

1 **Sex-specific competitive social feedback amplifies the role of early life contingency in male** 2 **mice**

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6 **Abstract:** Contingency (or ‘luck’) in early life plays an important role in shaping individuals’
7 development. When individuals live within larger societies, social experiences may cause the
8 importance of early contingencies to be magnified or dampened. Here we test the hypothesis that
9 competition magnifies the importance of early contingency in a sex-specific manner by comparing
10 the developmental trajectories of genetically identical, free-living mice who either experienced high
11 levels of territorial competition (males) or did not (females). We show that male territoriality results
12 in a competitive feedback loop that magnifies the importance of early contingency and pushes
13 individuals onto divergent, self-reinforcing life trajectories, while the same process appears absent
14 in females. Our results indicate that the strength of sexual selection may be self-limiting, as within-
15 sex competition increases the importance of early life contingency, thereby reducing the ability of
16 selection to lead to evolution. They also demonstrate the potential for contingency to lead to
17 dramatic differences in life outcomes, even in the absence of any underlying differences in ability
18 (‘merit’).

19 **Main:** Contingency (colloquially called ‘luck’ or ‘chance’) has long been recognized as an important
20 determinant of outcomes in ecology and evolution (and to varying degrees in other fields, including
21 philosophy, sociology, and economics (1–15)). The contingency hypothesis posits that an
22 individual’s behavior, health, social position, or fitness are strongly dependent on unpredictable,
23 uncontrollable events and experiences that occur across its life, and even in the lives of relatives
24 and other social contacts (5, 16–20). Contingent outcomes in early life are often especially
25 important, as they can set individuals onto divergent, self-reinforcing trajectories (1, 2, 5, 17, 18,
26 20). Recent evolutionary theory has argued that luck in an individual’s life largely swamps the
27 importance of individual quality in determining lifetime reproductive success, and that luck in early
28 life is especially important for such outcomes (1, 2). This heightened importance of contingency in
29 early life is consistent with the theoretical and observed limitations of phenotypic plasticity:
30 although some plasticity is maintained throughout life, plasticity is greatest during development,
31 and developmental decisions can restrict individuals’ future phenotypic options (18, 21–23).

32 Many animals naturally live within larger social groups, such that contingency in outcomes
33 is inextricably tied to individuals’ relationship to the behavior of others within societies (5, 24–28).
34 Through repeated social interactions, individuals adopt a consistent set of social phenotypes (i.e.,
35 their ‘social niche’ (25, 27, 29)). We hypothesize that competitive social processes magnify the
36 importance of contingency in early life. For example, animals that begin with zero or small
37 differences in competitive ability may differ in their access to resources due to variation in
38 contingent dominance or territorial interactions (19, 30–33). The resulting increased resource
39 access for a subset of the population then improves those animals’ condition relative to those with
40 reduced resource access, further entrenching the initial differences and magnifying the importance
41 of early contingency (19, 24, 33–36). This process is analogous to the ‘Matthew effect’ in the social

42 sciences, a phenomenon by which individuals or institutions that achieve early success tend to
43 achieve ever greater success in the future (37–39).

44 Experimentally studying of the role of contingency in individual outcomes is achievable with
45 the use of ‘replicate individuals’ that allow researchers to effectively ‘replay the tape of life’ for a
46 single genotype under different circumstances (40, 41). Studies of genetically identical animals
47 living in the lab have demonstrated the feasibility of this approach (e.g., inbred mice: (42–44),
48 inbred fruit flies: (45, 46), naturally clonal Amazon mollies: (47, 48)). In these studies, small
49 between-individual differences in early behavior increase in magnitude over time, despite animals’
50 sharing nearly identical genetics and macro-environments (42–48). Yet, assessing the ways in
51 which competitive social processes magnify or dampen the impact of early contingency requires
52 the study of replicate individuals living under realistic, complex, dynamic social conditions—
53 requirements that cannot be readily met under standardized laboratory conditions (49–51).

54 Here we overcome this limitation by studying the development of spatial and social
55 behavior in age-matched, genetically identical mice living outside in a large, shared macro-
56 environment. From infancy through adulthood, we tracked the development of the magnitude of
57 individual differences in ecologically relevant social and spatial behaviors among genetically
58 identical mice living under semi-natural field conditions (Fig S1).

59 We make two contributions to understanding the development of individuality and the role
60 that contingency and competitive processes play in that development. First, we present the most
61 detailed data to date on the development of semi-natural spatial and social behaviors in the
62 prototypical biomedical model mammal. We use this data to assess the developmental timing of
63 the emergence of individuality in genetically identical animals across a wide range of spatial and
64 social behaviors (Fig S2). Second, we show that small initial differences in males’ ability to acquire
65 and defend territories causes males—but not females—to enter onto divergent, self-reinforcing
66 behavioral trajectories, with downstream impacts on a wide range of male social and spatial
67 behaviors (Figs. 1-2). These divergent trajectories cause individual males to assume their
68 individually distinct adult behavioral phenotypes at an earlier age than do females. Using
69 quantitative agent-based simulations we also show that these differences between males and
70 females can be wholly explained by sex-specific social feedback loops, which magnify the
71 importance of early contingent experiences and shape the timing of the development of
72 individuality (Fig 1).

73

74 **Males Develop Individual Adult Behavioral Phenotypes Earlier than Females.**

75 We first assessed the developmental timing of individually distinct behavioral phenotypes
76 and whether this timing differed in males and females. In free-living C57BL/6J lab mice, males
77 compete for territorial control and resource access while females do not (52, 53). We hypothesized
78 that this difference in competitive experiences should cause males to diverge onto self-reinforcing
79 developmental trajectories as some males won competitive interactions and others lost. We expect
80 this same dynamic to be absent in females.

81 Over seven weeks from May to June 2022, we allowed 16 litters (n = 104 pups, 90 survived to
82 adulthood) of the C57BL/6J lab mouse strain to develop from infancy through adulthood outside in

83 a large (~560 m²) enclosure that emulates the natural foraging and social environment of
84 commensal house mice (Figure S1A-C). We placed litters of 2-week-old RFID microchipped pups
85 and their mothers inside nest boxes within one of 16 “resource zones” monitored with RFID
86 antennae. We inferred periods of social overlap using an established workflow to translate RFID
87 positional data into estimates of the duration of social aggregations within each of the 16 monitored
88 resource zones (Figure S1D, see (52) for details). Based on a total of 7.4 million RFID reads, we
89 traced the development of 17 social and spatial phenotypes from infancy through adulthood (~6.5
90 weeks, 14–58 days of age, Table S1), after which we trapped out the mice and terminated the
91 experiment.

92 We first leveraged our detailed behavioral dataset to answer an outstanding question in
93 social behavioral ecology—whether genetically identical animals display distinct, individually
94 repeatable social behaviors under ecologically relevant contexts and, if so, when these differences
95 emerge (40, 41, 47, 48, 54, 55). We measured repeatability as the proportion of a phenotype’s total
96 variation in each sex that was explained by individual identity (56) over a sliding five-day age
97 window, after controlling for maternal/litter identity. In total we assessed 17 phenotypes including
98 basic measures of movement patterns (e.g., the number of nightly resource zones that an animal
99 visited), measures of social phenotypes (e.g., the nightly number of opposite-sex animals
100 encountered and territory scores), and derived social network measures (e.g., eigen vector
101 centrality, see Table S1 for a description of phenotypes). We detect significant repeatability in all
102 measured phenotypes, for both sexes, with repeatability emerging as early as age 21 days (Fig S2),
103 roughly 1 month earlier than reported for spatial behavior of female populations of this strain in
104 enriched lab *vivaria* (11, 30). Animals’ behavior was repeatable prior to sexual maturity (~age 35
105 days) for 15 of 17 phenotypes in males and 16 of 17 phenotypes in females (range = 21–55 days,
106 median = 26 days, see Fig S2 G–H).

107 Having established that genetically identical mice still displayed strongly repeatable
108 individual suites of behavior, we next assessed the developmental timing at which males and
109 females assumed their individually distinct adult behavioral phenotypes. To generate an integrative
110 measure of animals’ spatial and social behavior, we used principal component analysis to reduce
111 the dimensionality of 16 of our 17 behavioral phenotypes into two principal components that
112 accounted for a majority of the total variation in our dataset (57% total across PC1 and PC2; ‘time
113 of first nightly transition’ phenotype could not be included because values were missing before
114 animals began moving between zones). Many phenotypes were loaded onto PCs 1 and 2 without
115 any one phenotype being particularly influential (see Table S2 for full loading information).

116 We identified animals’ final adult behavioral phenotypes by taking the average of each
117 individuals’ PC1 and PC2 scores during the last three days of the experiment (age 56–58 days, Fig
118 1A). For each sex we then assessed the relationship between individuals’ phenotypes at earlier time
119 points and these final adult behavioral phenotypes by building linear regressions between final
120 adult phenotype and individuals’ average phenotypes over five-day, non-overlapping windows (e.g.
121 age 21–25 days, 26–30 days, etc.). From each of these models we extracted the correlation between
122 earlier and adult phenotype and the estimated slope of the relationship between earlier and later
123 phenotypes (Fig 1B).

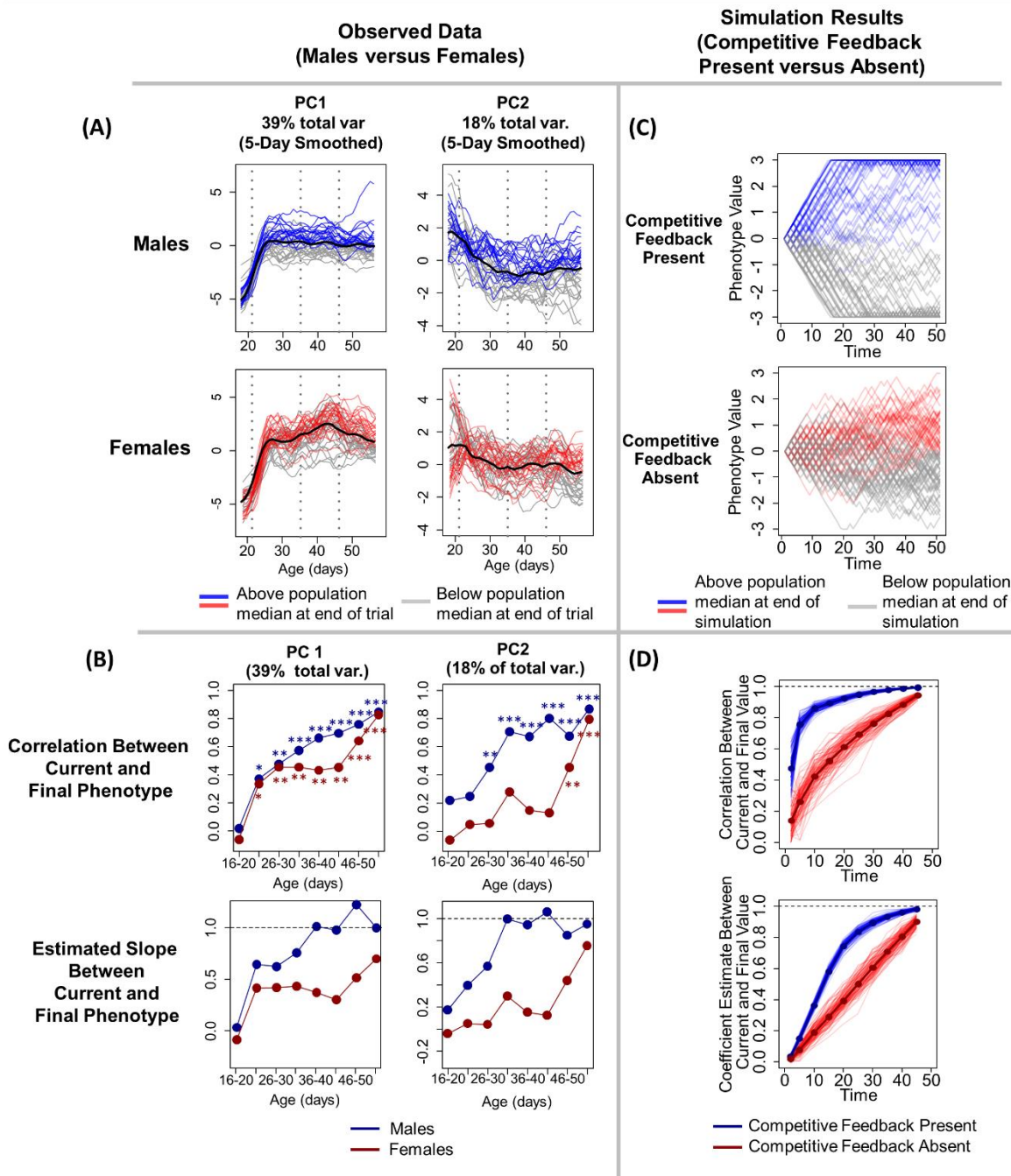
124 For both PC1 and PC2, males assumed their individually distinct adult behavioral
125 phenotypes earlier than females. Male behavior became predictive ($p < 0.05$) of final adult behavior
126 at or before females (PC1: 26 days vs. 26 days, PC2: 31 days vs 46 days, Fig 1B). The strength of the
127 correlation between earlier and later behavior for the same individual was also substantially higher
128 for males than for females across most or all of development (PC1: days 31-50; PC2: days 16-50,
129 Fig 1B). Males' behavior at earlier ages also more closely aligned with their adult behavior in
130 absolute terms. That is, the slope of the linear relationship between earlier behavior and adult
131 behavior was closer to 1 for males than for females, and this strong relationship developed at an
132 earlier age for both PC1 and PC2 (Fig 1B). We performed this principal component analysis using all
133 daily phenotype data for both males and females, but all of the above results hold if we instead
134 generate separate sex-specific PC values (Figure S3)

135 To aid in interpretation of Figure 1B, we provide an example of one set of models (Figure S4),
136 comparing the strength of the relationship between behavior immediately after sexual maturation
137 (ages 36-40 days) and individuals future behavior in adulthood (days 55-58) for males and females.
138 Here the strength of the relationship is much stronger for males for both PC1 (male $R^2 = 0.43$;
139 female $R^2 = 0.18$) and PC2 (male $R^2 = 0.44$; female $R^2 = 0.02$). And the slopes of the relationship
140 between earlier and later behavior is much closer to 1.00 for males than for females for both PC1
141 (male estimate = 1.01, 95% CI = 0.6-1.4; female estimate = 0.37, 95% CI = 0.1-0.6, non-overlapping
142 with males) and for PC2 (male estimate = 0.95, 95% CI = 0.6-1.3; female estimate = 0.2, 95% CI = -
143 0.2-0.5, non-overlapping with males).

144 We next assessed whether these sex differences in the developmental timing of
145 individuality could be fully explained by sex-specific difference in the importance of competitive
146 feedback in amplifying the importance of early contingency. To do so, we built a quantitative agent-
147 based model to generate empirical predictions of how competitive processes shape the long-term
148 phenotypic impacts of early contingency (Fig 1C-D). In this model we assumed that all individuals
149 start with the same value of a phenotype. Individuals' phenotypic value then changes at discrete
150 timesteps across their lives, with the nature of that change depending on the presence or absence
151 of competitive feedback. In simulations where competitive feedback was absent, the direction of
152 change in phenotypic value was randomly chosen to be positive or negative. When competitive
153 feedback was present, an individual's phenotype increased in value if it won a competitive
154 interaction with a randomly chosen individual and declined if they lost. The probability of winning
155 the interaction was dependent on the relative phenotypic values of the two interactants (see
156 methods for complete details).

157 The results of the simulation closely mirror our observations of differences in the
158 development of individuality in males and females in our system. Specifically, when competitive
159 feedback loops are present (i) the correlation between behavior at any given time and behavior at
160 the end of the modeled period is stronger, and (ii) the slope of the relationship between earlier and
161 later behavior is closer to 1.0. Thus, it appears that the sex-difference that we observe in the
162 development of behavioral individuality could be entirely explained by differences in sex-specific
163 competitive processes that amplify contingent early life differences in phenotype.

164



165 **Figure 1. Males adopt their adult phenotypes earlier than females.** (A) Traces of observed
 166 individual behavioral PC1 and PC2 values, smoothed over five days, across animals' development.
 167 Lines are color-coded to indicate individuals' behavior during the last three days of the experiment
 168 (age 56-58), with lines representing animals that displayed higher than median phenotype during
 169 this period in red or blue and animals that displayed lower than median phenotype in grey. (B, first
 170 row) The correlation between earlier and adult behavior is stronger in males for both PC1 (left
 171 column) and PC2 (right column). The y-axis represents the correlation coefficient between
 172 individuals' behavior at the age-window on the x-axis and their behavior at the end of the
 173 experiment (age 56-68 days). Asterisks denote significance of the correlations depicted in each
 174 point (* p < 0.05, ** p < 0.01, *** p < 0.001). (B, second row) The slope of the relationship between

175 earlier and adult behavior (y-axis). The slope of this relationship is consistently closer to 1 for males
176 than for females. (C-D) Each of the observed results in (A) and (B) are closely mirrored by agent-
177 based simulations in which simulated individuals' phenotypes develop either in the presence (blue)
178 or absence (red) of competitive feedback mechanisms. (C) Traces of individual phenotypes from a
179 single run of the simulation, with shading of traces matching (A). (D) Results from 1,000 iterations of
180 the simulation. Comparable to (B), relationships between current and future behavior are stronger
181 when competitive feedback is present. Detailed description of the simulation can be found in the
182 main text and methods.

183

184 **Territoriality acts as a sex-specific competitive feedback loop**

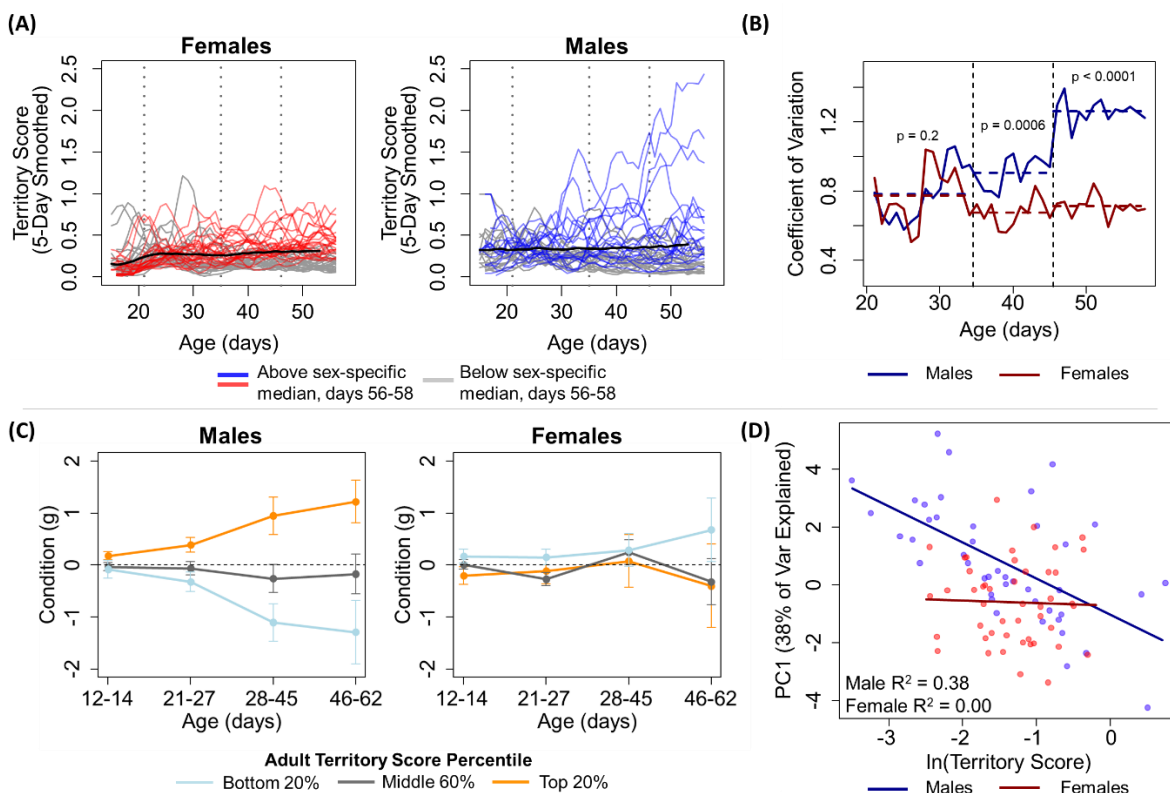
185 We next assessed whether males and females displayed differences in the strength of
186 resource competition in a fashion that would support this putative sex-biased competitive
187 feedback loop indicated by the model analysis in Figure 1. To do so, we estimated individuals'
188 nightly resource access by calculating a nightly territory score for each animal (see methods).
189 Consistent with males and females experiencing different levels of competition for resource
190 access, territory score varied more among males than it did among females (Fig 2A). This difference
191 emerged concurrently with the onset of sexual maturity, the period when we expect intrasexual
192 competition to increase in intensity. Although variation in territory score is comparable for males
193 and females during the juvenile period (ratio of variance = 1.5, $p = 0.2$, two-sided F test), following
194 the onset of sexual maturation (~age 35 days), males displayed significantly higher variation than
195 did females (ratio = 2.9, $p = 0.0006$), a difference that further increased following the onset of
196 successful mating (~age 46 days, ratio = 3.6, $p < 0.0001$, Fig2A).

197 Two additional pieces of evidence are consistent with males, but not females, experiencing
198 strong competitive feedback that set them on self-reinforcing divergent life trajectories. First, small
199 individual differences in early body mass (measured, days 21-27) predicted adult (days 46-58)
200 territory scores for males ($p < 0.05$, see Fig 2C, Fig S5) but not for females. Prior to release into the
201 enclosure, very minor differences in infant body condition did not predict future territory access in
202 either sex (days 12-14 compared to adult, $p > 0.05$, Fig S5), consistent with individuals starting out
203 on an approximately 'even playing field'. The magnitude of the differences in body mass between
204 males with differential resource access then increased over development (age x adult territory
205 score interaction: $p = 0.004$, Fig 3C, S5), consistent with males experiencing a competitive
206 feedback loop that increased the condition of winners relative to losers. This developmental
207 pattern was absent in females ($p = 0.19$, Fig 3C). In adulthood, this mass measure in females is
208 partially confounded by pregnancy status, but at no point (even before any pregnancies began) was
209 there a relationship between body condition in females and adult territory status (unlike in males,
210 Fig 2C).

211 Second, male territory scores strongly predicted the rest of males' behavioral phenotypes,
212 while the same was not true of females, indicating that our measure of competition in males has
213 major impacts on males' daily behaviors and ability to reproduce. Specifically, we performed a
214 principal component analysis using the other 16 phenotypes that we measured in adulthood (i.e.,
215 excluding territory score) to obtain a single integrative measure of animals' other behavior (PC1
216 explained 41% of the total variation in this dataset). Males' adult territory scores strongly predicted
217 this adult PC1 value (Fig 2D, $p < 0.0001$, $R^2 = 0.38$), while females' territory scores did not (Fig 2D, p

218 = 0.86, $R^2 = 0.00$). The same conclusion holds if we assess individual adult phenotypes, rather than
 219 this principal component measure (see Table S3 for all 16 comparisons). Individuals' access to
 220 members of the opposite sex provides a particularly striking, fitness-relevant example from this
 221 more granular analysis: for males, the average number of females met on a given night is very
 222 strongly, positively associated with territory score ($R^2 = 0.67$, $p < 0.0001$), while territory score does
 223 not predict the number of males met by females ($R^2 = 0$, $p = 0.7$).

224 Thus, male territorial competition appears to act as a sex-specific competitive feedback
 225 loop. Small initial differences in male body mass became magnified over time, depending on
 226 territorial control. Male territorial control then had downstream implications for a wide range of
 227 ecologically and fitness relevant spatial and social behaviors.



228
 229 **Figure 2. Territorial competition shapes males' phenotypes through a sex-specific competitive**
 230 **feedback loop.** (A) Traces of individual territory score values, smoothed over five days, across
 231 animals' development. Lines are color-coded to indicate individuals' scores during the last three
 232 days of the experiment (age 56-58), with lines of animals that display higher than median scores
 233 during this period in red or blue and animals that display lower than median phenotype in grey.
 234 Black lines indicate sex-specific means. Vertical dashed lines represent indicate approximate ages
 235 of weaning ('juvency', 21 days), sexual maturation ('adolescence', 35 days), and onset of
 236 conceptive mating ('adulthood', 46 days) (B) Male territory scores are more variable across
 237 individuals than female territory scores, a significant difference that emerges concurrent with
 238 sexual maturity and further increases following the onset of successful mating. Horizontal dashed
 239 line segments indicate the average coefficient of variation across the juvenile, adolescent, and
 240 adult stages. (C) Male adult territory scores are predicted by small differences in body mass in early

241 life, a difference that is magnified over time. The relationship is absent in females. The y-axes
242 represent deviations from age-predicted body mass. (D) Adult territory score strongly predicts an
243 integrative measure (PC1) of the 16 other spatial and social phenotypes in males but not in
244 females.

245 **Discussion:** Our results provide empirical support for the hypothesis that contingency (or ‘luck’) in
246 early life can have a major and sex-specific impact on the development of animals’ individual
247 differences in social and fitness-relevant phenotypes. Sex-specific competitive feedback loops
248 magnify the importance of contingency experienced early in life, such that young free-living male
249 lab mice enter onto divergent, self-reinforcing developmental trajectories. Our interpretation of our
250 empirical results is supported by their match to an agent-based simulation of expected differences
251 in the developmental timing of individuality in the presence and absence of competitive feedback.
252 We expect the sex-specificity of such competitive feedback loops to vary across different species,
253 depending on a given species’ specific social behavioral ecology. For example, in hyenas and other
254 female-dominant species, we would expect the reverse pattern to be present, such that females’
255 outcomes to be more dependent on early luck (e.g. the relative social status of the matriline into
256 which they were born, (57, 58)) than males’ outcomes.

257 Our results suggest an inevitable limitation of sexual selection to shape behaviors.
258 Intrasexual selection relies on within-sex competition resulting in differential reproductive success,
259 and for variation in this success to be heritable (59–61). But here we have shown that intrasexual
260 competition also magnifies the importance of contingency in later life outcomes in the sex
261 expressing that competition. As the importance of luck in determining individual phenotypic
262 outcomes increases, selection’s ability to cause evolution declines (1, 2). Thus, intrasexual
263 selection may be self-limiting, as an increase in the importance of competition in a single sex leads
264 in turn to an increase in the importance of contingency in determining individual outcomes. And to
265 the extent that intersexual choice is at least partially dependent on intrasexual competition, we
266 expect the increased importance of luck to act as a limit on the effectiveness of intersexual
267 selection as well. This increased importance of luck in systems with intrasexual competition may
268 help to explain why sexual selection fails to fully deplete genetic variation, despite strong selection
269 imposed by mate choice and intrasexual competition (i.e., the lek paradox (62–64)).

270 Our results provide a strong biological analog to the Matthew Effect, an often-observed
271 phenomenon in social science whereby small individual advantages earlier in life are correlated
272 with ever larger advantages over time (37–39). Such processes are understood to be the result of
273 social feedback mechanisms, by which an individual’s initial success improves their opportunities
274 for future success as well as the perception by other members of society of the individual’s
275 potential for success (39, 65). The extent to which Matthew Effects are specific to human societies
276 has remained an open question (39). Our results suggest that Matthew Effects (i) may have a
277 biological origin, (ii) are especially likely to occur in highly competitive environments or among
278 groups that face high levels of competition, and (iii) may emerge even in the absence of any
279 variation in underlying individual quality or ability.

280 The sources of inequality in human society are of central interest to both moral philosophy
281 and public policy (66–68). As with reproductive success in non-human animals, human outcomes
282 are likely to be partially explained by differences in genotypes (69). However, we show here that

283 even among isogenic animals, individuals still attain dramatically different phenotypic and fitness
284 outcomes. Our results add to sociological and biological literature that underscore the potential
285 importance of unpredictable, uncontrollable experiences in generating differences in outcomes
286 even when differences in underlying quality (or ‘talent’) are small or non-existent (12, 15, 16).

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294
295 **Data and Code Availability:** While this manuscript is under review, all data and code supporting
296 this manuscript and its analyses can be found in this Box folder:

297 <https://cornell.box.com/s/9jz4hp4kl1wnxhb5u3q275m650kfub7x>

299 **Supplementary Materials**

300 Materials and Methods

301 Supplementary Text

302 Tables S1 to S3

303 Figs. S1 to S5

304

305

306 **Materials and Methods:**

307 *Field Enclosure and RFID Data Collection:*

308 A detailed description of the enclosures at Cornell University’s Liddell Field Station can be
309 found elsewhere (52), so here we only describe those elements critical to the success of this
310 experiment. The enclosure is 15m x 38m, approximately 9,000 times the area of a typical mouse
311 cage. Within the enclosure we set up 16 plastic tubs (31 gallon storage totes, Rubbermaid, USA),
312 placed into four neighborhoods of (Figure S1E). Each tub (hereafter “resource zones”) contained *ad*
313 *libitum* food access along with a nestbox that provided insulation and shelter from adverse weather
314 conditions. We equipped each zone with a single joint entrance/exit made out of a 6-inch-long PVC
315 pipe (2” in diameter). These resources and the single entrance made the resource zones highly
316 valuable, defensible areas that are meant to mimic the foraging landscape of commensal mice. To
317 track the comings and goings of mouse visitors to each zone, we placed a 10-inch RFID antennae
318 (Biomark, USA), beneath the entrance tube of each zone. The antennas were connected to a central
319 monitoring system (Small Scale System, Biomark, USA) and transmitted RFID reads at a rate of 2-3
320 Hz.

321 *Study Subjects:*

322 We bred 16 litters of C57BL/6J mice by pairing 9-week old virgin males and females that we ordered
323 from Jackson Laboratory (Bar Harbor, ME). We timed pregnancies such that all litters were born

324 within 48 hours of each other, allowing infants to be approximately age-matched. Males were
325 removed from breeding cages two weeks after pairing to prevent mothers from becoming pregnant
326 again following parturition.

327 When pups were 8-10 days of age, we anesthetized litters and their mothers using isoflurane and
328 injected either 1 (pups) or 2 (mothers) PIT tags (Biomark Mini HPT10) subcutaneously. When
329 animals were 12-14 days old (12: n = 49 pups, 13: n = 51 pups, 14: n = 4 pups) we placed litters
330 along with their mothers and their nesting material in cardboard transfer containers. We then
331 transferred litters and mothers to our field enclosures and placed them inside of nest boxes within
332 resource zones. We balanced litter sizes across the four neighborhoods, placing 26 pups and 4
333 mothers in each neighborhood. 3 neighborhoods had litter sizes of 5, 6, 7 and 8 pups. The final
334 neighborhood had litter sizes of 4, 6, 7, and 9 pups.

335 We then allowed animals to develop and live largely undisturbed (but see “Mass Measures” below)
336 for 46 days, at which point we terminated the experiment. We selected this length of time to prevent
337 animals from giving birth in our enclosure. In total, 85 of the 104 pups that we placed outside
338 survived until the last three days prior to the end of the experiment (survival rate = 82%). These
339 animals’ data were included in all analyses. 5 other animals survived until at least 46 days of age
340 (the onset of conceptive mating). These animals (n = 90 total) were included in all analyses except
341 those appearing in Figure 4. An additional 5 animals (n = 95 total) survived until 30 days of age, and
342 we included these animals’ data in the repeatability analyses presented in Figure 2.

343 *Mass Measures:*

344 When pups were all 21-23 days of age, we caught by hand all living animals in the enclosure to
345 measure weaning mass. At this time, we also removed half of the mothers living within the
346 enclosure. This manipulation was performed to assess whether our animals relied on post-weaning
347 maternal care. Though we do not discuss these results in detail here, there was no impact of this
348 manipulation on dispersal, survival, juvenile behavior, or adult behavior. Following mass measures,
349 all other animals were returned to the resource zone in which they were found.

350 For the remainder of the experiment, we opportunistically caught animals by hand and took mass
351 measures. For five days a week we caught all animals present within and immediately below
352 resource zones from a single neighborhood. We rotated neighborhoods each day to try to prevent
353 discouraging animals from using the resource zones as a result of frequent disturbance.

354 On two occasions we re-captured an animal who had lost its PIT tag. To prevent these animals from
355 making unmeasured contributions to the social environment, we humanely euthanized these
356 animals. On one occasion we re-captured an animal that appeared to be in poor physical
357 condition. We humanely euthanized this animal to prevent future suffering. All other animals were
358 returned to the resource zone in which we found them.

359 At the conclusion of the experiment, we placed 48 Sherman live traps in resource zones for three
360 nights until all animals were successfully caught (all animals aged 61-64 days at time of trapping).
361 In the mornings following trapping we humanely euthanized animals, took their body masses for a
362 final time and then dissected and preserved a range of tissues for future analysis. We placed fewer

363 traps than there were animals due to logistical constraints on the number of daily dissections that
364 we could perform.

365 *Contingency Model (Fig 1C-D):*

366 To assess how the presence or absence of competitive feedback magnifies or dampens the
367 importance of early-life contingency on later life outcomes we built a probabilistic, agent-based
368 model.

369 We simulated populations of 100 replicate individuals that each began with an identical value (0) of
370 a given phenotype. We assumed that the phenotype had a range of possible values, which we took
371 to be [-3,3]. Individuals' phenotypes then changed contingently over a series of time steps. At each
372 time step, phenotypic values for each individual increased or decreased by a value drawn from a
373 normal distribution centered around 0.2 with a standard deviation of 0.02. Individuals continued to
374 change their phenotypic value for 50 time steps, at which point the simulation ended.

375 At each timestep, half of the individuals in our populations increased their phenotypic value and
376 the other half decreased their phenotypic value. Deciding the direction of these changes proceed
377 by the following steps. First, at each timestep the 100 individuals in a population were randomly
378 placed into pairs. Deciding the direction of phenotypic change for each member of the pair
379 depended on the presence or absence of competitive feedback in the population.

380 In the absence of a role for competition in the development process, the individual whose value
381 increased was selected at random. This approach is meant to simulate the impact of short-term
382 contingency, with individuals increasing or decreasing their phenotype as a result of recent
383 differences in the animal's internal state or by recent non-social environmental experiences (24).

384 In the presence of a competitive feedback loop, the identity of the animal whose phenotype
385 increased was determined by a contest. The probability of an animal winning the contest was
386 dependent on the difference in phenotypic values of the two animals in the pair.

387 Specifically, the probability of the first animal in a pair winning a contest was:

388
$$p(win_1) = 0.5 + \frac{value_1 - value_2}{2}$$

389 With $p(win_1)$ being truncated at 0 and 1. Thus, any contest between animals whose difference in
390 phenotypic values was greater than or equal to 1 had a deterministic outcome. Contests that had
391 smaller differences in values between contestants were probabilistic.

392 This approach is meant to model a competitive phenotype that determines access to resources.
393 The probability of an individual's phenotype increasing or decreasing depends on the outcome of a
394 contest, which in turn depends on the value of its phenotype compared to another individual in the
395 population. The winner of this contest acquires additional access to resources, which in turn
396 increases its competitive ability and its phenotypic value (thus generating a competitive feedback
397 loop (19, 34)).

398 To generate the data in Figure 1D, we built linear models in which each individual's final (time = 50)
399 phenotypic value was the response variable and the predictor variable was each individual's

400 phenotype value at an earlier point in time (times = {2, 5, 10, 15, 20, 25, 30, 35, 40, 45}). We then
401 extracted the correlation coefficients and slope estimates from the relationship between
402 phenotype values at these different points in time and individuals' final phenotypes.

403

404 **Statistical Analyses**

405 *Analysis of Acquisition of Adult Behavior in Males and Females (Fig 1, S2-S3).*

406 We first performed a principal components analysis to reduce the number of behavioral
407 phenotypes in our population to two variables that explained a majority of the total variation in our
408 dataset (PC1: 39% of variation explained, PC2 18% of variation explained). In this principal
409 component analysis, we included 16 of our 17 measured daily phenotypes for all individuals from
410 ages 14-58 days.

411 We then assessed the relationship between individuals' behavior during a given period and their
412 eventual final behavior in the experiment (measured during the last three days for which the
413 youngest animals were present, age 56-58 days).

414 As in the agent-based simulation (above), we built a series of linear models for each sex where the
415 response variable was each individual's average PC1 or PC2 value during age 56-58 days and the
416 predictor variable was each individual's average value during a series of non-overlapping 5 day
417 periods (16-20, 21-25, 26-30, 31-35, 36-40, 41-45, 46-50 and 51-55 days). We extracted the
418 correlation coefficients and slopes of the relationships between earlier and later behavior.

419 *Repeatability Analyses (Fig 3, S2):* We used the function rptGaussian (packaged 'rptR' (70)) to
420 calculate repeatability estimates for behavioral measures. We calculated sex-specific repeatability
421 across sliding 5-day age windows. We included pup age as a fixed effect and maternal/litter identity
422 as a random effect in models with which repeatability was estimated. Thus, our repeatability
423 estimates are the proportion of the variance in a five-day dataset of a given behavioral measure that
424 is explained by pup identity, after controlling for pup age and maternal/litter identity.

425 To measure the age at which repeatability in a phenotype emerged (Figure 2C), we identified the
426 earliest age at which animals displayed significant ($p < 0.05$) repeatability in a given phenotype and
427 then continued to be repeatable thereafter for the rest of the experiment.

428 *Territoriality Analysis (Figure 2, S5):* We calculated a nightly territory score for each animal. To do so,
429 we calculated the proportion of sex-specific nightly RFID reads at a given resource zone that
430 originated from each animal. We then summed these values across each of the sixteen resource
431 zones for each animal to calculate a measure of total nightly resource access. For example, if there
432 were 5000 male-sourced RFID reads at Resource Zone 1 on night 30 of the experiment and 4500 of
433 them came from Male 1, Male 1 was assigned a value of 0.9 for Resource Zone 1 for that night. If
434 Male 1 also visited exactly one other zone, where he accounted for 40% of the male-sourced RFID
435 reads at that zone, his total value of this measure for the night (hereafter 'territory score') would be
436 1.30.

437 We measured coefficients of variation in territory scores for each day from age 15 to 58. To assess
438 differences in variance in males' and females' territory scores we calculated each individuals'

439 average territory score across three different periods: (i) age 21-34 days, (ii) age 35-45 days, and (iii)
440 age 46-58 days. We then performed a difference in variance test for square-root transformed
441 average territory score values for the two sexes during each of these three periods ('var.test'
442 function).

443 For each sex we then built a mixed effects linear model (function 'glmmTMB' (71)) with body
444 condition as the response variable, predicted by the interaction between the age at which mass
445 was measured and the log of animals' average territory score during age 46-58 days (Fig 3C). We
446 also included a random effect of animal ID, with age nested within ID as a random slope.

447 Finally, we performed a principal components analysis using all behavioral data from the 46-58
448 day-old period, excluding territory score. We then built linear models for each sex in which the
449 response variable was an individual's first principal component value (PC 1 explained 38% of the
450 total variance in the dataset) and the predictor variable was the natural log of the individual's
451 average territory score in adulthood.

452

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- 609

610 **Supplement:**

611 **Table S1.** The spatial and social phenotypes measured on a daily basis in our animals, from age 15
612 to 58 days.

	Phenotype	Description
Spatial Phenotypes	Resource Zones Visited	The number of resource zones visited by an animal each night. Range = 0-16, mean = 6.0. Detected via at least one RFID read at a given zone on a given night.
	Transitions Between Zones	The number of times that an animal moved from one resource zone to another, each night. Range = 0-141, mean = 16. Detected by a change in an animal's zone location between subsequent RFID reads.
	Transitions Between Neighborhoods	The number of times that an animal moved from one neighborhood of resource zones to another, each night. Range = 0-26, mean = 2.9. Detected by a change in an animal's neighborhood location between subsequent RFID reads (see Figure 1 for neighborhood distribution).
	Time of First Nightly Transition	The number of hours past noon on a given night that an animal made its first transition between resource zones. 'NA' if no transitions occurred. Range = 2.1-23.1, mean = 5.7. Detected as the time stamp for the first transition each night.
	Proportion of Reads in Top Zone	The proportion of RFID reads that were recorded from an animal in its most visited zone (the zone with the most RFID reads for that animal). 'NA' if an animal did not visit any zones on a given night. A measure of spatial fidelity. Range = 0.15-1, mean = 0.62.
	Proportion of Reads in Top Neighborhood	The proportion of RFID reads that were recorded from an animal in its most visited neighborhood (the neighborhood with the most RFID reads for that animal). 'NA' if an animal did not visit any zones on a given night. A measure of spatial fidelity. Range = 0.32-1, mean = 0.89.
Basic Social Phenotypes	Number of Males Met	The number of males that an animal encountered in or around a resource zone each night. Range = 0-27, mean = 9.6. Measured based on the number of males that a given individual was inferred to overlap with for at least 1 second at a resource zone.
	Number of Females Met	The number of females that an animal encountered in or around a resource zone each night. Range = 0-35, mean = 12.3. Measured based on the number of males that a given individual was inferred to overlap with for at least 1 second at a resource zone.
	Total Number of Animals Met	The sum of the number of males and females that an animal met each night. Range = 0-54, mean = 21.9.
	Proportion Time Spent Alone	The proportion of all time that we inferred an animal spent in or around a resource zone for which it was the only animal inferred to be present. Range = 0-1, mean = 0.40.
	Proportion Time Spent with the Opposite Sex	The proportion of all time that we inferred an animal spent in or around a resource zone for which at least one member of the opposite sex was inferred to also be present. Range = 0-1, mean = 0.39.
	Territory Score	For each zone we calculated the proportion of all same-sex RFID reads that occurred at each zone. We then calculated the proportion of those reads that originated with each animal (sum = 1). For each night, we then summed this value across all 16 resource zones for each animal. For males, this is a measure of

		<p>competitive ability. For females, interpretation is difficult, but it is most closely a measure of isolation from other females. Range = 0-2.7, mean = 0.3.</p> <p>See methods for additional details.</p>
Social Network Phenotypes	Edge Strength	The average strength of the connection between each animal and all other animals that it was connected to in the network each night. A measure of the strength of its average social relationship. Range = 0-4.1, mean = 0.5.
	Opposite Sex Edge Strength	The average strength of the connection between each animal and all other animals of the opposite sex that it was connected to in the network each night. A measure of the strength of its average social relationship. Range = 0-3.3, mean = 0.2.
	Eigenvector Centrality	A measure of how connected an animal was to other members of the network, taking into consideration the strength of connectivity of each animal that the focal animal was connected to. Range = 0-1, mean = 0.28.
	Betweenness Centrality	A measure of centrality that is based on the extent to which an animal lay along the shortest path between other pairs of animals in the network. Range = 0-576, mean = 29.
	Closeness Centrality	A measure of centrality based on the length of the average path between any given animal and other animals in the network. Calculated as the inverse sum of the path length (number of connective steps) between the focal animal and each other animal in the network. Range = 0.27-1, mean = 0.61.

613

614

615 **Table S3.** Loadings of each of the 16 phenotypes included in the principal component analysis onto
616 principal components 1 and 2

Phenotype	PC1 Loading	PC2 Loading
Resource Zones Visited	0.35	0.03
Total Number of Animals Met	0.34	0.24
Number of Females Met	0.33	0.20
Transitions Between Neighborhoods	0.30	0.05
Transitions Between Zones	0.28	0.28
Number of Males Met	0.27	0.25
Betweenness Centrality	0.24	0.20
Eigenvector Centrality	0.20	0.23
Proportion Observed Time Spent Alone	0.20	-0.36
Resource Access	0.07	0.08
Closeness Centrality	-0.12	0.37
Opposite Sex Edge Strength	-0.18	0.42
Proportion Observed Time Spent with the Opposite Sex	-0.20	0.36
Edge Strength	-0.22	0.40
Proportion of Reads in Top Neighborhood	-0.23	-0.03
Proportion of Reads in Top Zone	-0.29	0.05

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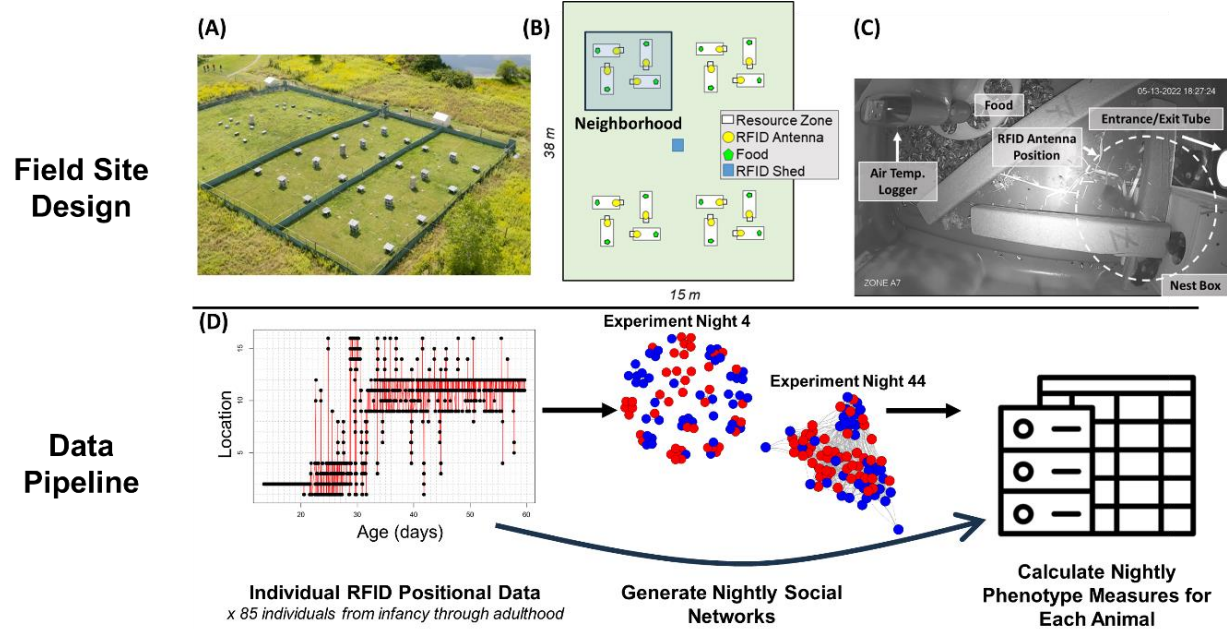
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619 **Table S3.** The relationship between average adult resource access and each other adult phenotype
 620 measured for each sex.

Phenotype	Sex	R ²	p value
Average Opposite Sex Edge Strength	Male	0.69	< 0.0001
	Female	0.02	0.32
Nightly Females Met	Male	0.68	< 0.0001
	Female	0.06	0.09
Number of Nightly Transitions Between Zones	Male	0.65	< 0.0001
	Female	0.05	0.11
Total Nightly Animals Met	Male	0.35	< 0.0001
	Female	0.04	0.16
Time of First Nightly Transition Between Zones	Male	0.37	< 0.0001
	Female	0.07	0.07
Betweenness Centrality	Male	0.27	< 0.0001
	Female	0.00	0.75
Closeness Centrality	Male	0.28	< 0.0001
	Female	0.03	0.25
Number of Nightly Transitions Between Neighborhoods [^]	Male	0.22	0.002
	Female	0.10	0.03
Proportion of Nightly Reads in Top Neighborhood	Male	0.34	< 0.0001
	Female	0.23	0.0008
Average Edge Strength	Male	0.32	< 0.0001
	Female	0.27	0.0002
Eigen Vector Centrality	Male	0.15	0.01
	Female	0.09	0.04
Proportion of Observed Time Spent With a Member of the Opposite Sex	Male	0.08	0.06
	Female	0.04	0.20
Nightly Males Met	Male	0.01	0.50
	Female	0.00	0.87
Nightly Resource Zones Visited	Male	0.00	0.78
	Female	0.08	0.06
Proportion of Nightly Reads in Top Resource Zone	Male	0.05	0.13
	Female	0.11	0.02
Proportion of Observed Time Spent Alone	Male	0.16	0.009
	Female	0.31	< 0.0001

621 [^]Analysis excludes animal 3059-1, which was an extreme outlier on this metric

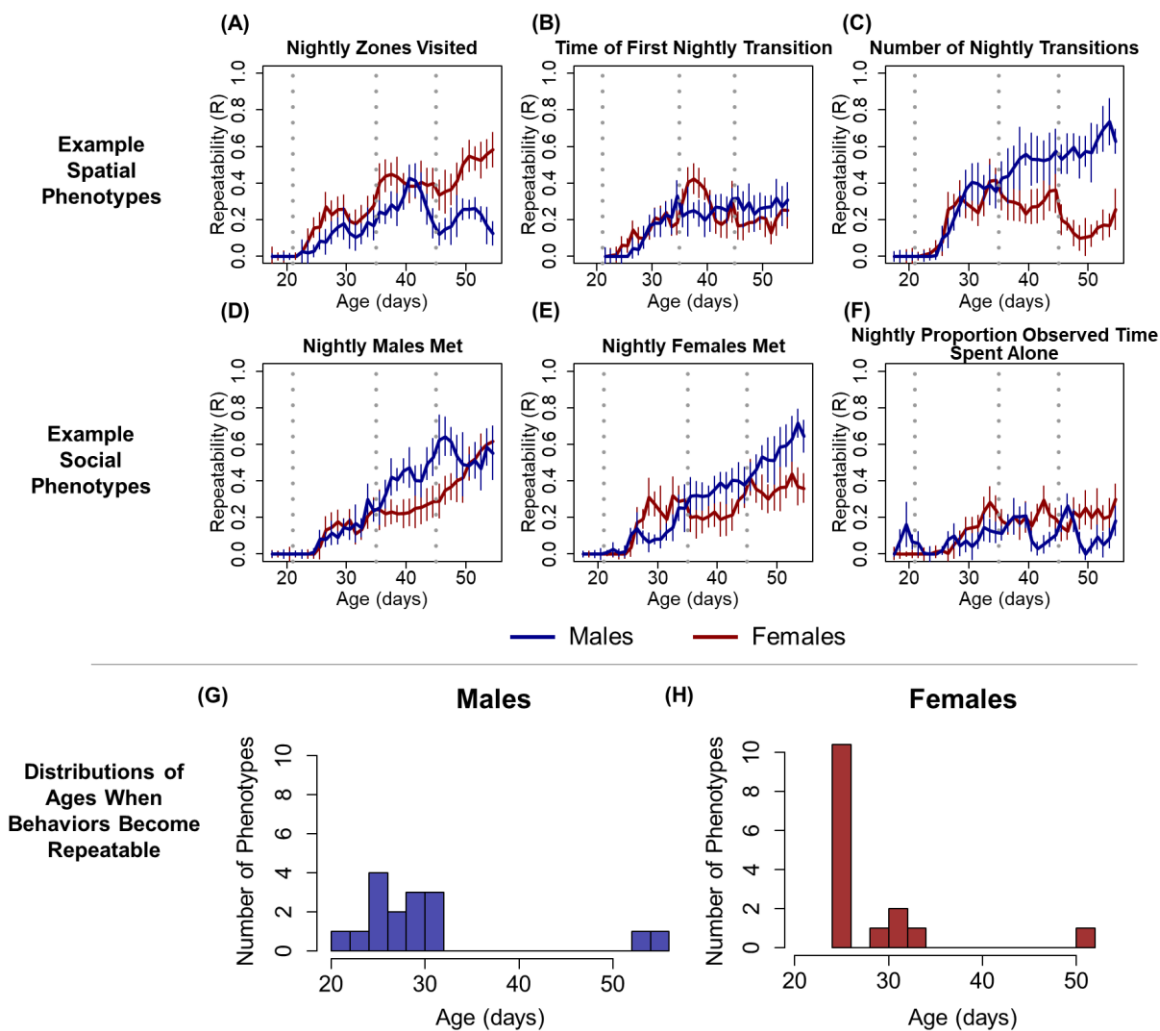
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623

624 **Figure S1. The experimental approach.** (A) An aerial view of our field site. Note that the
625 configuration of resource zones in this photograph is different from the configuration in this
626 experiment. (B) Schematic layout of our field enclosure in this experiment (not to scale). We placed
627 litters, along with their mothers inside of the nest box in one of 16 resource zones, which were
628 distributed into four “neighborhoods” of four zones each. (C) An interior view of one of our resource
629 zones. (D) Overview of data processing pipeline for our experiment. Example RFID positional data
630 show the known location of a single individual in our enclosure over the course of the experiment.
631 Each point represents an RFID read at a given resource zone (y-axis). Red lines between points
632 indicate transitions between resource zones.

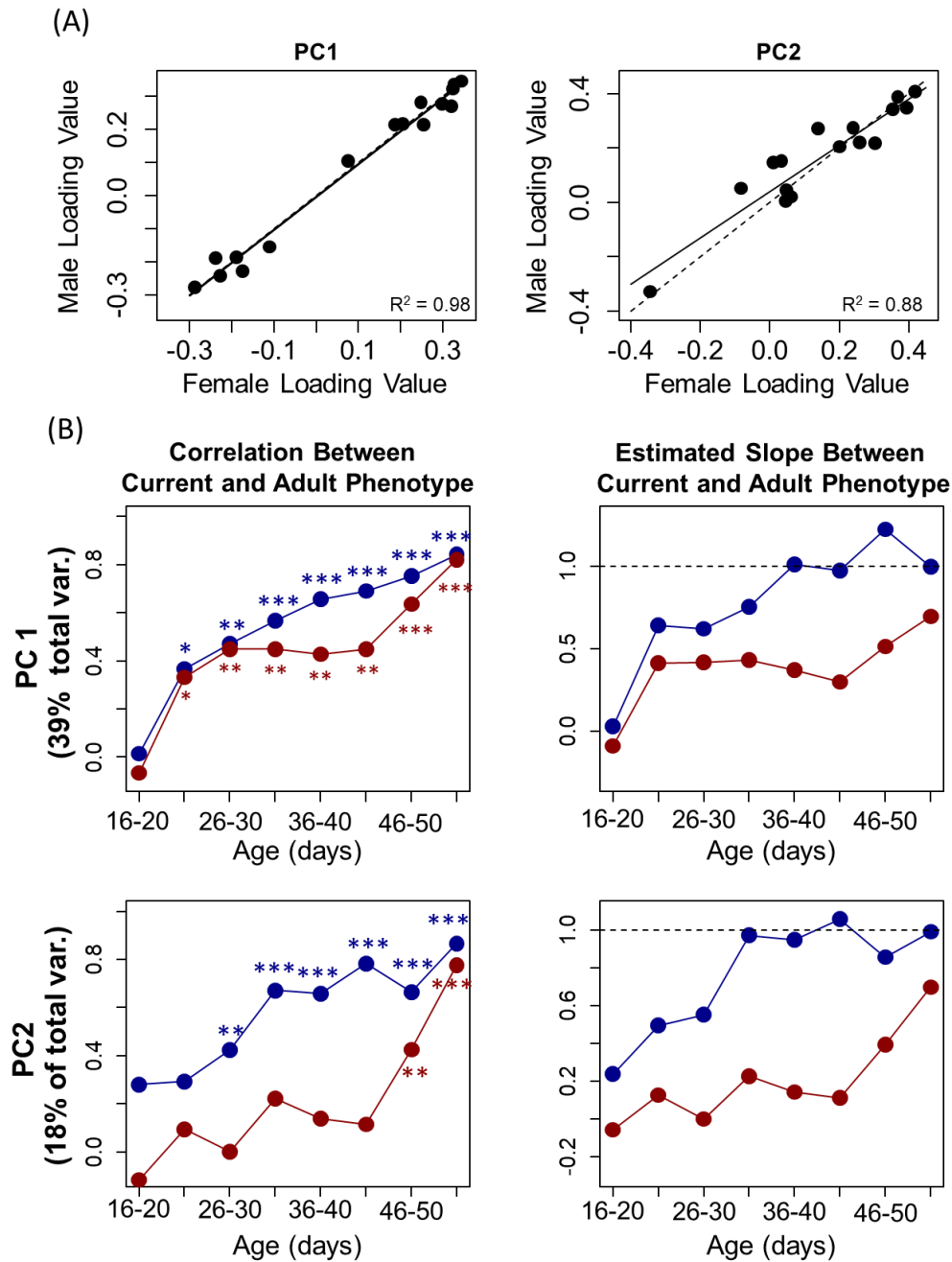
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634

635 **Figure S2. Both males and females developed repeatable individual differences in spatial and**
 636 **social phenotypes, beginning in the juvenile period.** (A-F) Examples of repeatability data for four
 637 representative spatial and social phenotypes. The repeatability measure on the y-axis controls for
 638 maternal/litter identity. Each point represents individual repeatability estimates from each sex
 639 during a sliding five-day window, with the x-axis value representing the center of that window. Error
 640 bars indicate standard error of repeatability estimates. Vertical dashed lines indicate approximate
 641 ages of weaning (21 days), sexual maturity (35 days), and first successful mating (46 days). (G-H)
 642 The distributions of the ages at which behaviors became repeatable for males and females.

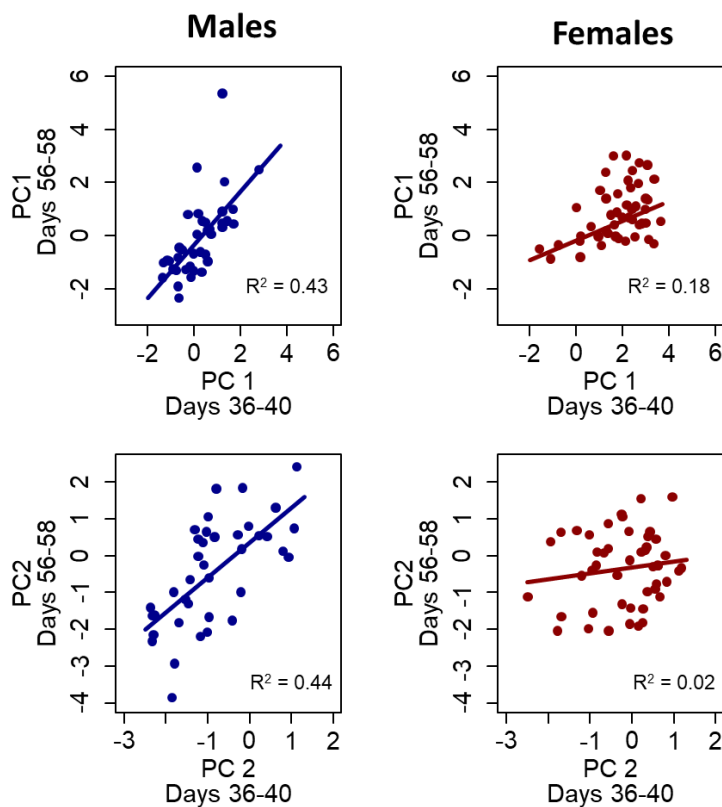
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644

645 **Figure S3.** Results in Figure 1 are unchanged if we use a sex-specific principal components
646 approach. (A) Loading coefficients of individual phenotypes are extremely similar in male-specific
647 and female-specific principal components 1 and 2. Solid line indicates modeled correlation,
648 dashed line indicates a one-to-one theoretical ideal. (B) The same analyses as in Figure 1B, except
649 using sex-specific principal components 1 and 2. The correlation between earlier and adult
650 behavior is stronger in males for both PC1 and PC2 and the slope of the relationship between
651 earlier and adult behavior is closer to 1. Asterisks denote significance of the correlations depicted
652 in each point (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

653



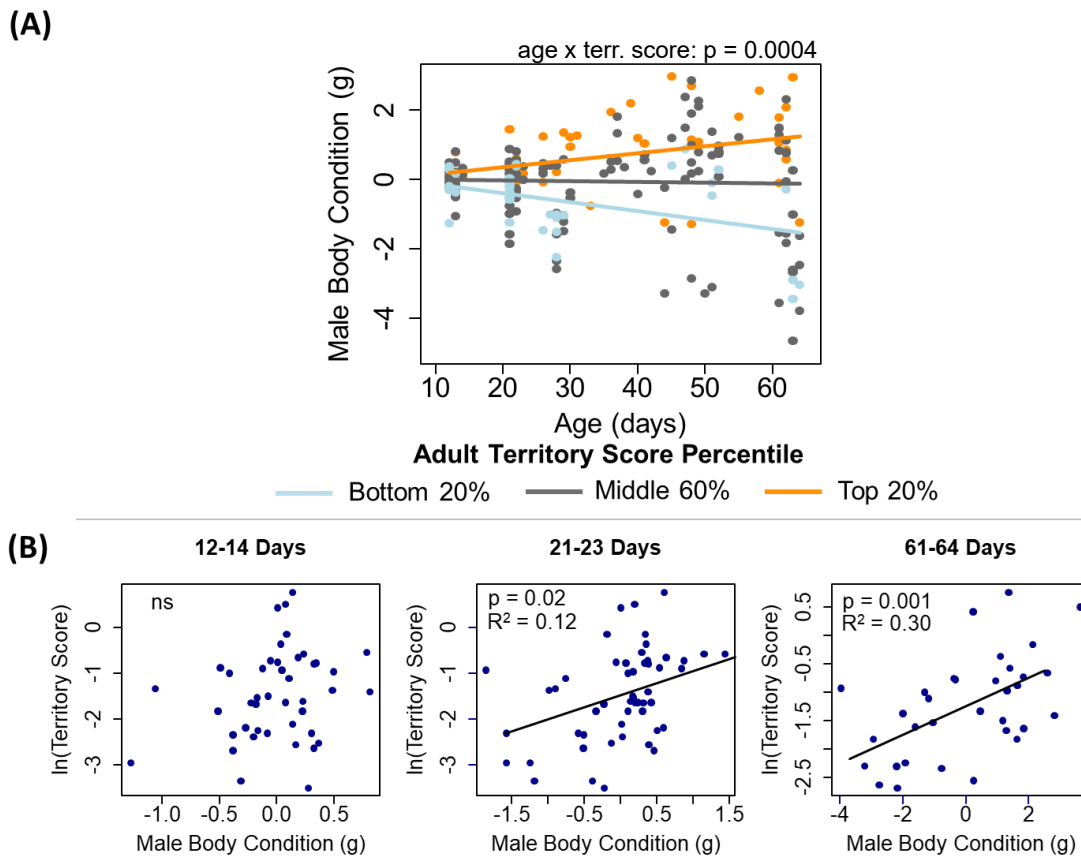
654

655 **Figure S4. An example of the sets of models contained in Figure 1B.** Here we compare the
656 relationship between behavior immediately after sexual maturity (age 36-40 days) and later
657 behavior in adulthood at the end of the experiment (days 56-68 days). For both PC1 (top row) and
658 PC2 (bottom row) the relationship is stronger and the slope estimates are closer to 1.00 for males
659 as compared to females.

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662



663 **Figure S5.** Small differences in initial male body mass are magnified by differential territorial
664 access. (A) The same data as in Figure 3C, but here presented as individual data points. Male adult
665 territory scores are predicted by small differences in body mass in early life, a difference that is
666 magnified over time. The y-axes represent deviations from age-predicted body mass. (B) The
667 strength of the relationship between body condition and adult territory score (days 46-58) increases
668 as males age. Although we collected opportunistic body masses from individuals throughout the
669 experiment, we collected body masses from all animals in the enclosure at three different points:
670 (1) prior to release (age 12-14 days), at weaning (21-23 days), and after we ended the experiment
671 (61-64 days). Initial body condition in infancy did not predict final territory scores (consistent with
672 individuals starting out on an approximately even playing field. However, as males aged, the
673 correlation between territorial behavior and body mass increased in strength, consistent with a
674 competitively induced feedback loop.

675