Individual and Population Age Impact Social Behavior and Network Structure in a Long-Lived Insect

Phoebe A. Cook,[1,2,*] Robin A. Costello,[1,2,3] Vincent A. Formica,[2,4,†] and Edmund D. Brodie III[1,2,†]

1. Department of Biology, University of Virginia, Charlottesville, Virginia 22904; 2. Mountain Lake Biological Station, University of Virginia, Pembroke, Virginia 24136; 3. Department of Biological Sciences, Auburn University, Auburn, Alabama 36849; 4. Department of Biology, Swarthmore College, Swarthmore, Pennsylvania 19081

ABSTRACT: Social behaviors vary among individuals, and social networks vary among groups. Understanding the causes of such variation is important for predicting or altering ecological processes such as infectious disease outbreaks. Here, we ask whether age contributes to variation in social behavior at multiple levels of organization: within individuals over time, among individuals of different ages, among local social environments, and among populations. We used experimental manipulations of captive populations and a longitudinal dataset to test whether social behavior is associated with age across these levels in a long-lived insect, the forked fungus beetle (*Bolitotherus cornutus*). In cross-sectional analyses, we found that older beetles were less connected in their social networks. Longitudinal data confirmed that this effect was due in part to changes in behavior over time; beetles became less social over 2 years, possibly because of increased social selectivity or reproductive investment. Beetles of different ages also occupied different local social neighborhoods. The effects of age on behavior scaled up: populations of older individuals had fewer interactions, fewer but more variable relationships, longer network path lengths, and lower clustering than populations of young individuals. Age therefore impacted not only individual sociality but also the network structures that mediate critical population processes.

Keywords: age, age structure, social behavior, animal social networks.

Introduction

Patterns of social interactions among conspecifics shape a variety of ecological and evolutionary processes, from the transmission of information and pathogens (VanderWaal et al. 2014; Aplin et al. 2015; Stroeymeyt et al. 2018) to the expression, fitness consequences, and heritability of traits (reviewed in Fisher and McAdam 2017; Brodie et al. 2022). Understanding the causes of variation in social behavior is therefore of use in a wide range of biological and sociological disciplines. In recent decades, animal social network analysis has been used to describe patterns of social interaction at multiple scales of organization, from the immediate neighborhood an individual experiences to its position in its population and up to the population-level structure of the network as a whole. Each of these levels has been demonstrated to have fitness consequences through natural (Bond et al. 2021), sexual (Schülke et al. 2010; Formica et al. 2021), social (Brodie et al. 2022), or multilevel (Barocas et al. 2011; Royle et al. 2012; Costello et al. 2023; Philson and Blumstein 2023) selection. Although significant progress has been made toward understanding the sources of variation in individual social behavior, much less is known about when and why network-level social structures vary in space and time. Here, we investigate the possibility that individual age may explain variation in social behavior at multiple scales of animal societies. Aging is often associated with a suite of phenotypic changes, many of which could produce changes in social behavior (reviewed in Siracusa et al. 2022a). The net costs of mating and other interactions could all change with age or stage and potentially change social network position (Rodrigues 2018). If reproduction or risk of mortality is age dependent, individuals may alter their investments in social behavior as part of their life history strategy (Tringali et al. 2020; Kroeger et al. 2021). Activity level and foraging patterns may also change, potentially resulting in shifts in social interactions. For example, red deer become less social with age, partially due to changes in home range size and location (Albery et al. 2022). Other mechanisms include cognitive changes; information accumulated over time can increase social competency and make older individuals sought-out social

* Corresponding author; email: pac6he@virginia.edu.
† Joint senior authors.
 ORCIDs: Cook, https://orcid.org/0000-0003-2108-0057; Costello, https://orcid.org/0000-0003-4528-2550; Formica, https://orcid.org/0000-0002-9709-5522; Brodie, https://orcid.org/0000-0001-9231-8347.

partners (Jaatinen and Öst 2011; Taborsky and Oliveira 2012). Alternatively, cognitive senescence can decrease the ability to learn new information, potentially making older individuals less valuable partners that are therefore avoided (Kulahci and Quinn 2019). All of these factors could create differences between old and young individuals in the social environments they experience and the positions they occupy within the overall population social network.

Individual behavioral change is not the only mechanism that can produce a relationship between age and social behavior. In humans and many other taxa, studies have found that sociality is correlated with life span, such that either more or less social individuals die earlier than others (reviewed in Korb and Heinze 2021). This selective disappearance means that the individuals surviving to old age represent a nonrandom sample of the initial population with respect to social behavior, creating a correlation between age and behavior. A similar result could be found if viability selection acts on a trait correlated with sociality, such as boldness. In any of these cases, social behavior will vary with age across individuals despite there being no within-individual change in behavior over time. Longitudinal analyses are often required to understand whether a filtering process or true individual changes due to aging are generating the covariance between age and social behavior.

At the level of the group, the composition of individual ages (or the age structure) can also vary among populations or subpopulations. The field of population dynamics has done extensive work on the factors producing variation in age structures. Across a metapopulation, the age structure of subpopulations may vary because of differences in recruitment (Cooper and Shanks 2011) and local environmental factors, such as predation regimes or harvesting (Miaud et al. 1993). Even within a population, age structure is not stable; fluctuations in age structure have been found to be of a similar magnitude to those in population size (Hoy et al. 2020).

Although there is a rapidly growing body of research on sociality and age, few studies have looked at levels of organization above the individual. The spatial and temporal variation in age structure suggests a possible source of variation in social networks: if individuals of different ages behave differently, we expect that the age structure of a population will shape its network structure and therefore the many processes mediated by these structures. Social network structures are known to depend on the frequencies of individual physiological and behavioral traits (Cantor et al. 2021; Cook et al. 2022), and there is a growing body of knowledge about age-related behavioral changes, but to our knowledge no work has connected the two.

We used an experimental approach to study the relationship between age and social interactions at several levels of social organization in a long-lived insect. Insects make up over half of all described species (Mayhew 2007) and contain enormous inter- and intraspecific variation in both social behavior and life span. Despite this rich diversity, most studies of age in insects are limited to lab studies of *Drosophila* (Brenman-Suttner et al. 2020; Guo et al. 2020; Zajitschek et al. 2020; Quigley and Amdam 2021), and comparatively few have examined aging or senescence in the wild (but see Bonduriansky and Brassil 2002; Hassall et al. 2015; Rodríguez-Muñoz et al. 2019). The forked fungus beetle (*Bolitotherus cornutus*) has been suggested as suitable for studies of aging and age-related variation in natural conditions (Zajitschek et al. 2020). Screened enclosures placed in the beetle's natural habitat closely match natural conditions while eliminating extrinsic mortality from predation. These mesocosms allow us to create replicate experimental populations, a powerful tool for understanding the drivers of variation in network structure (Krause et al. 2010; Smith et al. 2019). Using this approach, we manipulated the age structure of populations to test whether there is a relationship between individual age and social behavior and whether the composition of ages within a group alters the structure of the group social network. We then used a multi-year longitudinal dataset to test whether observed age-related behavioral differences were due to behavioral changes as individuals aged.

Material and Methods

Study System

Bolitotherus cornutus is a tenebrionid beetle that lives on wood-decaying shelf fungi in the forests of eastern North America (Liles 1956). In the wild, they live clustered together in subpopulations on resource patches created by fallen logs. These fungi provide food, shelter, oviposition sites, and arenas for social interactions (Pace 1967). Larvae, pupae, and newly eclosed adults develop inside the fungus fruiting bodies, or "brackets," for months to years before emerging as sexually mature adults (V. A. Formica and E. D. Brodie III, unpublished data). After emergence, many individuals survive for only one breeding season, but some live as long as 5 years (Brown and Rockwood 1986). Adult age is calculated from the year of emergence and does not include the period of development within the fungus bracket. Because they are holometabolous, adults do not grow in size as they age.

The age structure of forked fungus beetle subpopulations is highly variable. In the Pond Drain metapopulation near Mountain Lake Biological Station in southwestern Virginia, where beetles have been exhaustively collected and labeled since 2015, the proportion of adult beetles on a single log that are more than 1 year old ranges from 5% to 64% (V. A. Formica and E. D. Brodie III, unpublished data). This

variation may be caused by the age of the resource patch, local predation regimes, dispersal patterns, and other processes. Nothing is yet known about the consequences of age structure at the subpopulation level in this species.

At the individual level, variation in age is known to be associated with variation in dyadic social behavior. Older individuals of both sexes participate in more courting and mating interactions (Conner 1989*b*; V. A. Formica and E. D. Brodie III, unpublished data). Older males initiate more aggressive interactions than younger males (L. D. Mitchem, V. A. Formica, and E. D. Brodie III, unpublished data), which may make them more likely to win fights in male-male contests (Mitchem et al. 2019). It is unknown whether these differences between ages are caused by longitudinal change, differential survival, or both.

Experimental Design

We established a captive breeding population of *B. cornutus* at Mountain Lake Biological Station (37°22′37.0″N, 80°31′17.5″W) that was founded with wild beetles collected from the surrounding area in autumn 2017 and spring 2018. We created 12 experimental populations of 36 beetles each and surveyed their social interactions for 3 weeks for a different research project in summer 2018 (Costello et al. 2022, 2023). Although the exact age of these wild-caught founders is unknown, we know their minimum age from their time of capture. Several years of field surveys of a nearby metapopulation have found that 60% of all observations are of individuals not observed in previous years (V. A. Formica and E. D. Brodie III, unpublished data), so this minimum is likely correct for the majority of individuals and conservative for the rest. For the next 2 years, we allowed all beetles to breed and deposit eggs on fungus brackets in screen enclosures exposed to natural abiotic conditions. Adults were shuffled among enclosures to mimic natural migration and promote genetic diversity. Offspring developed inside the old fungus brackets until emergence, just as in the wild. Each year, we searched the populations for newly emerged offspring and marked them with a unique three-character code affixed to their elytra with a ultraviolet-cured acrylic epoxy (Tuffleye; Wet A Hook Technologies, San Antonio, TX). Beetles captured as adults in early spring were assumed to have emerged late in the previous year and to therefore be 1 year old.

By late summer 2020, we had three age cohorts: young of the year (hereafter, "first-years") newly emerged earlier that summer, 2-year-olds first caught in spring 2019, and beetles wild caught in 2017 or spring 2018 and therefore at least 3 years old. Note that we are excluding 1-year-olds, meaning beetles that had emerged in autumn 2019 and overwintered, because sampling was not possible during early spring 2020 due to pandemic constraints.

In August 2020, we tested the effects of both individual age and social group age on behavior by creating two different experimental treatments. We replicated our methodology from 2018 to create 12 experimental populations of 36 beetles each, but this time with six replicates in both of the two treatments. The six "young" populations consisted of 18 first-years and 18 beetles that were 2 years old, and the six "old" populations consisted of 18 beetles that were 2 years old and 18 that were 3 (or more) years old. These compositions approximate two ends of the range in age structure observed in natural populations.

We minimized differences among these populations in sex ratio, body size, relatedness, and past interaction history. The body size of each individual was measured as the length of the elytra from an image taken on a flatbed scanner (Epson Perfection V600 Photo) using ImageJ (Abràmoff et al. 2004). We then used structured sampling from sex- and age-specific size quantiles to create populations that had equal sex ratios and did not differ from each other in body size ($F_{11, 402} = 0.21, P = .997$; for details, see the supplemental material of Cook et al. 2022). This process was repeatedly simulated until the population assignments also minimized the number of beetles placed together that had overwintered or emerged from the same enclosure. All were held in isolation for at least 7 days before the start of the experiment, which past studies suggest is enough time for patterns of social interaction to "reset" (Formica et al. 2017).

In both 2018 and 2020, populations interacted freely within 2.4 × 2.4 × 1.2-m screened experimental enclosures built to mimic natural resource patches in the forest. Enclosures contained mulch floors and artificial logs, which were wooden shelving units holding 54 bags of hardwood sawdust. Eighteen of those bags were inoculated with the same strain of the *B. cornutus* host fungus species *Ganoderma tsugae* (Sharondale Mushroom Farm) and allowed to produce brackets. These shelves mimic the logs on which beetles live in the wild but with fungus age, size, genotype, and spacing all controlled so as not to vary between populations (for details, see Costello et al. 2022). Population densities were within the range observed in wild populations (Conner 1989*a*). The screened enclosures were placed in an area of forest where this species naturally occurs and were exposed to natural abiotic conditions. At the start of the experiment, individuals were allowed to acclimatize to the enclosures for 36 h before behavioral observation began. After acclimatization, we performed scan sampling of all activity and dyadic interactions three times a day (0630–0930, 1430–1630, and 2130–0030 hours) for 21 days. Any beetles that were visible to observers had emerged onto an exposed surface and were considered active; beetles that were not visible to observers were assumed to be sheltering within fungus brackets or tight crevices, with very little

space for locomotion or social interaction. Individuals were defined as social partners if they were in physical contact or close proximity (within 5 cm) of one another, following past work in this system (Formica et al. 2012). Courtship and mating interactions were excluded because they are not included in measures of sociability (Gartland et al. 2022).

Both the order in which populations were surveyed and the individual observer identity were randomized to control for possible time and observer biases. Observers in 2020 could not be made fully blind to the age composition treatment because the individual identification codes used to label beetles have progressed in a predictable sequence over the years. However, the majority of the observers were not aware of the questions that would be answered with the data, and a priori predictions as to the direction of effects had not been made when data collection was underway.

Network Creation

We constructed a social network from the nonmating interactions, as defined above, between all individuals in each of the 12 populations. Ties in these networks are undirected and weighted by the simple ratio index, which describes associations as the fraction of times that a pair was observed together out of the total observation periods where at least one individual was observed (scored as active, see above; Ginsberg and Young 1992). Our 63 observation periods are sufficient to estimate association strengths precisely (Whitehead 2008).

Twenty-three beetles died during the 3 weeks of sampling in 2020: 3 of 108 first-years, 6 of 219 beetles that were 2 years old, and 14 of 110 beetles that were 3 years old or older. The five that died in the first 3 days of surveying were replaced with beetles of the same age, sex, and size. Individuals that died were included in the networks for accurate description of social structures and environments but were removed from other analyses. Any observations that could not be confidently assigned to an existing beetle ID (e.g., if an ID label was not readable) were excluded from network creation to avoid the creation of false nodes. Networks were visualized using the R package igraph (Csardi and Nepusz 2006). All analysis was performed in R version 4.1 (R Core Team 2021).

Age and Network Position: Cross-Sectional Analysis

We compared three measures of social network position between beetles of different ages in the 2020 experimental populations. Network strength (hereafter, "strength") is a measure of local connectivity, quantifying the number and weight of all of a node's ties. In accordance with past work

in this system (Formica et al. 2012), we calculated strength using a tuning parameter of 0.5, meaning that each additional partner increases strength by 1 and repeated interactions between the same partners increase strength by 0.5 each (Opsahl 2009). An individual that interacts often and with many partners would have high strength. Betweenness measures an individual's centrality in the overall network as the number of the shortest paths between all other members of the population that pass through that individual. Individuals along paths connecting many dyads in the population have high betweenness. Clustering coefficient is a measure of cliquishness, calculated as the proportion of an individual's social partners that interact with each other (Croft et al. 2011). Strength and betweenness are often somewhat correlated, which may be because they capture different aspects of an underlying tendency to be socially central. These metrics have previously been shown to be under strong, highly variable selection in this species (Formica et al. 2012, 2021), and strength and betweenness are known to be repeatable on the scale of weeks (Formica et al. 2017).

We modeled each of these three metrics of network position using generalized linear mixed models. We treated age as a categorical variable. Body size and number of times seen have previously been shown to covary with social behavior in this system (e.g., Costello et al. 2023), so these variables were included in the model. To improve model fits, both were globally standardized across all individuals, such that the mean of all values was 0 and the standard deviation was 1. A sex-by-age interaction allowed us to test whether the relationship between age and sociality differs between males and females. We did not include other interaction terms because we had no a priori reasons to do so. A fixed effect of the age composition treatment (young or old population) allowed us to test for effects of group age structure on individual network position. Last, a random effect of population was included. Sample size was 414 for strength and betweenness but 396 for clustering coefficient, which can be calculated only for individuals that interact with two or more social partners. The strength and clustering models were fitted with a Tweedie error distribution, and the betweenness model was fitted with a negative binomial distribution, in the R package glmmTMB (Brooks et al. 2017). All three models assumed that zero inflation was constant across the dataset, with a single intercept dispersion term. Assumptions of residual homogeneity, dispersion, and zero inflation were tested visually and statistically with DHARMa (Hartig 2021). Marginal means were calculated and compared in post hoc tests using the emmeans package (Lenth 2023). No model simplification was used; inferences were made from the full fitted models including interaction terms.

There is currently debate over how best to test hypotheses in social network data, which are inherently

nonindependent. Various permutation approaches have been proposed (Croft et al. 2011; Farine and Whitehead 2015; Farine 2017) and critiqued (Farine and Carter 2022). Of these, node permutation approaches are less prone to false positive errors than datastream permutation approaches and may be appropriate when datasets are complete and free of observation biases (Puga-Gonzalez et al. 2021; Weiss et al. 2021*a*). Our experimental setup, labeling, and observation methods were designed to meet these criteria (see Costello et al. 2022). However, new work suggests that node permutations analyses still violate the assumption of exchangeability of residuals and do not perform better than standard regression approaches (Hart et al. 2022). In addition, standard regression approaches have the advantage of allowing the calculation of accurate effect sizes. Therefore, in the main text we present the results of our generalized linear mixed models run only in the observed data. To confirm that our results are robust to this choice of method, we also used a node permutation approach in which we compared our observed results to the distribution of results from the same models run in 10,000 node-permuted datasets. Details and results of this method are presented in the supplemental PDF. In both cases, our models included a random effect of population. Although this does not solve the issue of nonindependence, it does account for some of the potential similarities of network metrics among members of the same network.

We measured effect sizes for all fixed effects in our models with Cohen's f^2 (Cohen 1988). Cohen's f^2 measures how much variance is explained by each fixed effect relative to the variance unexplained by the model. We measured variance explained by each full or partial model using Nakagawa's marginal R^2 in the R package performance (Nakagawa et al. 2017; Lüdecke et al. 2021). In our interpretation, we follow Cohen's guidance to consider $f^2 \geq 0.15$ as moderate and $f^2 \geq 0.35$ as large.

Age and Social Network Position: Longitudinal Analysis

In a post hoc analysis made after the above analyses were completed, we asked whether differences in social network position among age classes are due to longitudinal changes over an individual's lifetime rather than to an association between social behavior and early mortality. The 96 individuals in the 2020 experiment that were at least 3 years old had all been phenotyped using the same experimental methods and group sizes as in 2018, so we were able to calculate the change in their number of social partners (network degree). To account for weather and other factors that might influence activity level, we compared this change to the difference between the 2018 and 2020 yearly baseline groups. We calculated the differences in degree between one set of 96 randomly selected young beetles in 2018

and another in 2020. We then used a two-sided *t*-test to ask whether the within-individual changes in sociality over time were greater than the differences between randomly selected young beetles during the 2 years. Unlike the cross-sectional analyses described above, this analysis could not include a random effect of population because individuals did not remain in the same group.

Individual Age and Age of Social Partners

Returning to the cross-sectional dataset, we asked whether individuals assort by age, such that an individual's age is associated with the age of their local social environment. Such phenotypic correlations between interactants can influence the outcomes of social selection. Note that this is different from the network measure "assortativity" (Brodie et al. 2022). The mean age of social partners, weighted by the frequency of interaction with each partner, was calculated for each individual and then compared between age classes using *t*-tests. Because a positive correlation across treatments could be an artifact of design in which similarly aged individuals were deliberately sorted together, we analyzed each treatment separately, examining patterns of association within the old and young populations.

Population Age Structure and Network Metrics

We tested whether population age structure affects five metrics of global network structure. The total number of interactions is simply how many nonmating social interactions occurred. Tie density quantifies how many of all possible dyads interacted, and the coefficient of variation of tie weight measures how unevenly interactions were distributed among those pairs. Global clustering coefficient is determined by how many possible triads are closed. The average shortest path length measures how closely linked the network is. Tie densities were calculated in the package igraph (Csardi and Nepusz 2006), and weighted clustering and shortest path lengths were calculated in the package tnet (Opsahl 2009).

Unlike individual-level metrics, measures of network structure are independent of one another (Croft et al. 2011). The comparison for groups of equal size sampled with equal effort under the same conditions is simple, as the null hypothesis is that network structures do not differ because of nuisance effects (James et al. 2009; Farine and Carter 2022). We used two-sided *t*-tests to compare each of the five network metrics between the age treatments, with six replicates in each treatment. A similar experiment with only 10 populations showed significant effects of manipulating group composition—in that case, with regard to individual personality rather than age—on four of these metrics (Cook et al. 2022), suggesting

that this design and sample size are powerful enough to detect large differences in network structures between treatments.

Results

Our final dataset consists of 12 networks composed of 2,986 nonmating interactions among 414 beetles (fig. 1). Individuals were observed, and therefore considered active, in an average of 44 of 63 surveys (range = 4–63), and the number of observations of active beetles did not differ between the old and young populations ($t = -0.80$, df = 9.89, $P = .44$). Beetles interacted with an average of nine unique social partners but with as few as zero and as many as 21. They varied in strength (mean = 1.58, SD = 0.80), betweenness (mean = 22, SD = 27), and clustering coefficient
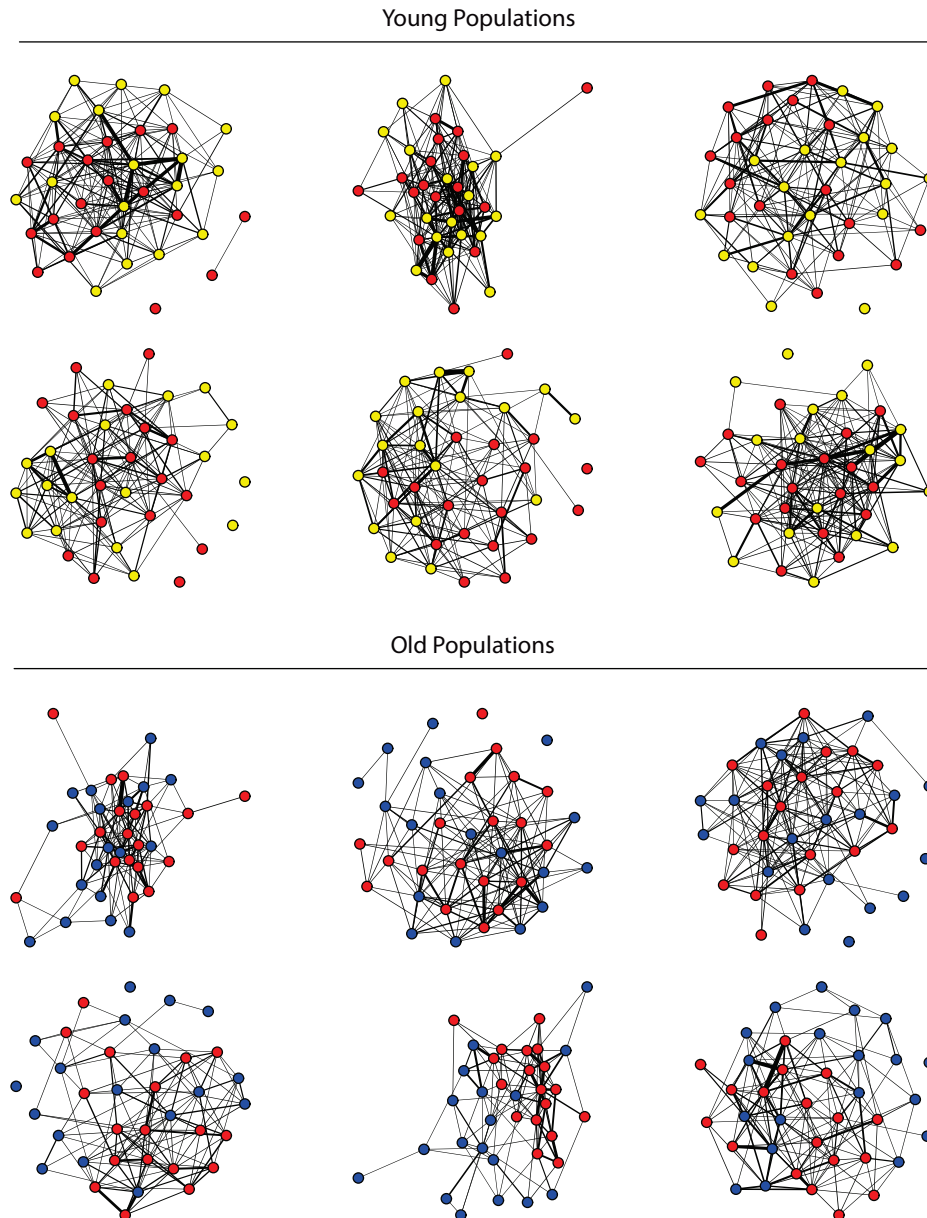
Young Populations

Old Populations

Figure 1: Networks from six young populations composed of first-years (yellow nodes) and 2-year-olds (red nodes) and six old populations composed of 2-year-olds and beetles 3 years old or older (blue nodes). Tie thickness is proportional to the simple ratio index, and nodes are plotted using the Fruchterman-Reingold layout algorithm, which places tightly connected pairs close together. Three-year-olds have fewer connections and are less central to their networks than members of the other age classes. Old populations have sparser and more variable ties, fewer closed triads, and longer paths between individuals than young populations.

Table 1: Predictors of individual network strength

	Estimate ± SE	*F*	*P*	Effect size (*f*²)
Fixed effect:				
Body size (mm)	−.02 ± .03	.3	.546	.01
Scans active	.13 ± .03	25.7	**<.001**	.21
	Mean (95% CI)			
Individual age		24.1	**<.001**	.29
First-years	1.67 (1.48–1.88)			
2 years old	1.69 (1.55–1.84)			
≥3 years old	1.17 (1.02–1.34)			
Sex		3.0	.082	.03
Female	1.56 (1.42–1.70)			
Male	1.42 (1.30–1.56)			
Individual age × sex	...	.2	.909	.01
Population age composition		3.6	.056*	.60
Young	1.61 (1.44–1.80)			
Old	1.38 (1.23–1.54)			
	Variance	SD	*N*	
Random effect:				
Population ID	.010	.099	12	

Note: Unstandardized estimates (slopes) ± SEs are reported for continuous variables, and back-transformed marginal means with 95% confidence intervals (CIs) are reported for categorical variables. *P* values below the $\alpha = .05$ level are indicated in bold. Marginal *P* values are indicated with an asterisk. Total number of individuals = 414.

(mean = 0.41, SD = 0.16, with 18 beetles not having a defined value). Strength was positively correlated with betweenness ($r = 0.60$, $t = 15.2$, df = 412, $P < .001$) but not clustering coefficient ($r = 0.08$, $t = 1.65$, df = 394, $P = .10$), while betweenness and clustering coefficient had a slight negative correlation ($r = -0.16$, $t = -3.25$, df = 394, $P = .001$).

Age and Individual Network Position

The oldest beetles in our experimental populations had lower strength than first-years and 2-year-olds (post hoc test of marginal means: $t = -0.21$, df = 402, $P = .977$; table 1; fig. 2) and lower betweenness than 2-year-olds (post hoc test of marginal means: $t = -0.21$, df = 402,
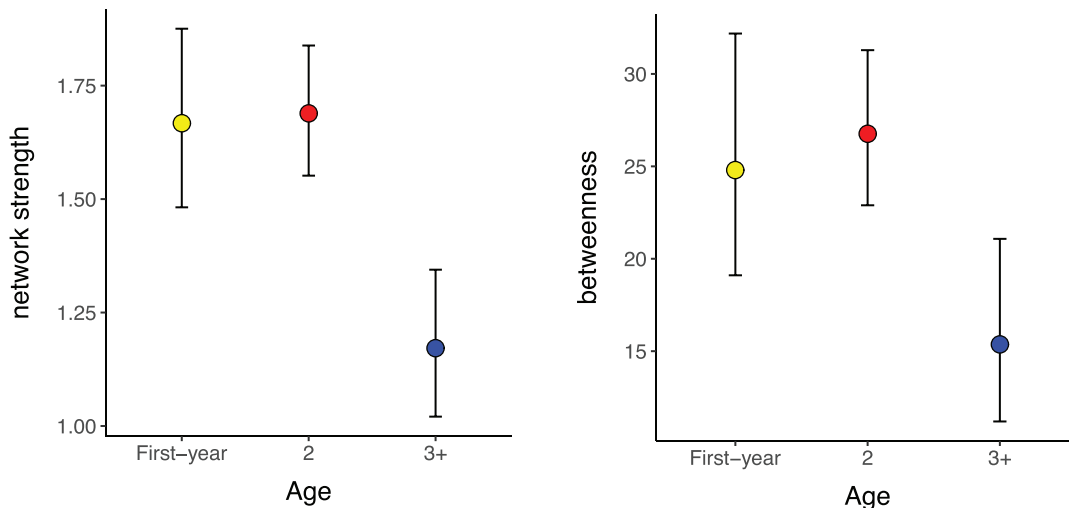

Figure 2: Back-transformed marginal means of network strength (*left*) and betweenness (*right*) for the three age cohorts. The sexes have been combined here because the effects do not differ significantly by sex. Error bars represent 95% confidence intervals. First-years (yellow points) and 2-year-olds (red points) occupy similar network positions. The oldest age class (blue points) has significantly lower strength than first-years and 2-year-olds and lower betweenness than 2-year-olds.

Table 2: Predictors of individual betweenness

	Estimate ± SE	F	P	Effect size (f^2)
Fixed effect:				
Body size (mm)	.01 ± .96	.0	.838	.00
Scans active	.25 ± .06	17.9	**<.001**	.06
	Mean (95% CI)			
Individual age		10.9	**.004**	.03
First-years	24.8 (19.1–32.2)			
2 years old	26.8 (22.9–31.3)			
≥3 years old	15.4 (11.2–21.1)			
Sex		3.7	.054[*]	.01
Female	24.4 (20.5–29.1)			
Male	19.3 (15.8–23.5)			
Individual age × sex	...	.8	.666	.00
Population age composition		4.8	**.029**	.01
Young	18.7 (15.2–22.9)			
Old	25.2 (20.9–30.4)			
	Variance	SD	N	
Random effect:				
Population	<.001	<.001	12	

Note: Unstandardized estimates (slopes) ± SEs are reported for continuous variables, and back-transformed marginal means with 95% confidence intervals (CIs) are reported for categorical variables. *P* values significant at the $\alpha = .05$ level are indicated in bold. Marginal *P* values are indicated with an asterisk. Total number of individuals = 414.

$P = .877$; table 2; fig. 2) but did not differ from younger beetles in clustering coefficient (table 3). There was no significant interaction between age and sex in any model, meaning that these patterns did not differ between males and females. Individuals in the older populations had higher betweenness (population age composition effect; table 2), and there was a nonsignificant trend toward lower individual strength in these populations as well

Table 3: Predictors of individual clustering coefficient

	Estimate ± SE	F	P	Effect size (f^2)
Fixed effect:				
Body size (mm)	.01 ± .02	.5	.478	.01
Scans active	−.03 ± .02	2.2	.135	.07
	Mean (95% CI)			
Individual age		.8	.656	.04
First-years	.413 (.377–.452)			
2 years old	.422 (.396–.451)			
≥3 years old	.404 (.366–.446)			
Sex		.3	.616	.02
Female	.409 (.383–.437)			
Male	.417 (.390–.445)			
Individual age × sex	...	.5	.791	.02
Population age composition		1.9	.164	.32
Young	.431 (.397–.469)			
Old	.395 (.363–.430)			
	Variance	SD	N	
Random effect:				
Population	.005	.076	12	

Note: Unstandardized estimates (slopes) ± SEs are reported for continuous variables, and back-transformed marginal means with 95% confidence intervals (CIs) are reported for categorical variables. Total number of individuals with a measurable clustering coefficient = 396.

(table 1). Interestingly, the effect size of the relationship between population age composition and individual strength is large (Cohen's $f^2 = 0.60$) but nonsignificant, which suggests the possibility that the sample size was too small or the data too variable to detect an existing relationship. There is also a small to moderate but nonsignificant effect of population age composition on clustering coefficient (Cohen's $f^2 = 0.32$). Beetles observed more frequently had higher strength and betweenness (number of scans active; tables 1, 2) but not a higher clustering coefficient (table 3), and all effect sizes of activity level were small.

All tests of statistical significance in the cross-sectional study were qualitatively identical and quantitatively very similar whether or not node permutations were used (compare tables 1–3 with tables S1–S3).

In the longitudinal data, the 96 beetles phenotyped in both 2018 and 2020 declined in the number of social partners they interacted with over that time, from an average of 12.4 social partners during a 3-week study period in 2018 to 7.0 partners 2 years later (fig. 3). This average 5.4-partner decline was significantly greater than the average 1.9-partner difference in network degree between the baseline groups of randomly selected young beetles ($t = -3.77$, df $= 185.68$, $P = .002$).
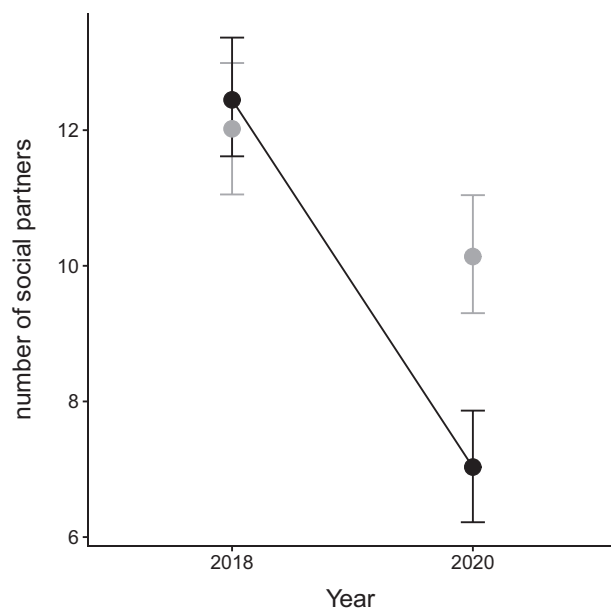

Figure 3: Change in the number of social partners (network degree) over time for the same individuals phenotyped in both 2018 and 2020 (black points, connected by the line) compared with that for the two groups of randomly selected young beetles in each year (gray points). Error bars represent bootstrapped 95% confidence intervals around means.

Individual Age and Age of Social Partners

In both treatments, individual age was positively associated with the mean age of the social partners with whom they interacted. In populations composed of younger beetles, first-years interacted with younger partners than did 2-year-olds ($t = -6.97$, df $= 199.08$, $P < .0001$). In populations composed of older beetles, 2-year-olds had lower mean social partner ages than beetles 3 years old or older ($t = -3.63$, df $= 170.29$, $P = .0004$).

Population Age Structure and Network Metrics

Populations in the two age composition treatments differed in every group-level network metric we tested (figs. 1, 4). Populations composed of older individuals had fewer nonmating interactions ($t = -3.34$, df $= 6.72$, $P = .01$), lower tie densities ($t = -3.92$, df $= 8.65$, $P = .003$), higher variation in tie weight ($t = 3.18$, df $= 8.28$, $P = .012$), lower global clustering ($t = -2.27$, df $= 9.14$, $P = .049$), and longer average shortest path lengths ($t = 4.98$, df $= 9.26$, $P < .001$) than populations with younger average ages.

Discussion

We found that age explains variation in social behavior at multiple scales. At the individual level, we found a correlation between age and social network position, caused at least in part by within-individual change to interact with fewer partners over time. Additionally, we found a positive relationship between individual age and age of social partners, meaning that beetles of different ages experienced different local social environments even within the same population. At the group level, population age composition determined overall social network structure. This is, to our knowledge, the first demonstration that group age structure shapes emergent social structures and, potentially, processes that network structures mediate, such as social selection and disease transmission. The combination of our longitudinal data, experimental manipulation, and analysis at multiple scales allows us to understand both the causes and the consequences of age-related variation among individuals.

Age and Network Position

Older beetles of both sexes were less connected and occupied more peripheral social positions in their populations than younger beetles. The fact that these two aspects of social network position are correlated suggests that they both may measure the same underlying behavioral
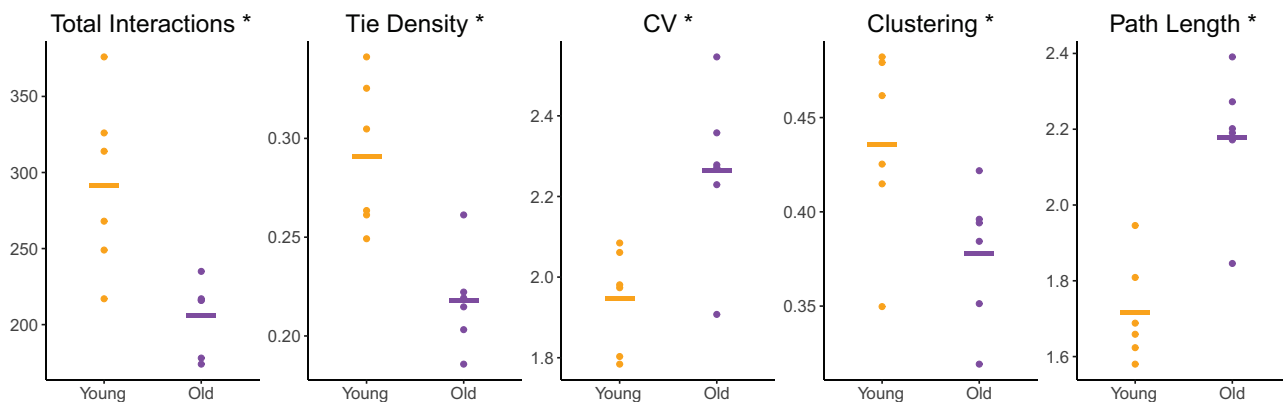
Figure 4: Five metrics of group network structure for the 12 experimental populations, by age composition. Each point represents a network of 36 individuals, and horizontal lines mark means. Asterisks denote metrics that differ significantly between the young and old populations. CV = coefficient of variation.

difference between age classes. In the cross-sectional analysis, we saw that beetles in the oldest age class had lower strength than those in the other age classes, even in a model controlling for the number of times individuals were observed to be active. These same beetles declined dramatically over time in their number of unique social partners, much more so than could be accounted for by differences in baseline activity rates between the 2 years. We therefore conclude that individual social network position changes longitudinally. This change does not rule out the possibility that selective disappearance could also occur if natural selection acts on social traits, either reinforcing the within-individual change (if individuals that remain highly social as they age are more likely to die) or opposing it.

A similar decline in social connectivity with age has been interpreted as social senescence in red deer (Albery et al. 2022), but there are several reasons not to assume that a reduction in nonmating interactions constitutes deterioration in all cases. First, they may simply be reducing their movement and coming into contact with fewer social partners. Alternatively, they may be more efficiently converting an initial contact into a mating. Both competitive ability and mating success increase from the first to third year of adulthood in forked fungus beetles (Mitchem 2021; V. Dos Anjos and V. A. Formica, unpublished data). Instead of senescing, beetles may be shifting their energy into mating interactions instead of nonmating interactions, which expose them to costs such as disease without major fitness benefits (Siracusa et al. 2022*a*). Therefore, we do not consider the patterns we see to be equivalent to those seen in red deer. More studies in a wide range of taxa may help us identify both diversity and similarity of age-related social changes (Machanda and Rosati 2020).

Longitudinal changes in social behavior might be due to social experience accumulated over time or change intrinsic to aging. A plausible source of such intrinsic change often invoked in life history evolution is the increased risk of mortality with age (Promislow and Harvey 1990). Although this experiment was not designed to measure survivorship curves and extrinsic mortality from predation was limited by the enclosures, we do observe that mortality during the experiment was higher in our oldest age class than in the younger two age classes. Further work could investigate whether this effect holds; if older individuals do indeed have higher mortality, they might be altering their behavior as part of a terminal investment strategy. Regardless of the cause, reduced social connectivity likely means that older beetles have lower exposure to parasites, pathogens, and social information than young ones.

Individual social network position also depended on the age composition of the population. There was a large but nonsignificant effect that individuals in the younger populations had higher strength, which is consistent with the finding from the longitudinal analysis that beetles decrease in strength over time. However, individuals in younger populations had lower betweenness centrality, despite the fact that young individuals tended to be more central to their networks. This result is not as paradoxical as it may appear. Populations with younger age structures tended to be quite well and evenly connected, as seen in their high tie density and global clustering, and therefore connections were not tightly funneled through a few highly central nodes. This pattern suggests that the most central individuals were the relatively young members of old populations, which potentially exert high influence on flows of parasites, pathogens, or information through the network. More generally, our results suggest that both individual age and

population age structure are axes of variation that we must account for in studies of social behavior.

Individual Age and Age of Social Partners

Individual age was weakly but positively correlated with the age of social partners, suggesting a positive assortment by age even among the artificially constrained social options offered in the experimental enclosures. This assortment may reinforce effects of age on social behavior because the most and least social age groups tend to interact with similarly behaving partners. Similar patterns of age homophily are documented in many other systems (Lusseau and Newman 2004; Wey and Blumstein 2010; Ozella et al. 2020; Weiss et al. 2021*b*). Age homophily might be due to passive processes, such as older beetles sharing similar resource use and activity patterns because of age-related changes; active processes, such as assortative mate preferences or younger individuals avoiding competitive interactions with aggressive older beetles; or cohort effects (Brodie et al. 2022). Whatever the mechanism, the outcome is that individuals of different ages experience different social environments, even within the same population. The fitness consequences of social interaction may depend on the age of social partners (Rodrigues 2018), and the pattern of assortment will determine the effects of social selection (Brodie et al. 2022).

Population Age Structure and Network Metrics

The individual-level effects of age scale up, such that the age structure of a population shapes its global social network structure. Populations of older individuals had fewer and more variably weighted ties, longer path lengths, and lower clustering than populations of young individuals. We note that group clustering was affected by group age composition, even though we did not detect a relationship between individual clustering and individual age, which highlights the importance of studying social behaviors at multiple levels of organization (see also Costello et al. 2022). Although mortality was higher in the oldest age class, we do not think these midexperiment deaths can account for the substantial differences in network structures we observe. Populations of old beetles had the same number of total observations of active beetles as populations of young beetles but still differed in the number of social interactions and how these interactions were distributed through the population.

Social network structure is hypothesized to change population processes, such as disease transmission, that affect individual fitness (reviewed in Kurvers et al. 2014), and a few studies have shown evidence of multilevel selection on network structure (Royle et al. 2012; Costello et al.

2023). Further work should investigate whether population age structure alters group member fitness via effects on network structure. If so, this would be a novel path by which age structure can affect population dynamics.

The tie density and tie strength results suggest that beetles shift from interacting indiscriminately early in life to having fewer and less randomly distributed social ties as they age. This fits the pattern of increasing social selectivity with age, a phenomenon that is well documented in humans and seen in other mammals (Almeling et al. 2016; Rosati et al. 2020; Siracusa et al. 2022*b*; reviewed in Siracusa et al. 2022*a*) and potentially beneficial for any long-lived species with a slow pace of life (Silk and Hodgson 2021; but see Machanda and Rosati 2020; Bond et al. 2021; Aubier and Kokko 2022). Other recent studies may identify related trends, despite their wide diversity of systems and methods: older female eiders form smaller brood-rearing coalitions (Jaatinen and Öst 2011), older elephants have more stable network positions (Murphy et al. 2020), garter snakes become more selective in their associations over time (Skinner and Miller 2020), and older Arabian babblers occupy more similar positions across multilayer interactions than young individuals (Dragić et al. 2021). A larger body of data on sociality and aging in diverse long-lived organisms will help shed light on whether these are truly comparable trends and perhaps even represent similar mechanisms operating across species. We encourage other researchers to devote more attention to age in studies of social structures.

Statement of Authorship

P.A.C. contributed to conceptualization, funding acquisition, data curation, formal analysis, investigation, experimental design, project administration, software development, analysis and visualization, writing—original draft, and writing—review and editing. R.A.C. contributed to methods development, project administration, software development, and writing—review and editing. V.A.F. contributed

to conceptualization, funding acquisition, methods development, analysis, supervision, and writing—review and editing. E.D.B. contributed to conceptualization, funding acquisition, methods development, supervision, and writing—review and editing. All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Data and Code Availability

Data and code are available from the Dryad Digital Repository (https://doi.org/10.5061/dryad.8931zcrt2; Cook et al. 2023).

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A proximity interaction between two adult *Bolitotherus cornutus* on the lip of a fungus bracket. Photo credit: Hazel Galloway.