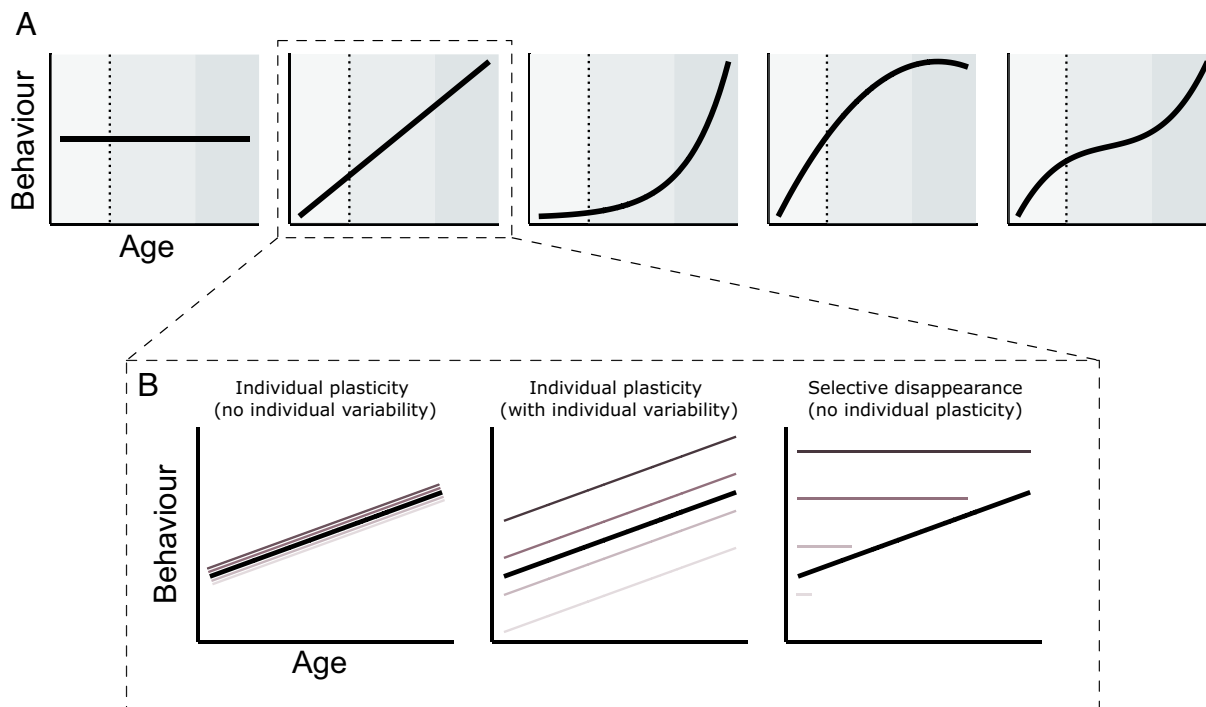


Fig. 1. Theoretical relationships and potential mechanisms of behavioral aging. (A) Five theoretical relationships between age and behavior at the population level: no relationship; a linear relationship (monotonic change in behavior with age); an exponential, convex, relationship (sharp change in behavior in old individuals); a quadratic, saturating, relationship (drastic change before maturation and then a stabilization in behavior); and a third-degree polynomial relationship (different behavior 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 behavior, but, depending on the behavior, a decreasing relationship is possible too. The vertical dotted line indicates the age of maturation, and the different gray hues represent distinct life stages (e.g., juvenile, reproducing, old). (B) Mechanisms that may explain population-level relationships between age and behavior: individual plasticity without individual variability (all individuals behave and change their behavior in the same way); individual plasticity with individual variability (individuals differ in their average behavior but change it similarly with age); variation in behavior among individuals with no behavioral plasticity, instead, selective disappearance of individuals with a particular behavioral traits leads to population-level behavioral aging. These three mechanisms can apply to any of the patterns in A. Thick black lines are the population-level relationship between behavior and age and the thinner gray lines are individual-level relationships between age and behavior.

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).

In this study, our main goal is to examine patterns of behavioral aging 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 aging patterns in movement and social behaviors. To do so, we use a dataset of 15-y 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 y (29). Griffons have a low 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 centers, 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 behavioral aging 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 behavioral aging 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 hypothesized that site fidelity, movement routines, and social behaviors will change with age either gradually or more sharply early or late in life (Fig. 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 analyzed different measures of roosting behavior as a proxy for movement and social behavior [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 to 2022). Using a subset of 142 griffons, aged 0 to 24 y (Fig. 2B), that remained in the main study area and that were tracked for a minimum of 30 d and maximum of over 12 y (Fig. 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 whether these population-level behavioral changes

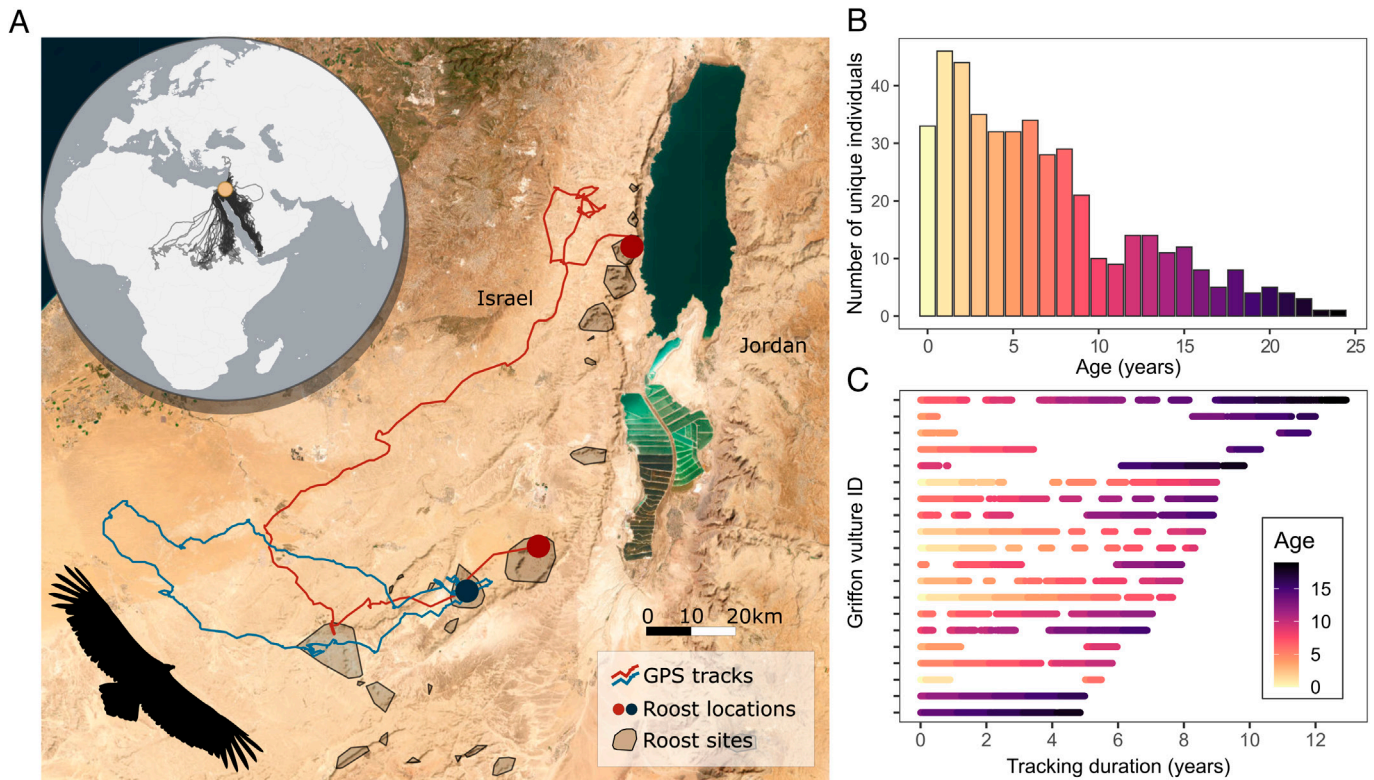


Fig. 2. Study area and GPS-tracking dataset. (A) Map showing GPS tracks of two griffon vultures in a single day: one individual remained at the same roost-site on consecutive nights (blue), and the other switched between roost sites on consecutive nights (red). The inset shows the location of the study area, as well as the movements of griffon vultures traveling 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 *SI Appendix, Fig. S7*. In *B* and *C*, colors indicate the age of each individual, with younger individuals represented in lighter colors.

arise from individuals changing their movement and social behaviors 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 behavioral aging.

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 y, 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 (Fig. 3A and *SI Appendix, Tables S1 and 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 (Fig. 2 and *SI Appendix, Fig. S1*). This population trend was mostly shaped by individual plasticity (individuals increasing roost fidelity throughout their lives, *SI Appendix, Fig. S2*) and not by selective disappearance, despite the slight, nonsignificant indication that individuals with higher roost fidelity may live shorter lives (Fig. 4 and *SI Appendix, 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 -> ... , Fig. 3B and *SI Appendix, Tables S4 and S5*). Furthermore, the strength of these roost-switching routines [index of routine (40)] increased exponentially - changing most drastically after the age of 15 y (Fig. 3C and *SI Appendix, Tables S6 and S7*). Due to the smaller sample size in this analysis, we could not evaluate whether this pattern emerged from individual plasticity or selective disappearance. Thus, we could not determine whether behavioral predictability provides a selective advantage over the course of an individual's 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.

Past research, from a single population in France, found that actuarial senescence (an increase in mortality rates) in griffon vultures starts at 28 y (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 y 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 behavior of older griffons emerge from changes in their breeding duties.

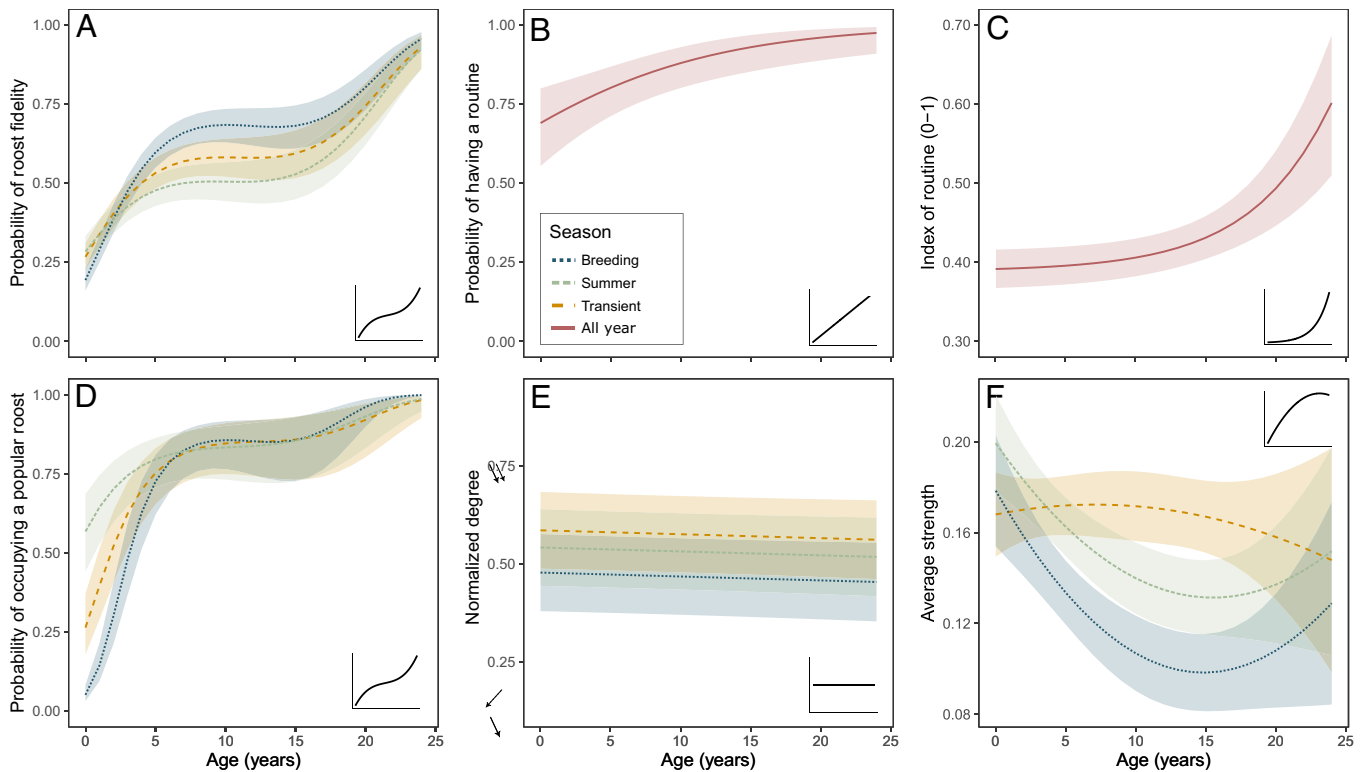


Fig. 3. Age-related changes in movement and social behavior of griffon vultures. Each panel A–F represents the model predictions, backtransformed to the original data scale, and the 95% CI for the effect of age on movement (A–C) and social behaviors (D–F): (A) probability of remaining at the same roost-site 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). Colors 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 Fig. 1.

However, to the best of our knowledge, there are 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 underlie behavioral aging. 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," Fig. 3D and *SI Appendix*, Tables S8 and S9), which tend to be closer to supplementary feeding stations (*SI Appendix*, Fig. 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 (Fig. 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 y 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 (*SI Appendix*, Fig. S2), despite the slightly, nonsignificant, lower longevity of the individuals that occupy the most popular roosts (*SI Appendix*, Fig. S4 and 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 whether 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.

Griffons Decrease the Strength of Social Relationships with Age.

In addition to the changes in movement behavior, there was also an effect of age on the social behavior of griffons. Contrary to studies in other species (24), the proportion of the population that an individual coroosted with (normalized degree) remained constant at all ages (Fig. 3E and *SI Appendix*, 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

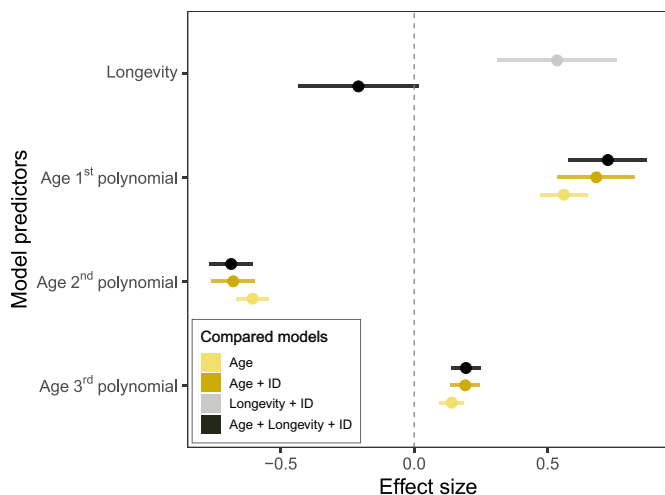


Fig. 4. Individual plasticity, rather than selective disappearance, shapes the increase in roost fidelity with age. To isolate the effect of individual plasticity (i.e., within-individual behavioral changes) from the effect of selective disappearance (i.e., between-individual behavioral differences and selection acting on different behaviors), 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 (gray); 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% CI of age (modeled 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 nonsignificant negative effect size for longevity, suggesting that behavioral 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 *SI Appendix, Fig. S4*.

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 y, during the breeding and summer seasons, but not during the transient season, suggesting that the breeding behavior of adult individuals limits their interaction rates (Fig. 3*F* and *SI Appendix, Tables S11 and 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 behavior would result in low average strength of social relationships between breeding individuals. Future studies analyzing the movement and social behaviors 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 behaviors are intertwined (47), the changes we observe in social behavior may also emerge from changes in spatial behavior 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 whether the population-level change in average strength resulted from individuals reducing their reliance on social information with age (6) or whether the pattern is due to the selective disappearance of individuals with higher average strength, for example, due to higher exposure to pathogens (1) (*SI Appendix, Figs. S2 and S4 and Table S3*).

Our results support our hypothesis that behaviors 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 analyzing behavioral aging in a multitude of vertebrate species (for example, nonhuman primates (2, 24), red deer *Cervus elaphus* (6), black kites *Milvus migrans* (25), among 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, behaviors that are commonly attributed to aging humans (49, 50). While we found that within-individual behavioral plasticity is a major driving force of behavioral aging in a long-lived bird, selection may still act on the rate of behavioral change, for example, by favoring individuals that change more drastically earlier in life (17, 25). At the population level, the rate of behavioral change, and its timing in life, seem to differ among behaviors: 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 behavior (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 behavior 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 behavioral changes from changes in the environment. Nevertheless, it is plausible that the observed sharp increase in behavioral 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 behaviors exhibited by older individuals can hamper the ability of populations to 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 (160 g E-Obs GmbH) and GPS-GSM Accelerometer transmitters (50 g Ornitrack from Ornitela) on 319 griffons in Israel, using Teflon harnesses in backpack (2008 to 2015) and leg-loop (2016 onward) configurations. Vultures were captured in cage traps (62) and a small fraction were released from rehabilitation centers, captive-breeding, and translocation programs (61). During tagging, all griffons were ringed with metal and color rings and marked with patagial tags for field identification. During capture, they were aged based on their morphological characteristics, including feather shape and molting patterns (flight feathers, great coverts, and neck ruff feathers), and the bill and eye colors (63, 64). Every year, about 100 griffons are trapped or retrapped; therefore, almost all individuals are aged when they are still younger than 4 y 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 y 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 y old. On average, their roost fidelity was not different from the cohort of 18 y old, and therefore, we assumed this was their average age (*SI Appendix, Fig. 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 (*SI Appendix, Fig. 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 457 d (min = 1, max = 2962, including only terminated deployments, *SI Appendix, Fig. S7*), and the median number of deployments per bird was 1 (mean = 1.5). Yet, one individual was redeployed with new GPS devices 6 times during its life. Overall, the gap between deployments was 543 d (min = 0 d, max = 3,622 d).

The GPS transmitters typically recorded location and ground speed every 10 min during the day (average 13 min, SD = 68 min), 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 1 Hz (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 50 m/s, or if two consecutive nighttime locations were over 10 km 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 (postbreeding 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 (67) and the data is available in Zenodo (68).

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 60 min 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 60 min 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 2 km 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 1 km 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 Fig. 2A). This analysis was performed using R package "fpc" (69).

Roost Fidelity and Routine Behaviors. 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 1 km and 20 km for considering two consecutive nights as using the same roost-site (*SI Appendix, Fig. 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 (*SI Appendix, Fig. S1*).

We then investigated movement routine for griffons that switched roosts within our main study area (Israel and surrounding areas: longitude 34.2 to 36.5, latitude 29.3 to 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 to 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 two roost locations) (*SI Appendix, Fig. S8*). In total, we identified six 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 whether the results were influenced by the popularity threshold, we repeated our analyses using 25% and 30% thresholds for roost popularity. We also investigated whether 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 (*SI Appendix, Fig. 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 (Fig. 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 (*SI Appendix, Fig. S10*).

Social Behavior. To quantify the social behavior 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 to 2022, *SI Appendix, Fig. 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 ($N = 20$ y-season combinations), in which vultures that roosted within 1 km 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 (70–72). 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 to 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 Behavior with Age. To evaluate the influence of age on the movement behavior of griffon vultures, we fitted a series of generalized linear mixed models (GLMMs), using the R package “glmmTMB” (73). We considered three response variables to describe the movement behavior 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 = 3,120). 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 d (6 mo) and again, only with individuals that were tracked for 365 d (1 y) or more (*SI Appendix, Fig. S12*). The results of both analyses did not differ from results of the full dataset (*SI Appendix, Figs. S13 and S14*). Overall, using the 30 d threshold, we identified the roost fidelity for 142 griffons (86,192 roost locations); we modeled the probability of routine for 135 griffons (627 roost switching sequences); and we modeled 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 behavior and age: linear ($y = ax + b$), quadratic ($y = ax^2 + bx + c$), exponential ($y = a^x$), and third-degree polynomial ($y = ax^3 + bx^2 + cx + d$) (Fig. 1). Depending on the behavior, these models may represent an increasing or decreasing relationship between behavior and age. We also fitted a null model with only random effects. We analyzed the model residuals using R package “DHARMA” (74). 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 analyze how age affects griffon vultures’ social behavior, 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 behavior 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 Behaviors. To assess the relative importance of selective disappearance and/or individual plasticity for shaping behavioral aging in movement and social behavior 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 to 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 mo, then it would be considered dead if it was not seen for 10 mo; if individual B was seen every 36 mo, then it would be considered dead if it was not seen for 180 mo). 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 y-gap since the last observation (for all individuals). All three age-at-death estimates provided similar results for the relative importance of longevity and behavioral plasticity (*SI Appendix, Figs. S15 and S16*). For the analysis of the mechanism of behavioral aging, 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 analyzed, 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 and 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 whether plasticity or selection drives the changes in average strength. To ensure that our results were not driven by the complex relationship between behavior and age, or by a nonlinear relationship between behavior 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 behavioral aging in griffons (SI Appendix, Table S13, Figs. S17, 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, Materials, and Software Availability. Analysis code is available at https://github.com/msa2015/Ageing_Vultures (67). The data are available in Zenodo, under the DOI: [10.5281/zenodo.10651582](https://doi.org/10.5281/zenodo.10651582) (68). The GPS coordinates were shifted a few kilometers from the original location to ensure species safety, while maintaining all geometric attributes needed for reconstructing the analyses.

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Author affiliations: ^aSchool of Zoology, Faculty of Life Sciences, Tel Aviv University, Tel Aviv, Israel; ^bDepartment of Ecology and Evolutionary Biology, University of California Los Angeles, Los Angeles, CA; ^cScience Division, Israel Nature and Parks Authority, Jerusalem, Israel; ^dDepartment for the Ecology of Animal Societies, Max Planck Institute of Animal Behavior, Konstanz, Germany; ^eMitrani Department of Desert Ecology, Jacob Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Midreshet Ben-Gurion, Israel; and ^fDepartment of Ecology, Evolution and Behavior, The Hebrew University of Jerusalem, Jerusalem, Israel

Author contributions: M.A., N.P.-W., and O.S. designed research; M.A., K.G., and O.S. performed research; M.A. and K.G. analyzed data; M.A. and K.G. critically revised the paper; N.A., G.V., R.H., and R.E. collected data; critically revised the paper; O.H. collected data; critically revised the paper; secured funding; R.N., N.P.-W., and O.S. critically revised the paper; Secured funding; and M.A. wrote the paper.

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