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Genetically identical mice express alternative reproductive tactics depending on social conditions in the field

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In many species, establishing and maintaining a territory is critical to survival and reproduction, and an animal's ability to do so is strongly influenced by the presence and density of competitors. Here we manipulate social conditions to study the alternative reproductive tactics displayed by genetically identical, age-matched laboratory mice competing for territories under ecologically realistic social environmental conditions. We introduced adult males and females of the laboratory mouse strain C57BL/6J into a large, outdoor field enclosure containing defendable resource zones under one of two social conditions. We first created a low-density social environment, such that the number of available territories exceeded the number of males. After males established stable territories, we introduced a pulse of intruder males and observed the resulting defensive and invasive tactics employed. In response to this change in social environment, males with large territories invested more in patrolling but were less effective at excluding intruder males as compared with males with small territories. Intruding males failed to establish territories and displayed an alternative tactic featuring greater exploration as compared with genetically identical territorial males. Alternative tactics did not lead to equal reproductive success—males that acquired territories experienced greater survival and had greater access to females.

1. Introduction

To deal with dynamic and unpredictable physical and social environmental conditions, animals are predicted to evolve plastic behavioural responses that allow them to make the best of a wide range of scenarios [1,2]. When different environmental conditions lead to different optimal reproductive behaviours, these plastic behaviours are referred to as 'alternative reproductive tactics' or 'conditional reproductive strategies' [3,4]. For many species, establishing and maintaining a territory is a central aspect of individuals' reproductive life history, as territorial control allows them to reliably access physical resources and attract mates [5–11]. We therefore expect behaviours related to territory formation, defence, and invasion to have been under strong selection in these species and for animals to plastically alter their territorial behaviour in response to a wide range of social environmental conditions.

Animals seeking to establish territories may encounter radically different social environments that vary widely in their intensity of competition. At one extreme, animals may seek to establish a territory in a relatively unoccupied environment with an abundance of resources and a lack of competitors for space. This is the situation faced by, for example, rodents living in low-density populations at the start of a breeding season [12–15] or the earliest migratory birds to arrive at a breeding ground [16–20]. On the other extreme, an animal might develop or compete in a world where suitable territories are either largely or entirely filled. Such is the world often encountered by rodents born later in a breeding season after colonization and population growth has already occurred or migratory birds arriving relatively late to a breeding ground [12–20].

In some species, genetic differences determine an animal's reproductive strategy (e.g. the swordtail fish, *Xiphophorus nigrensis* [21], and the pentamorphic guppy *Poecilia parae* [22]). But what if the exact same animal—with the same genotype—found itself in a more or less competitive social environment? How would its territorial behaviour change? In many species, males that are unable to establish territoriality control or social dominance adopt an alternative 'sneaker' tactic to attempt to furtively mate with females as a conditional strategy to make the best of a bad situation [4,23–27]. Yet, in natural populations it is difficult to know whether these differences in tactics are caused by an individual's quality, its history of social interactions, the broader current social context in which it lives, or even indirect genetic effects caused by the genotypes of other animals in its environment. The simplest way to establish unambiguous causality regarding the effect of social environment on individual behavioural decisions is by manipulating a single aspect of social environment while holding genotype and developmental conditions constant. But such manipulations of environmental conditions are rarely, if ever, possible in wild populations [28].

Experimental populations of inbred mouse strains (*Mus musculus domesticus*) living in semi-natural enclosures provide the ideal opportunity for studying the causal impact of social environment on individual competitive and reproductive behaviours. Wild and laboratory mice establish and defend territories when given the space to do so, and territories allow males to monopolize or nearly monopolize access to food and mates [29–37]. And the identical genetics and standardized rearing conditions of inbred strains represent an extreme uniformity across individuals as compared with wild populations, allowing us to manipulate a single aspect of animals' social environments and draw causal conclusions about the impact of this manipulation [28].

In this paper, we characterize the behavioural tactics of genetically identical mice that encounter either (a) a world of abundant, unfilled territorial spaces and limited conspecific competition, or (b) a world in which residents already occupy territories. The resulting data allow us to test the hypothesis that animals with similar prior experiences will rapidly develop alternative tactics in response to the current social environment in which they find themselves. Additionally, we use this data to test three hypotheses regarding mouse territorial behaviour, in particular: (1) that territory size is constrained by social factors, such that males with larger territories face greater invasion pressure than males with smaller territories, (2) that territorial males monitor their social environment and respond to changes in it caused by immigration or death, and (3) that territories confer benefits to males in the form of both survival and access to females. The data also allow us to describe the dynamics of territory formation and defence in the most studied biomedical model organism in finer-grain detail than ever before. Given recent public attention to the constraints of the laboratory environment on drawing useful inferences from laboratory mice, this latter contribution is particularly timely [38].

2. Material and methods

(a) Field enclosure and study subjects

A detailed description of the enclosures at Cornell University's Liddell Field Station can be found elsewhere [39], so here we will only describe those elements critical to the success of this experiment. The enclosure is 15 × 38 m, approximately 9000 times the area of a typical mouse cage. Within the enclosure we set up 12 plastic tubs (31 gallon storage totes, Rubbermaid, USA), placed in an equally spaced 3 × 4 grid across the enclosure (electronic supplementary material, figure S1). Each tub (hereafter 'resource zones') contained ad libitum food access and provided insulation and shelter from adverse weather conditions. We equipped each zone with a single entrance and exit made out of a 6-inch-long PVC pipe (2 inch in diameter). These resources and the single entrance made the resource zones highly valuable, defensible areas that are meant to mimic the foraging landscape of commensal mice. To track the comings and goings of mouse visitors to each zone, we placed a 10 inch radio-frequency identification (RFID) antenna (Biomark, USA) beneath the entrance tube of each zone. The antennas were connected to a central monitoring system (Small Scale System, Biomark, USA) and transmitted RFID reads at a rate of 2–3 Hz.

Our study subjects were 20 male and 20 female eight-week-old laboratory mice (C57BL/6J strain), obtained from The Jackson Laboratory (Bar Harbor, Maine, USA). After arrival at our laboratory, we separated individuals into smaller holding cages containing either two males or four females. After allowing animals to acclimate for 8 days, we administered isoflurane (an inhaled anaesthetic) and injected two subcutaneous passive integrative transponders (PIT) tags in the flank and between the scapulae of each mouse (MINI HPT10, Biomark, USA) using 16-gauge needles. Inserting two PIT tags allowed us to continue to monitor individuals in the field even if one of the tags was lost. Based on past experience, we anticipated PIT tag loss at <5%, making it quite unlikely that any individual mouse would lose both tags during the experiment.

(b) Manipulating the social environment of genetically identical animals

We studied a population of isogenic mice over the course of 35 days in our large outdoor enclosure. On the afternoon of 24 September 2021 (first day) we simultaneously released eight male and eight female mice in the centre of the enclosure. We allowed mice to explore the enclosure and establish territories over the first five nights of the experiment. During this initial stage the number of male mice (8 animals) was substantially smaller than the number of resource zones (12 zones). These animals were entering a world of abundant resources with relatively few competitors.

Then, on the afternoon of 29 September (the sixth night of the experiment) we released 12 additional males (hereafter 'intruding' males) and 12 additional females into the enclosure. We observed mouse movement and spatio-temporal dynamics between the first and second waves of mice. Here we focus on the dynamics of territorial and intruding males, focusing on the first two weeks after the intrusion (day 20 of the experiment). For the remainder of the 35-day experiment, we continued to collect data regarding the long-term stability of social relationships in our study system (not described here) as well as longer-term survival data (described here). We then trapped and removed all surviving animals on day 35.

(c) Radio-frequency identification data analysis

For all analyses below, we used the data collected from the RFID system. We calculated the number of zones that animals visited each night to assess the breadth of animals' movement in the enclosures. We also identified movements between zones each time that an

animal appeared in one zone, followed by the same animal appearing in a different zone. To assess territorial control, we calculated the proportion of male-sourced reads at a zone originating from the male with the highest proportion of reads on each night.

For social network analyses, we inferred the amount of time that animals overlapped in the same zone based on their patterns of RFID reads. We have described the process for inferring the duration of overlap elsewhere in detail [39]. Briefly, if a mouse registered consecutive RFID reads in the same zone within a given time window, we assume that the mouse had been in the zone for the period between those reads. Because the zones are approximately 400% larger than the area of the antennae, mice will often spend substantial time in a zone but only register RFID reads occasionally. To estimate the duration of different visits to a given zone we first identified the 95th percentile of the distribution of the amount of time that passed between reads of the same individual in the same zone across all individuals and all zones in our experiment (211 s). If a mouse registered an RFID read in the same zone with less than this length of time passing between reads, we assumed that it had been present in or around the zone for the entirety of the interim period. We then calculated periods of spatio-temporal overlap with other animals. While this assumption about animals' presence in the zone is of course imperfect, this approach provides a noisy but informative view of the social world of these animals.

(d) Statistical analyses

We performed all statistical analyses in R [40]. We built mixed effects models using the glmmTMB package [41]. For each analysis any transformations of response or predictor variables were chosen based on visual inspection of the relationship between the two variables as well as the resulting residuals from models of untransformed variables. We included relevant random intercepts and random slopes in each mixed effects model, as appropriate. We identify the random effects structure for each analysis in the results tables below. We performed the repeatability analysis described below using the rptR package [42] and the time-varying survival analysis using the survival package [43].

3. Results

In this experiment, we exposed genetically identical, age-matched male mice to two different social environments—one in which territories were empty and resources were abundant and one in which territories were full and resources were restricted. Below we first describe the social and spatial behaviour of the first group of males in an empty social environment, followed by their different reactions to the addition of the second group of males. We then compare the alternative socio-spatial behaviour of the two groups of males, depending on the social environment that they encountered. We close by describing the differential survival and apparent reproductive outcomes obtained by the males that encountered the two different social environments.

(a) Behaviour of males entering an empty social environment

For the first 5 days in the enclosure, the eight original males experienced an environment with abundant resources and relatively low levels of competition. During this time, the number of available resource zones exceeded the number of males, and the eight males rapidly established territorial control over each of the 12 resource zones. Across all 12 zones, the proportion of all RFID reads belonging to the eventual territory male increased during the first five nights of the experiment, such that nearly all (99.97%) of those reads recorded on night 5 were reads from the territory holder (electronic supplementary material, figures S2 and S3). The pattern of increasing control over each zone by a single male resembles patterns observed for this strain in a previous experiment [39]. Animals showed strongly nocturnal behavioural patterns, with 83% of transitions between resource zones occurring between 18.00 and 6.00 (and 97% occurring between 16.00 and 8.00; electronic supplementary material, figure S4). To reflect this activity pattern, hereafter we refer to 'nights' and 'nightly' behaviour to mean the behaviour that animals engage in between noon on one day and noon on the following day.

By night 5, each male accounted for the majority of male reads in either one ($n = 4$) or two ($n = 4$) resource zones. Males displayed strikingly different patterns of space use depending on the number of zones contained within the territories that they established. Those males that established territories containing a single zone (hereafter 'one-zone males') very rarely visited another zone (figure 1; electronic supplementary material, figure S3), averaging only 2.5 transitions between zones each night during these first five nights of the experiment. By contrast, males holding two territories (hereafter 'two-zone males') consistently spent time in one resource zone during the day and made frequent excursions between the two zones at night (figure 1; electronic supplementary material, figure S3), averaging 11.0 transitions between zones during the same period.

(i) Territory size influences resident male behaviour in the face of intruders

On day 6 of the experiment, we added an additional 12 males (hereafter 'intruder males') and 12 females to the enclosure. Territorial males responded differently to this introduction depending on whether they held one or two resource zones within their territory. On the night of the introduction, two-zone males responded by significantly increasing the frequency with which they moved between their two zones ($p < 0.0001$). The magnitude of this increase varied among these four males, but was substantial in all four cases, ranging from a 200 to a 383% increase as compared with the average number of zone transitions during their first five nights (figure 1). By contrast, males holding a territory containing a single resource zone significantly *decreased* the number of nightly transitions that they made between zones—these males essentially never moved between zones again after the introduction of additional males (figure 1, table 1). These results indicate (1) that males were monitoring their social environment and scaling their behaviour in response to changes in it, (2) that males with larger territories needed to expend more energy on patrolling and defending their territories as compared with males with smaller territories, and (3) that this energetic cost of territory size was especially acute under dense social conditions, when intruder males were present (i.e. after night 5 of the experiment).

No successful takeover event appeared to occur during the two weeks following the introduction of new males (up to and including night 20 of the experiment). A successful takeover would have been visible in our data as an event in which a new male became responsible for a plurality of RFID reads within a zone on a given night and maintained that position thereafter.

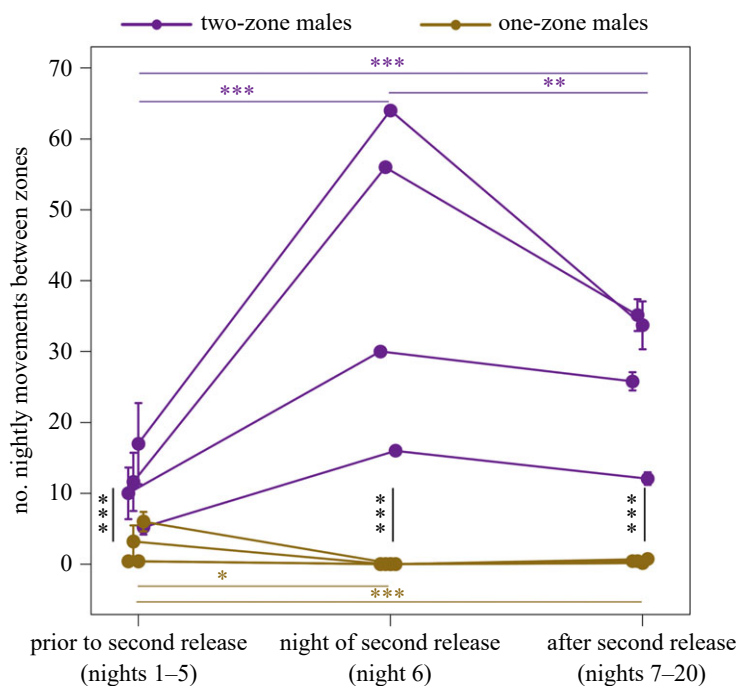


Figure 1. Males responded to the introduction of intruder males differently, depending on the size of their territory. The y-axis represents the average number of nightly transitions between resource zones that males performed, with each point representing a single male during a different period of the experiment. Males with larger territories, containing two resource zones (purple points and lines), increased their number of nightly trips between zones in response to the introduction of intruding males on night 6, and maintained elevated patrolling behaviour thereafter. By contrast, males with smaller territories, containing only one resource zone (gold points and lines) responded by reducing their number of nightly transitions between zones and essentially never moving between zones again. Asterisks indicate levels of statistical significance for comparisons, extracted from mixed-effects models (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$; table 1).

Table 1. Comparisons of the average number of transitions between zones made by males with different territory sizes at different points in the experiment. Bold type indicates statistical significance ($p < 0.05$).

comparison	mean 1	mean 2	z-value	p-value ^a
<i>two-zone males over time</i>				
nights 1–5 versus night 6	11.0	41.5	6.4	<0.0001
nights 1–5 versus nights 7–20	11.0	26.7	6.9	<0.0001
night 6 versus nights 7–20	41.5	26.7	−3.4	0.0006
<i>one-zone males over time</i>				
nights 1–5 versus night 6	2.5	0.0	−2.5	0.01
nights 1–5 versus nights 7–20	2.5	0.4	−4.3	<0.0001
night 6 versus nights 7–20	0.0	0.4	1.0	0.33
<i>one-zone males versus two-zone males</i>				
nights 1–5	2.5	11.0	3.5	0.0004
night 6	0.0	41.5	4.3	<0.0001
nights 7–20	0.4	26.7	5.7	<0.0001

^aExtracted from mixed effects models including a random effect of male ID.

In two cases, an intruder male was responsible for a plurality of RFID reads at an antenna for a brief period, but the original territorial male then quickly reclaimed the territory.

(ii) Relative defensibility of differently sized territories

Given their increased effort to maintain the integrity of their territories, we next asked whether two-zone males were able to defend their territories with a comparable degree of success to one-zone males. Figure 2 displays the average proportion of reads in a given zone that originated from the territory-holding male, depending on whether that male held one or two zones in his territory. Although there was no significant difference between these values on night 5 of the experiment ($p = 0.45$, before the introduction of new males), a large difference emerged following the introduction of additional males on night 6.

While one-zone males experienced only a negligible reduction in their ability to exclude other males from their territories, zones controlled by two-zone males experienced substantial incursion (figure 2a, table 2). Across nights 6 to 20, the proportion of reads in a given zone belonging to the territory holder was significantly lower if the territory holder was a two-zone male

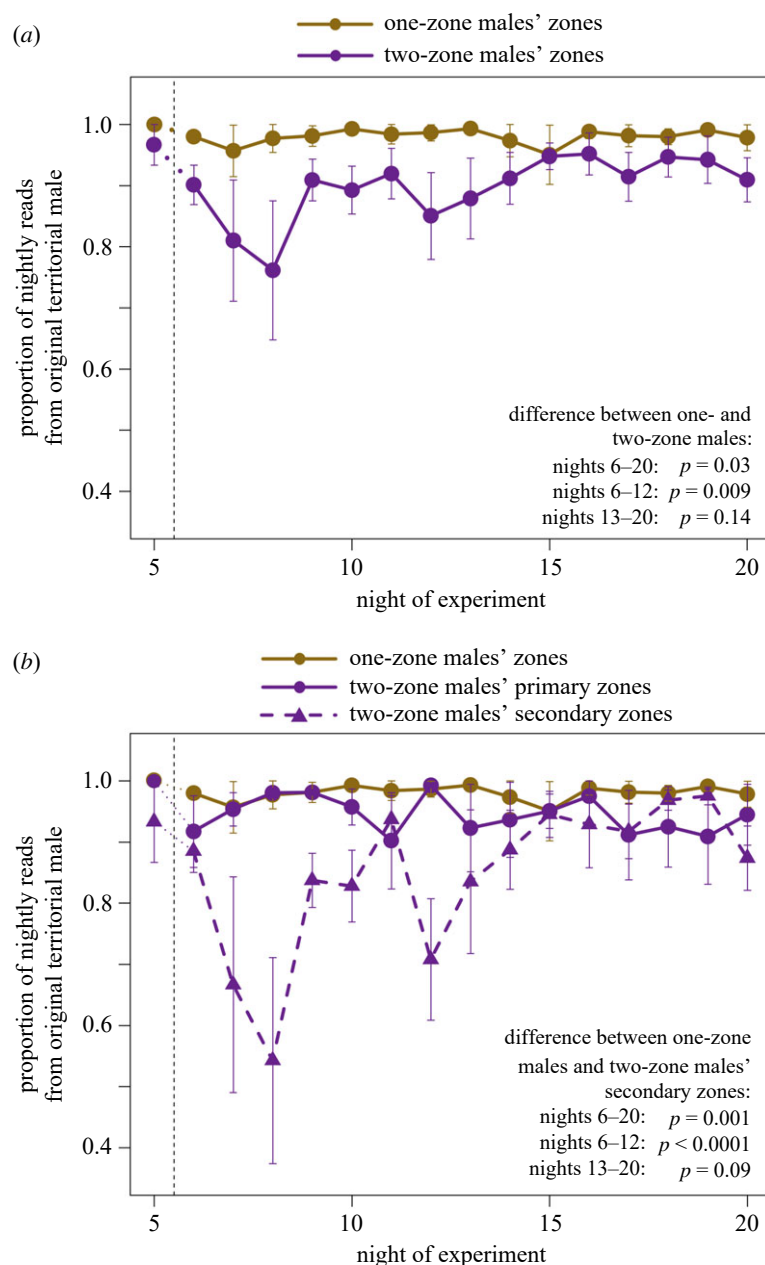


Figure 2. Two-zone males were somewhat less able to defend their territories from intruders. (a) The y-axis represents the average across zones of the proportion of nightly RFID reads that originated from the territorial male that controlled the zone. Higher values correspond to a zone being more defensible and suffering fewer incursions by non-territory holders. Following the introduction of new males (indicated by the vertical dashed line), zones contained in larger territories became significantly less defensible than zones contained in smaller territories. (b) This difference in defensibility was true only of one of the two-zone males' zones (their 'secondary' zones). Two-zone males were able to maintain territorial integrity comparable to one-zone males in their primary zones. In both panels, p -values refer to mixed effects models that included random effect of territorial male ID.

Table 2. Comparisons of the average proportion of RFID reads in a given resource zone that originated from the territory holder (a measure of defensibility), depending on territory size. Bold type indicates statistical significance ($p < 0.05$).

period of comparison	one-zone males' zones	two-zone males, both zones (z-value; p -value) ^b	two-zone males' primary zones only (z-value; p -value) ^b	two-zone males' secondary zones only (z-value; p -value) ^b
night 5	1.00	0.97 (−0.8; 0.45)	1.00 (0.0; 1.00)	0.94 (−1.4, 0.16)
nights 6–20 ^a	0.98	0.90 (−2.2; 0.03)	0.94 (−0.9, 0.37)	0.85 (−3.3, 0.001)
nights 6–12 ^a	0.98	0.86 (−2.6, 0.009)	0.95 (−0.5, 0.59)	0.77 (−4.5, <0.0001)
nights 13–20 ^a	0.98	0.93 (−1.5, 0.14)	0.93 (−1.2, 0.24)	0.92 (−1.7, 0.10)

^aExtracted from mixed effects models including a random effect of territory holder ID.

^bAll z- and p -values are in comparison with one-zone males' zones.

(mean = 0.90) rather than a one-zone male (mean = 0.98, difference: $p = 0.03$). This effect was strongest during the week starting on the night of male introduction (nights 6–12), when the mean proportion of reads from the territory holder was only 0.86 in zones held by two-zone males, but remained at 0.98 in zones controlled by one-zone males ($p = 0.009$).

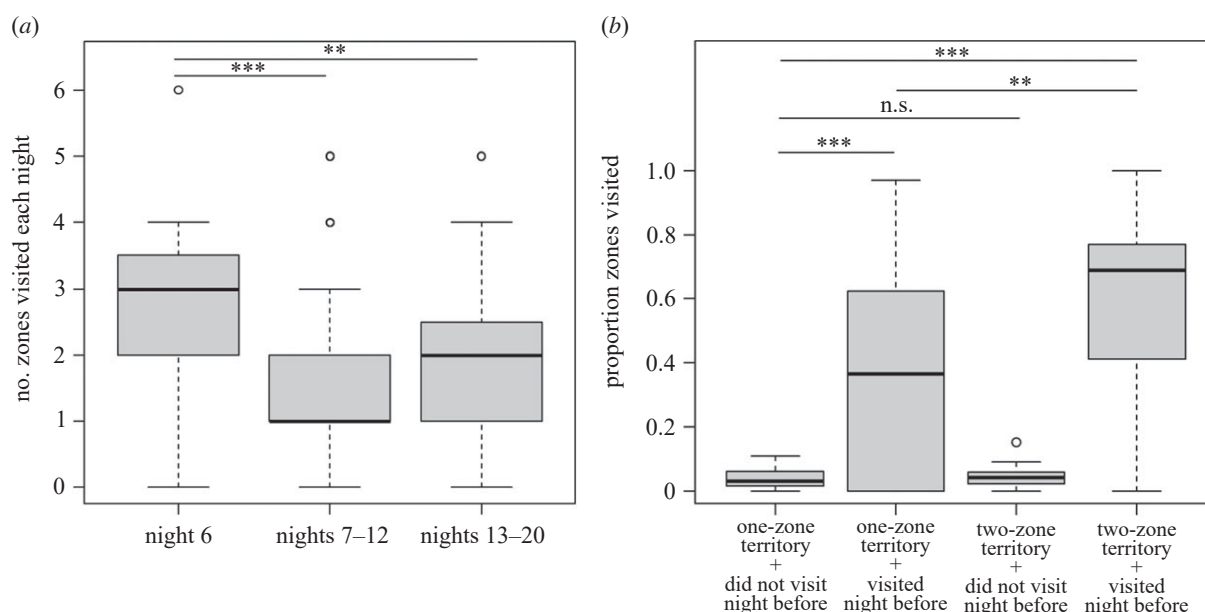


Figure 3. The zone visitation patterns of intruding males. (a) Intruding males made nightly visits to occupied resource zones, but visited fewer zones after their first night in the enclosure (night 6). Boxplots represent the distribution of nightly visits in each period for all intruding males. (b) Intruding males were more likely to visit a zone on a given night if they had visited the zone the night before. This site fidelity was especially strong when the zone belonged to a two-zone male. In both panels significant differences (identified with a mixed effects model) are identified with asterisks (** $p < 0.01$, *** $p < 0.001$). n.s., not significant.

Table 3. Results from mixed effects models regarding the behaviour of intruding males. Bold type indicates statistical significance ($p < 0.05$).

parameter	estimate	s.e.	z-value	p-value	interpretation
<i>number of zones that intruding males visited on a given night^a</i>					
intercept (reference = night 6)	2.9	0.3			intruding males visited more zones on their first night in
nights 7–12	−1.2	0.3	−3.5	0.0004	the enclosure as compared with subsequent nights
nights 13–20	−1.1	0.3	−3.3	0.001	
<i>probability that an intruding male visited a given zone on a given night^b</i>					
intercept	−3.3	0.5			
zone held by two-zone male	0.7	0.7	0.9	0.34	
did the the same male visit the zone on the previous night? (yes versus no)	1.3	0.4	3.4	0.0007	an intruding male was much more likely to visit a zone if he had visited the same zone the previous night
zone held by two-zone male × same male visited yesterday	1.2	0.4	2.7	0.006	the effect of visiting a zone on the previous night was stronger when the zone was controlled by a two-zone male

^aEstimates extracted from linear mixed models including random effects of intruding male ID.

^bEstimates extracted from generalized linear mixed model (binomial error distribution) including random effects of intruding male ID, territorial male ID and zone ID, as well as a random slope of territory size nested within intruding male ID.

Additional investigation revealed that two-zone males did not suffer incursions into their two zones at equal rates. Instead, two-zone males appeared to prioritize defensive attention on one of their two zones, from which they were able to almost entirely exclude intruding males (their 'primary' zone; figure 2b, table 2), mirroring the ability of one-zone males. By contrast, the second zone that they controlled (their 'secondary' zone) was significantly less defensible than zones controlled by single males (figure 2b, table 2).

(b) Behaviour of males entering a filled social environment

The males that we added on night 6 of the experiment entered a filled social environment that lacked any available resource zones. Although no intruding males successfully took over any resource zones in the first two weeks after their addition, they did make frequent visits to existing males' territories. Intruding males' space use and exploratory behaviour changed over the course of the experiment. Intruding males explored the greatest number of zones on their first night in the enclosure (mean = 2.9, 95% CI: 2.2–3.7), before visiting fewer zones on ensuing nights (mean = 1.8, 95% CI: 1.4–2.1, $p = 0.0004$; figure 3a, table 3).

Given our finding that zones controlled by two-zone males were more prone to intrusion by non-territorial males (figure 2, table 2), we sought to gain a better understanding of the decision-making processes among intruding males that led to this outcome. To do so, we built a mixed effects logistic regression model to interrogate the decision-making process at the level of an individual intruding male mouse on a given night. This analysis yielded two results. First, intruding males appeared to show

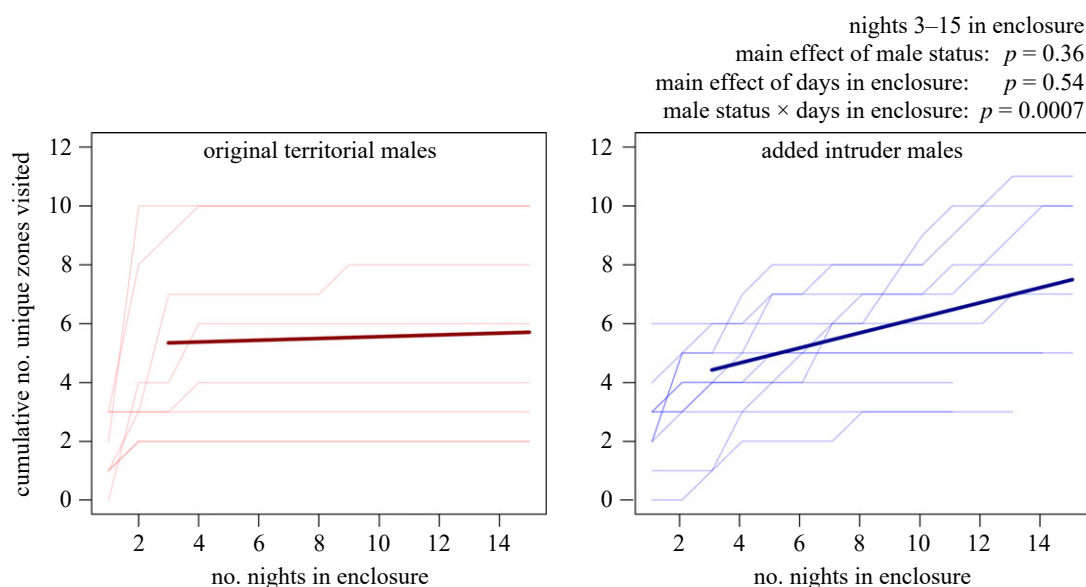


Figure 4. Male exploratory behaviour differed, depending on whether the male encountered an environment without any occupied territories (left) or an environment with all territories already filled (right). The y-axis represents the cumulative number of resource zones that males visited and the x-axis represents how many nights males had been in an enclosure. Intruding, but not territorial, males continued to explore the enclosure after initial exploration, such that the intruding males had visited substantially more zones by the end of the experiment. Faint lines represent data from individual males and thick curves represent model estimates from the mixed effects model described in [table 4](#).

Table 4. Results from a mixed effects model predicting the number of cumulative unique zones visited by a male after its first three nights in the enclosure. Results are from a linear mixed effects model that also included a random intercept of male ID along with a random slope of total nights spent in the enclosure. Bold type indicates statistical significance ($p < 0.05$).

parameter	estimate	s.e.	z-value	p-value	interpretation
intercept (reference = original males)	5.3	0.8			
total no. nights spent in enclosure (nights 3–15)	0.03	0.05	0.6	0.54	original males visited very few new zones after their first three nights in the enclosure
male was an intruding male	−0.9	1.0	−0.9	0.36	original and intruding males visited a comparable number of unique zones during their first three nights in the enclosure
intruding male × nights	0.23	0.07	3.4	0.0007	intruding males continued to visit new zones throughout their time in the enclosure

some spatial fidelity, despite not holding territories in resource zones. Intruding males were much more likely to visit a zone on a given night if they had visited that zone on the previous night ($p < 0.0001$; [figure 3b](#), [table 3](#)). And this site fidelity was especially strong when the zone the intruder had visited the night before belonged to a two-zone male (interaction with territory size, $p = 0.006$; [figure 3b](#), [table 3](#)).

(c) Alternative tactics between males entering different social environments

We found strikingly different patterns of exploratory behaviour, depending on whether males entered an environment of unoccupied territories (the first males) or instead entered an environment in which all territories were already occupied ([figure 4](#)). While both sets of males explored similar numbers of resource zones during their first three nights in the enclosure, the original males that were able to find and acquire territories largely ceased exploration after these first three nights. In fact, after these first three nights, four of the eight original males never entered a new zone again during their next 12 nights in the enclosure (the remaining four entered one or two new zones each, mean for all eight original males = 0.6; see electronic supplementary material, [figure S5](#)). By contrast, the males added on night 6 (which were unable to establish territories in the zones that they had explored after three nights) continued to explore new zones (mean new zones among surviving intruders = 4.2 zones; interaction between status and time in enclosure, $p = 0.0007$; [table 4](#)). The outcome of this difference in exploratory behaviour was that the group of intruding males on average had explored substantially more zones by their 15th night in the enclosure than the original territorial males (night 20 of the experiment, 7.5 zones versus 5.7 zones; [figure 4](#)). A comparable analysis that considers as the unit of analysis the number of nightly new zones that a male visited yields the same results (electronic supplementary material, [figure S5](#)).

A cursory examination of [figures 3](#) and [4](#) reveals substantial variation in intruding males' space use, which may reflect differences in efforts to explore and monitor territories and the males that controlled them. Indeed, while some intruding males

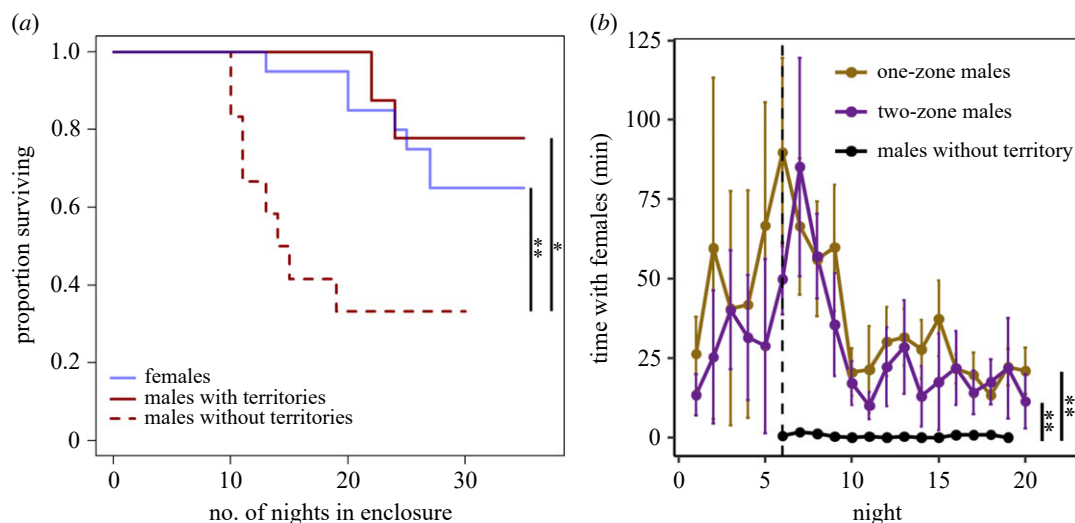


Figure 5. (a) Males with territories experienced a survival advantage as compared with males without territories and survived at comparable rates to females. (b) Males with territories spent more time overlapping with females in resource zones than males without territories. Asterisks indicate statistically significant differences between groups (*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$).

generally visited one zone each night after their first night in the enclosure, others consistently visited two or more zones. Overall, male identity explained an estimated 25% of the variance in the number of zones that an intruding male visited on each of nights 7–20 of the experiment (95% CI = 0.06–0.45, $p < 0.0001$). In the current paper we are unable to assess whether such variation in space use among intruding males shapes eventual territory acquisition or reproductive success, but the presence of such variation suggests a fruitful path for future studies.

(d) Survival and reproductive opportunities of males expressing alternative behavioural tactics

Finally, we assessed whether males expressing alternative behavioural tactics achieved apparent differences in fitness, as measured by (a) survival and (b) access to females.

Over the full 35-day experiment (figure 5a), males without territories died at significantly higher rates than did either (a) males with territories (hazard ratio = 5.9, 95% CI = 1.2–29.1, $p = 0.03$) or (b) females (hazard ratio = 4.7, 95% CI = 1.6–14.3, $p = 0.005$). Given the low levels of mortality in territorial males, we were unable to assess whether territory size (i.e. two zones versus one zone) had an additional effect on territorial male mortality.

We are unsure of the cause of inferred mortality for any given individual. The bias towards increased mortality in males, especially non-territorial males, suggests that exclusion from resources or injury during competition may have played a role in some mortality. This male-biased mortality mirrors findings from populations of wild mice (reviewed in [44]). At the same time, female mortality did occur, which indicates that animals can die even in the absence of these challenges. Females were relatively unconstrained in their movement and unlikely to have experienced either resource scarcity or violent competition. The causes of these female deaths are especially unclear, but might have included predation (our netting is predator resistant, but is imperfect in excluding some small predators), infectious disease or parasitism, or exposure.

We also assessed whether territorial males achieved greater access to females than males without territories. Territorial males spent much more time overlapping with females in resource zones than did males without territories (linear mixed effects model $t_{98} > 4.3$, $p < 0.0001$; figure 5b), independently replicating recently published results from a different study in this system [39]. In addition, we found that one- and two-zone males spent comparable amounts of time overlapping with females ($p > 0.05$; figure 5b). Thus, we identified major differences in reproductive success in our system that were not the result of any differences in genetics or developmental environment (i.e. animals' life in the laboratory prior to release), but instead were the result of the competitive social environment that a male happened to encounter in our enclosures.

4. Discussion

By manipulating the social environment experienced by genetically identical, age-matched mice, we have identified causal impacts of the current social environment on individuals' behavioural tactics. When placed in semi-natural field enclosures that reproduced ecologically relevant physical and social conditions, the canonical strain of laboratory mouse (C57BL/6J) expressed at least three alternative reproductive tactics, depending on the social environment that individuals encountered. Males that entered a world of abundant resources and a low number of competitors established territories and rarely left these spaces after establishing control over them. By contrast, age-matched, genetically identical males that encountered a filled social landscape without available territories failed to monopolize space and instead continued to explore a wider range of the physical space in the enclosure. For territorial males, the size of their territory and the addition of intruder males had strong impacts on their space use and movement patterns, indicating that males are acutely aware of changes to their social environment and alter their behaviour in response to such changes.

Unlike many studies of conditional strategies or alternative mating strategies under natural conditions, which examine the role of nutritional [45,46], abiotic [47] or genetic [48,49] factors in determining behaviour, here we controlled genetic and developmental variation by using a single inbred strain of laboratory mice. The only difference between those males expressing territorial behaviour and those expressing intruder behaviour was the social environment into which they were placed. This study joins recent advances in laboratory-based manipulations of social status in monkeys [50] and mice [51] and social experience in flies [52] that reveal the individual and society-level impacts of variation in a controlled social environment. Though not measured here, our social manipulation likely also led to differences in males' physiology and resource deployment, such as differences in gene expression or metabolism and signal allocation. In the laboratory, dominant animals show different gene expression profiles from subordinate animals [53], and animals that experience competitive success or failure rapidly alter their patterns of chemical signalling through urination [54].

The alternative reproductive tactics that males expressed were accompanied by apparent differences in survival and access to females. Males that entered a filled social environment and were forced to pursue a territory-less tactic died more quickly and spent less observed time overlapping with females while they were alive. We expect that it is exceedingly likely that territorial males produced more offspring than non-territorial males. Females do not seem to be repelled by territorial aggressiveness from males and they build both tunnels and nests under the resource zones that males control (M. N. Zippel & C. C. Vogt 2020–2023, personal observations). Still, it is possible that non-territorial males managed to occasionally mate successfully with females during their incursions into other males' territories. Thus, these different tactics that we observed are not two genetically determined strategies that yield approximately equal reproductive success. Instead, males pursue alternative tactics within a single reproductive strategy, depending on the social environment that they encounter.

Within the group of territory-holding males, maintaining larger territories appeared to come with a socially imposed cost. After the addition of intruder males, those zones that were controlled by two-zone males were more vulnerable to incursion. Territories (in particular, 'secondary zones') were less well monopolized, and intruding males' tendency to return to the same zones on subsequent nights was particularly strong when that zone was controlled by a two-zone male (figures 2 and 3). This latter finding suggests that by visiting the territory of a two-zone male, intruders assess that the territory may be relatively porous or otherwise attractive, causing them to be particularly likely to return the following night (a version of a 'win–stay, lose–shift' tactic [55]). We suspect that two-zone males treat their secondary zone as a valuable 'backup' territory in an effort to hedge their bets in the event that they are overthrown by an intruder male in their primary territory.

The primary limitation of this study is that we were only able to measure space use within the resource zones that we set up, which likely represent a small, though extremely important, part of a male's territory. We infer that all territorial mice spent a substantial, but minority, portion of their time in and immediately around these zones (on the order of 3–10 h per day on average). We suspect that the remainder of males' time was spent outside of zones, but within the rest of their territories, which we suspect comprised approximately 10–30 square metres surrounding the zone(s) that the male controlled, as well as the series of tunnels that mice regularly dug below their zones. Still, we expect our measures of male space use within zones to largely predict space use within the larger territories outside of the zones. This expectation is bolstered by results from Smith *et al.* [56], who reported that in California ground squirrels space use below ground (inferred by a similar RFID approach taken here) strongly predicted above-ground social networks that were observed directly.

What implications do our results have for wild mice? We intentionally matched the starting and ending densities of our enclosures to fall within the range of densities published for wild house mice (our densities ranged from 0.03 to 0.07 mice m⁻²; published range = 0.003–5.0+ mice m² [57,58]). Nevertheless, although our semi-natural enclosures are much larger and naturalistic than standard laboratory conditions, unsuccessful individuals are still constrained in their ability to disperse. Under fully wild conditions, males that are unable to form a territory in a given space could eventually disperse over a greater distance in search of an available territory. Alternatively, the overall social structure of *Mus musculus* could be density dependent, mirroring the density dependence of some other rodents (e.g. African striped mice [59,60]). Indeed, Anderson [30] suggested just such a density-dependent social structure based on the limited demographic evidence available at the time [30].

No non-territorial males visited all 12 resource zones, suggesting that males at this density might engage in the floater reproductive tactic for weeks, even when additional space remains unexplored. What is more, under substantially denser conditions (but short of plague-level densities), available territories may be limited or non-existent. Under such conditions, floater males may still encounter consistent resistance from territorial males and have no better luck finding available territories by dispersing over a wider range. Indeed, it has been previously observed that wild male house mice have greater mortality than females, and hypothesized that this differential mortality is borne by territory-less males [44]. We therefore suspect that the floater behaviour that we observe in our enclosure, and its associated survival costs, are likely generally consistent with those that occur under at least some fully natural conditions [44].

Although the focus of our study here is territorial behaviour in males, evidence from a long-term study of wild mice in Switzerland suggests that wild female mice also display alternative reproductive tactics. Specifically, females seem to follow a condition- and density-dependent strategy when deciding whether to rear litters as a solitary mother or communally with other females. In this system, younger, lighter females are more likely to rear pups communally with other females, while older females often shift to a more successful solitary rearing tactic [61]. The balance of these tactics is also density dependent, with communal breeding being more common under high-density (lower-quality) environmental conditions [62].

The approach that we take here—studying the impacts of variation in social environment in model organisms living outside of a highly artificial laboratory environment—holds great potential for additional advances [28]. By focusing on what is important to these animals' natural history, in combination with using high-throughput approaches to study animals whose genetics, demography, and social environment we can control, we are able to test hypotheses and draw causal conclusions about behaviour, individuality and society. These same conclusions are extremely difficult if not impossible to obtain with unambiguous causality in either fully wild populations or the overly constrained social conditions of the laboratory.

Ethics. The research described in this manuscript was approved by the Cornell Institutional Animal Care and Use Committee under protocol 2015-0060. This protocol was first approved in 2015 and has since been repeatedly amended and updated, most recently prior to this experiment on 24 June 2021. Studying animals in semi-natural enclosures rather than the laboratory creates some challenges that may be unfamiliar to some readers. For example, we are unable to monitor the health of individual mice during the experiment. Because mortality is often high in experiments like these (e.g. [63,64]), we made an effort to reduce the total number of animals that we used in our experiment.

Data accessibility. Data and code supporting these analysis can be found at the following link: <https://doi.org/10.5061/dryad.2ngf1vvhv1> [65].

Supplementary material is available online [66].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. M.N.Z.: conceptualization, data curation, formal analysis, funding acquisition, investigation, visualization, writing—original draft, writing—review and editing; C.C.V.: conceptualization, data curation, formal analysis, methodology, visualization, writing—original draft, writing—review and editing; M.J.S.: conceptualization, funding acquisition, project administration, resources, supervision, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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