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The tendency for social submission predicts superior cognitive performance in previously isolated male mice

Louis D. Matzel^{a,*}, Stefan Kolata^a, Kenneth Light^b, Bruno Sauce^a

^a Department of Psychology, Program in Behavioral Systems Neuroscience Rutgers University Piscataway, NJ, 08854, United States

^b Department of Psychology, Barnard College of Columbia University, New York, NY, 10027, United States

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ABSTRACT

The imposition of subordination may negatively impact cognitive performance in common social settings (e.g., the classroom), and likewise, laboratory studies of animals indicate that the stress associated with social defeat can impair cognitive performance. It is less clear whether an animal's *predisposition* for social subordination (i.e., a tendency that is expressed *prior* to experience with social defeat) is related to its cognitive abilities (e.g., "general" intelligence). Using genetically diverse CD-1 male mice, here we determined that in the absence of adult experience with social hierarchies or social defeat, the predisposition for social subordination was associated with superior general cognitive ability (aggregate performance across a battery of five learning tasks). The tendency for social subordination was not dependent on the mice' body weight, but both general cognitive ability and the tendency for social subordination were directly related to high stress reactivity (i.e., free corticosterone elevations induced by mild stress). This pattern of results suggests that submissive behavior and sensitivity to stress may be associated with superior cognitive *potential*, and this can reflect a native predisposition that precedes exposure to social pressures. More broadly, these results raise the possibility that socially subordinate animals evolved compensatory strategies to facilitate their survival, and that absent the *imposition* of subordination, normally submissive individuals may be better prepared for cognitive/academic achievement.

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* Corresponding author at: Department of Psychology, Rutgers University, Piscataway, NJ 08854, United states.
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1. Introduction

Among humans, the imposition of subordination (e.g., in the classroom) may produce circumstances that are detrimental to learning, such as elevated stress levels or a failure to effectively engage one's environment (Baumeister et al., 2002). Like humans, in their native environments, mice live in social groups, and socialization can improve cognitive performance in laboratory mice relative to mice housed in social isolation (Chida et al., 2006; Voiker et al., 2005). However, it has also been observed that the imposition of social subordination (which is often imposed on subsets of animals in many social groups) can impair cognitive performance in mice (Colas-Zelin et al., 2012; Fitchett et al., 2005). These patterns of results indicate that the benefits of social interactions can vary according to an animal's position in a social hierarchy, a conclusion supported by the observation that stress reactivity (e.g., corticosterone elevations) can covary with an animal's social status (Sapolsky, 2005). Despite the ramifications of these observations, there have been few attempts to elucidate the relationship between an animal's predisposition to behave in a dominant or subordinate manner and its innate cognitive abilities (but see Mery and Kawecki, 2003; for an example in *Drosophila*, and Cole and Quinn, 2012; for an example in birds). This neglect is significant, given that recent theories in evolutionary biology have suggested that humans began to form social groups at a time when testosterone levels (which is associated with aggressive behaviors) among males dropped (Cashdan and Downes, 2012). Not surprisingly, with decreased testosterone levels and socialization came a pattern of advances indicative of rapid increases in intelligence (Dawson, 1972).

To fully understand the relationship between innate tendencies toward submissiveness and intelligence, it would be necessary to isolate individuals from prior experience with social hierarchies (and the aggressive behaviors that are embedded in them) and then assess their cognitive abilities. In this regard, the use of mammalian animal models such as the mouse can be especially useful because individuals can be safely housed individually after the time of weaning (and long prior to adolescence). In the past, we have developed behavioral and analysis methods with which it is possible to characterize the general cognitive ability of outbred laboratory mice (Kolata et al., 2005; Matzel et al., 2003; Matzel et al., 2006; Wass et al., 2012), and this cognitive trait has been described as qualitatively analogous to what is described in humans as intelligence (Blinkhorn, 2003). This approach makes it possible to ascertain the degree to which social submission and general cognitive ability are related. Furthermore, we can then assess whether either of these innate traits are associated with other possible influences such as physical stature (e.g., body weight) or stress reactivity. While this issue has been partially addressed with both an experimental approach (i.e., selective breeding of *Drosophila* for their ability to form a simple associations, followed by an assessment of their competitive fitness; Mery and Kawecki, 2003) as well as a correlational approach (a comparison of problem solving ability to competition for food among wild great tits; Cole and Quinn, 2012), the present approach extends these prior results in three principal ways. First, we explored the relationship between general cognitive performance and tendencies for social submission in a mammalian species (genetically heterogeneous mice). Second, rather than a single learning task, in this study we assessed the performance of mice on a battery of five diverse learning tasks, and

thus can draw conclusions about the animals' more general cognitive ability (c.f., "intelligence"). Lastly, in the present case, all mice were socially isolated since prior to adolescence, and were thus naïve to experience with aggression-based social hierarchies. Consequently, any relationship between submissive tendencies and general cognitive ability is not likely to reflect prior experience with defeat stress or aggressive social interactions.

Here, we used 64 outbred, non-littermate CD-1 mice that were individually-housed before sexual maturity (the time at which dominance hierarchies begin to emerge in mice). The mice were approximately 70 days of age (young adults) at the start of testing. CD-1 mice were chosen because they express genetic variability comparable to wild mice, and non-littermates' social interactions are less likely to be influenced by innate or acquired familial interactions. We first assessed these mice on a battery of five cognitive tasks designed to evaluate abilities in different learning domains, and the general cognitive ability of each animal was characterized according to its aggregate performance across all tests. Following the completion of the learning battery, we categorized the mice within a dominance hierarchy based on a test of aggressive social interactions. We assessed a subset of these animals (n = 32) on an additional test of social dominance (urine marking, which does not require interactions between animals) prior to the social aggression test. In addition, we measured in this same subset of animals the levels of corticosterone elevation in response to mild environmental stress (isolation on an elevated platform, which induces an intermediate level of corticosterone elevation). In this manner, it was possible to determine the relationship of general cognitive abilities to social dominance in adult animals not previously exposed to a social hierarchy. In addition, we tested the relationships between cognitive abilities and the tendency for social submission to the animals' physical "stature" (measured by body weight) and/or their hormonal responses to environmental stressors.

2. Methods

2.1. Subjects

Sixty-four outbred, male, non-littermate CD-1 mice were obtained from Harlan Sprague-Dawley, and arrived in our laboratory at approximately 35 days of age. This strain exhibits wide behavioral and genetic variability (similar to wild populations), and thus are well-suited for the study of individual differences. We used non-siblings to avoid familial and genetic similarities that might influence social interactions.

Upon arrival (and before sexual maturity, which occurs between 50 and 60 days of age), the mice were individually-housed in clear shoe-box cages and were maintained on ad libitum food and water (unless otherwise noted) in a temperature-controlled vivarium on a 12-h light/dark cycle. The mice were adapted to these conditions for 4–5 weeks prior to the start of experimentation. During this period, each mouse was handled daily (removed from its cage and held by an experimenter for 60 s/day). All mice were approximately 70 days of age at the start of behavioral testing (at which time body weights ranged from 26 to 32 g), and testing was complete by 130 days of age.

2.2. General cognitive ability

Using previously reported methods (Kolata et al., 2005; Matzel et al., 2006), all animals were tested in a series of five independent learning tasks: Lashley III maze, passive avoidance, spatial water maze, odor discrimination, and cued fear conditioning. By design, these tasks place unique sensory, motor, motivational and information processing demands on the animals.

The 64 CD-1 mice used in this experiment were assessed in two replications on the five learning tests which represent core tasks we used in the past to evaluate general cognitive ability. These five tests were administered in an order that separated any two tasks that are motivated by either food or water deprivation, and that separate tasks that have similar patterns of action (e.g. activity or passivity). This ordering prevented excessive physical strain and minimizes any potential cross-task influences due to motivational factors. The order in which animals were tested was: Lashley maze, passive avoidance, odor discrimination, fear conditioning and spatial water maze. A different experimenter tested the animals on each of the learning tasks, and these experimenters were unaware of the animals' history or social status.

In all learning tasks, the animals' performance was assessed during the acquisition phase of learning (i.e., prior to reaching their stable, asymptotic level of performance). Thus the dependent measure for each task was analogous to the animals' rate of learning on that task, and these measures of each individual's performance could be ranked (through the application of exploratory factor analysis and the resultant factor scores; see below) relative to other animals in the sample. To quantify an animal's performance in tasks in which there were multiple training/test trials, performance during trials that fell within the acquisition phase were averaged. In tasks in which there was only one test trial (i.e. fear conditioning and passive avoidance), training parameters were used that were previously determined to result in sub-asymptotic responding by most animals (Matzel et al., 2003), and as such, performance on this single test trial were in part a reflection of differences in animal's rate of learning.

2.2.1. Spatial water maze

This task requires animals to locate a submerged platform in a round pool of opaque water. Absent distinct intra-maze cues, animals' performance in this task is highly reliant on the extra-maze spatial cues. The animals are motivated by their aversion to the water. The latency and path length to locate the platform decreases over successive trials, despite entering the pool from different locations.

A round black pool (140 cm diameter, 56 cm deep) was filled to within 24 cm of the top with water made opaque by the addition of a nontoxic, water soluble black paint. A hidden 11 cm diameter perforated black platform was in a fixed location 1.5 cm below the surface of the water midway between the center and perimeter of the pool. The pool was enclosed in a ceiling-high black curtain on which five different shapes (landmark cues) were variously positioned at heights (relative to water surface) ranging from 24 to 150 cm. Four of these shapes were constructed of strings of white LEDs (spaced at 2.5 cm intervals) and include an "X" (66 cm arms crossing at angles 40° from the pool surface), a vertical "spiral" (80 cm long, 7 cm diameter, 11 cm revolutions), a vertical line (31 cm) and a horizontal line (31 cm). The fifth cue was constructed of two adjacent 7-W light bulbs (each 4 cm diameter). A video camera was mounted 180 cm above the center of the water surface. These cues provided the only illumination of the maze, totaling 172 lx at the water surface.

On the day prior to training, each animal was confined to the escape platform for 5 min. Training was conducted on the two subsequent days. On Day 1 of training, animals were started from one of

three unique locations on each of five trials. The pool was conceptually divided into four quadrants, and one starting point was located in each of the three quadrants that did not contain the escape platform. The starting point on each trial alternated between the three available quadrants. An animal was judged to have escaped from the water (i.e., located the platform) at the moment at which all four paws were situated on the platform, provided that the animal remained on the platform for at least 5 s. Each animal was left on the platform for a total of 20 s, after which the trial was terminated. Trials were spaced at 10 min intervals, during which time the animals were held in their home cages. On each trial, a 90 s limit on swimming was imposed, at which time any animal that had not located the escape platform was placed onto the platform by the experimenter, where it remained for 20 s. The time it took for the animal to escape (latency) as well as the distance traveled (path length) to reach the platform were recorded.

Animals were observed from a remote (outside of the pool's enclosure) video monitor, and animals' performance was recorded on videotape for subsequent analysis. Day 2 of training proceeded, as did Day 1, albeit with four trials only. After the last training trial, a 90 min retention period began, after which animals were tested with a "probe" trial. On the probe test, the escape platform was removed from the pool, and all animals were started from the first position for that day. A 60 s test was conducted and the animals' time searching in the target quadrant (that in which the escape platform was previously located) and non-target quadrants was recorded.

2.2.2. Lashley III maze

The Lashley III maze consisted of a start box, four interconnected alleys and a goal box containing a food reward. Previous studies have shown that over successive trials, the latency of rats to locate the goal box decreased, as does their number of errors (i.e., wrong turns or retracing). A Lashley III maze scaled for mice was constructed of black Plexiglas and a goal box marked by white electrical tape was located in the rear portion of the maze where 45 mg BioServe (rodent grain) pellet served as a reinforcer. Illumination was 80 lx at the floor of the maze. The maze was isolated behind a shield of white Plexiglas to prevent the use of extra-maze landmark cues.

For the two days prior to training, the mice' access to food was limited to 60 min per day at the end of the light cycle. The food-deprived mice were acclimated and trained on two successive days. On the day prior to acclimation, all animals were provided with three food pellets in their home cages to familiarize them with the novel reinforcer. On the acclimation day, each mouse was placed in the four alleys of the maze, but the openings between the alleys were blocked so that the animals could not navigate the maze. Each animal was confined to the start box and subsequent two alleys for 4 min, and for 6 min in the last (goal) alley, where three food pellets were present in the goal box. This acclimation period promotes stable and high levels of activity on the subsequent training day. On the training day, each animal was placed in the start box and allowed to traverse the maze until it reached the goal box and consumed the single food pellet present in the cup (a 1 cm depression in the floor at the rear of the box). Upon consuming the food, the animal was returned to its home cage for a 20 min interval (ITI) during which the apparatus was cleaned. After the ITI, the mouse was returned to the start box to begin the next trial, and this sequence was repeated for five trials. The latency and errors (i.e., a turn in an incorrect direction, including those which result in path retracing) to enter the goal box were recorded on each trial.

2.2.3. Associative fear conditioning

In this task, mice received a tone (CS) paired with a mild foot shock (US). Two distinct experimental chambers (i.e., contexts)

were used, each of which was contained in a sound- and light attenuating enclosure. These boxes were designated as training and novel contexts, and differed as follows: The training chamber (16.5 × 26.5 × 20 cm) was brightly illuminated (100 lx), had clear Plexiglas walls, and parallel stainless-steel rods (5 mm, 10 mm spacing) forming the floor. The novel chamber (23 × 21.5 × 19 cm) was dimly illuminated (6 lx) and all of the walls and floor were constructed of clear plexiglass. In both boxes, the auditory stimulus (60 dB, 2.9 kHz) was delivered by a piezoelectric buzzer.

On Day 1 subjects were acclimated in both novel and training contexts for a 20 min period in each box. On Day 2 subjects received an 18 min training session in the training chamber. All training sessions were videotaped for subsequent offline scoring. Subjects received three tone/shock presentations at 4, 10 and 16 min into the session. The CS presentation consisted of a pulsed (0.7 s on 0.3 s off) 20 s tone. Immediately following the tone offset, the shock US (0.6-mA, constant-current foot shock) was presented for 500 msec.

Freezing was measured during the 20 s before (baseline freezing), during (tone freezing) and after (post shock freezing) the 20 s tone presentation. A measure for freezing during the training period (training freezing) was calculated by subtracting the time spent freezing in baseline from the time spent freezing during the tone.

On Day 3, freezing was measured during a 5 min session in the novel chamber during which time, tone, but no shock was presented.

2.2.4. Odor discrimination

Rodents rapidly learn to use odors to guide appetitively-reinforced behaviors. In a procedure based on one designed for rats (Sara et al., 2001), mice learned to navigate a square field in which unique odor-marked (e.g., almond, lemon, mint) food cups were located in three corners. Although food was present in each cup, it was accessible to the animals in only one cup, the one marked by mint odor. An animal was placed in the empty corner of the field, after which it explored the field and eventually retrieved the single piece of available food. On subsequent trials, the location of the food cups was changed, but the accessible food was consistently marked by the same odor (mint). On successive trials, animals required less time to retrieve the food and made fewer approaches (i.e., “errors”) to those food cups in which food was not available. Using this procedure, errorless performance was typically observed within three to four training trials.

A black Plexiglas 60 cm square field with 30 cm high walls was located in a dimly lit (10 fc) testing room with a high ventilation rate (3 min volume exchange). Three 4 × 4 × 2.0 cm (l, w, h) aluminum food cups were placed in three corners of the field. A food reinforcer (30 mg portions of chocolate flavored puffed rice) was placed in a 1.6 cm deep, 1 cm diameter depression in the center of each cup. The food in two of the cups was covered (1.0 cm below the surface of the cup) with a wire mesh so that it was not accessible to the animal, while in the third cup (the “target” cup), the food could be retrieved and consumed. A cotton-tipped laboratory swab, located between the center and rear corner of each cup, extended vertically 3 cm from the cups’ surface.

Immediately prior to each trial, fresh swabs were loaded with 25 µl of lemon, almond, or mint odorants (McCormick flavor extracts). The mint odor was always associated with the target food cup. It should be noted that in pilot studies, the odor associated with food was counterbalanced across animals and no discernible differences in performance could be detected in response to the different odors.

On the day prior to test animals were given 60 min of free feeding (in the home cage) at the same time of day they would receive have been acclimated. On test day, animals received four training trials in the field with all three food cups present. On each trial, a mouse was placed in the empty corner of the field. On Trial 1, the

reinforcing food (one piece of chocolate flavored puffed rice) was available to the animal in the cup marked by mint odor. An additional portion of food was placed on the top surface of the same cup for the first trial only. The trial continued until the animal retrieved and consumed the food from the target cup, after which the animal was left in the chamber for an additional 20 s and then returned to its home cage to begin a 6 min ITI. On Trials 2–4, the location of the food cups was rearranged, but the baited cup remained consistently marked by the mint odor. Both the corner location of the mint odor and its position relative to the remaining odors was changed on each trial. On each trial, the latency to retrieve the food and errors was recorded. An error was recorded any time an animal made contact with an incorrect cup, or its nose crossed a plane parallel to the perimeter of an incorrect cup. Similarly, an error was recorded when an animal sampled (as above) the target cup but did not retrieve the available food.

2.2.5. Passive avoidance

A chamber illuminated by dim (<20 lx) red light was used for training and testing. Animals were confined to a circular (“safe”) chamber (10 cm diameter, 8 cm high). The walls and floor of this chamber were white, and the ceiling was translucent orange. The floor was comprised of plastic rods (2 mm diameter) arranged to form a pattern of 1 cm square grids. A clear exit door (3 cm square) was flush with the floor of the safe compartment, and the door was able to slide horizontally to open or close the compartment. The bottom of the exit door was located 4 cm above the floor of a second circular chamber (20 cm diameter, 12 cm high). This “unsafe” chamber had a clear ceiling and a floor comprised of 4 mm wide aluminum planks that formed a pattern of 1.5 cm square grids oriented at a 45° angle relative to the grids in the safe compartment. When an animal stepped from the safe compartment through the exit door onto the floor of the unsafe compartment, a compound aversive stimulus comprised of a bright (550 lx) white light and “siren” (60 dB above the 50 dB background) was initiated.

Animals learn to suppress movement to avoid contact with aversive stimuli. This “passive avoidance” response is exemplified in step-down avoidance procedures, where commonly, an animal is placed on a platform, whereupon stepping off of the platform it encounters a foot shock. Following just a single encounter with shock, animals are subsequently reluctant to step off of the safe platform. The animals’ reluctance to leave the platform is believed to *not* reflect fear, because typical fear responses are not expressed in animals engaged in the avoidance response [78–79]. Upon stepping off the platform, animals here were exposed to a compound of bright light and loud oscillating noise rather than shock, so as not to duplicate stimuli between tasks (see fear conditioning, above). Like more common procedures, our variant of this task supports learning after only a single trial (i.e., subsequent step-down latencies will be markedly increased).

Animals were placed on the platform behind the exit blocked by the Plexiglas door. After 4 min of confinement, the door was retracted and the latency of the animal to leave the platform and make contact with the grid floor was recorded. Prior to training, baseline step-down latencies typically ranged from 8 to 20 s. Upon contact with the floor, the door to the platform was closed and the aversive stimulus (light, noise, and vibration) was presented for 4 s, at which time the platform door was opened to allow animals to return to the platform, where they were again confined for 5 min. At the end of this interval, the door was opened and the latency of the animal to exit the platform and step onto the grid floor (with no aversive stimulation) was recorded. The ratio of post-training to pre-training step-down latencies was calculated for each animal and this served to index learning. We have determined that asymptotic performance is apparent in group averages following

2–3 training trials; thus performance after a single trial reflects, in most instances, sub-asymptotic learning.

2.3. Social dominance

Three weeks after completion of the learning battery, all 64 animals underwent a test of social dominance based on aggressive interactions between pairs of animals. 32 pairs of animals were tested for four days. From each of these pairs, one was classified (dependent on the outcome of the test) as either dominant or submissive. Pairs of animals were placed in start boxes (10 cm long \times 6 cm \times 6 cm) lined with bedding from the animal's home cage. Animals were immediately allowed to enter a tube (40 cm long \times 4 cm wide Plexiglas, covered in translucent yellow acetate) from opposite ends (start locations). Upon each animal reaching the center of the tube, a guillotine door was opened at which time one animal would typically retreat and the other would advance (a behavior usually accompanied by aggressive biting on the part of the advancing animal). The first animal to advance into the 20% of the tube occupied by the retreating animal's start location was scored as the winner of that bout. Both animals were then immediately removed from the tube. The procedure was repeated with new pairs of animals on four successive days (one trial per day, a winner from the prior trial paired against another winner and a loser from the prior trial paired against another loser.) For each test pair, animals were matched for body weights. Upon completion of testing, each animal received a hierarchy score from 0 (having lost all bouts) to four (having won all bouts).

An animal's behavior may be altered by its initial experience with an aggressive conspecific. Thus in the previous test, performance on Bouts 2–4 may have been influenced by the animals' experience on Bout 1. Thus a second measure of social dominance was used which did not rely on interactions between animals. This test was conducted in the week *prior* to tests of paired interactions. Previous studies have revealed that the urine marking patterns of mice in a novel environment covary with its position in a dominance hierarchy, such that submissive animals tend to urinate near the outer walls of the field while dominant animals urinate closer to the center, unwall portions of the field (Desjardins et al., 1973). These differences exist in the absence of previous experience in a dominance hierarchy (Drickamer, 2001). Here, we used a subset of 32 animals (those which comprised the second replication), and placed them in an opaque plastic chamber (35 cm \times 30 cm \times 25 cm) with a grid floor on top of a paper liner for 6 h (during the middle of the 12 h light cycle). Following this exposure, we visualized urine markings using a Bio-Rad Multilmager fluorescent imager (Desjardins et al., 1973). For each animal, we recorded the percent of the total area of urine that fell in the interior of the chamber (beyond 6 cm from the wall) relative to the exterior of the chamber.

2.4. Post-Stress free corticosterone levels

Fourteen days after the last cognitive test, the 32 mice from our second replication were exposed to a mild environmental stressor (confinement on an elevated platform in a novel, bright, noisy room, during the middle two hours of the light cycle). We have previously reported that this treatment induces an intermediate level of stress, as indicated by an elevation of free corticosterone (Matzel et al., 2006). Ten min after removal from the platform, each animal was decapitated and trunk blood was collected. From this blood, we determined levels of free corticosterone (as in (Matzel et al., 2006)). Higher values reflect an elevated stress response.

2.5. Statistical analyses

Learning performance was assessed during acquisition (Kolata et al., 2008; Matzel et al., 2003). To ensure normalization across the two replications (32 animals/replication), animals' performance on each task was converted to a z score. So as to simplify the interpretation of our factor analyses, on tasks where lower performance values were indicative of better learning, we changed signs of the performance measures so higher values represent better learning across all tasks. Using SPSS 23, we first performed an exploratory factor analysis in all learning tasks to verify the existence of a general cognitive ability similar to our previous studies. After this, we proceeded with testing theoretical models about our data by using the method of structural equation modeling.

We used structural equation modeling (SEM) to test the relationships among general cognitive ability (measured by the five learning tasks), social dominance (measured by the social aggression and the urination task), body weight, and stress reactivity (measured by level of corticosterone after a mild stressor). SEM is a hybrid of multiple regression and factor analysis techniques, and it allows simultaneous assessment of the strength of the interrelationships among multiple dependent and independent variables, examining the direct and indirect effects of one variable upon another (Kline, 2011). Since an SEM can have multiple indicators for a single (latent) variable, this reduces measurement error (i.e., only the shared variance between measures are considered). In the present case, the latent variables of general cognitive ability and social dominance were of interest. This leads to more accurate and often stronger relationships between latent variables than in other multivariate methods such as MANOVA or multiple regression (Kline, 2011). We designed three main models here: a Dominance Model, D1, as well as two Stress Reactivity Models, S1 and S2.

Our Dominance Model (D1) can be seen in Fig. 1. The model states that the innate tendency for social dominance (measured by the social aggression tests and the urination test) influences the variation in general cognitive ability (measured by the five learning tasks in our battery), and that body weight is correlated with social dominance. Thus, this is a model informed by the prior expectations we had regarding the relationship between intelligence, dominance, and physical "stature". In evolutionary terms, a compensatory mechanism may have promoted increases in intelligence among individuals low in the hierarchy of dominance. We described the assessment of this model below. Furthermore, we also compared our primary Dominance Model (D1) to two alternative models (D2 and D3). To assess the alternative possibility, that social dominance was unrelated to general cognitive ability, we tested model (D2) in which Social Dominance is not connected with General Cognitive Ability. In addition, in order to test the importance of physical "stature" in our Dominance Model, we tested another alternative model (D3) in which body Weight is not related to Social Dominance. For comparisons between our Dominance Model and these two alternative (and nested) models, we performed the Chi-Square Difference Test (χ^2_D), where the null hypothesis represents no differences between the models (Kline, 2011).

For our stress reactivity model, initially we assessed the relationship of all variables from the dominance model plus the corticosterone measure as potential influences on both Social Dominance and General Cognitive Ability. However, this led to a Heywood Case (standardized loading larger than one and negative error variance) in our latent variable of Social Dominance. This problem was likely due to the model having too many parameters relative to sample size (as the measures of corticosterone and urine marking were only obtained from the second replication of animals). Due to this problem, we split the variables of Social Dominance apart and built two versions of our corticosterone model,

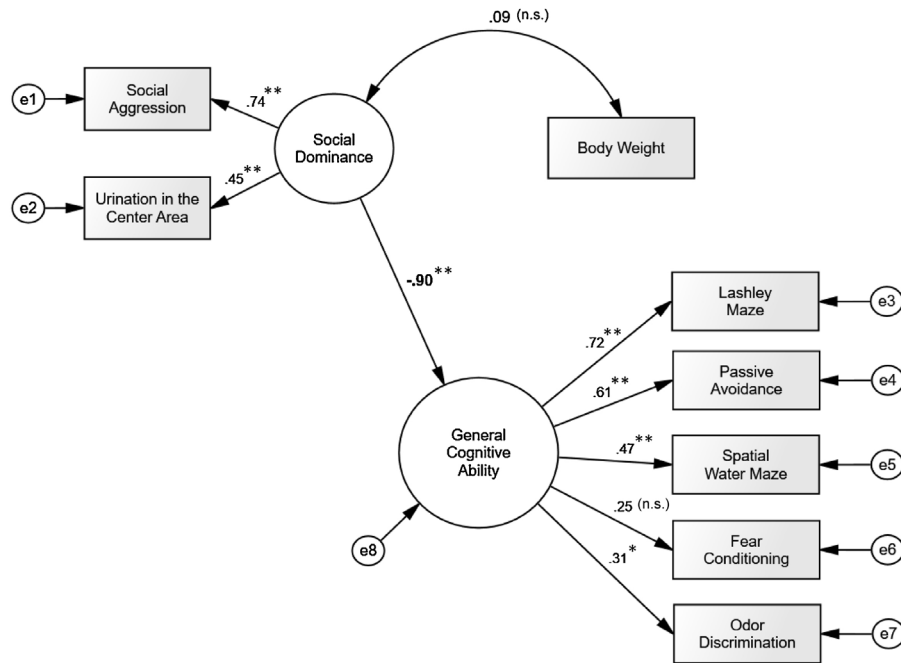


Fig. 1. SEM results of our Dominance Model (D1). The model overall had an excellent fit to the data. Arrows going out of the latent factors represent factor loadings. Circles with an “e” represent error. The arrow from Social Dominance to General Cognitive Ability represents a regression weight, which was significant. Curved, double sided arrow between Social Dominance and Body Weight represent a correlation coefficient, which was not significant. All parameters shown are standardized.

*p < 0.05.
 ** p < 0.01.

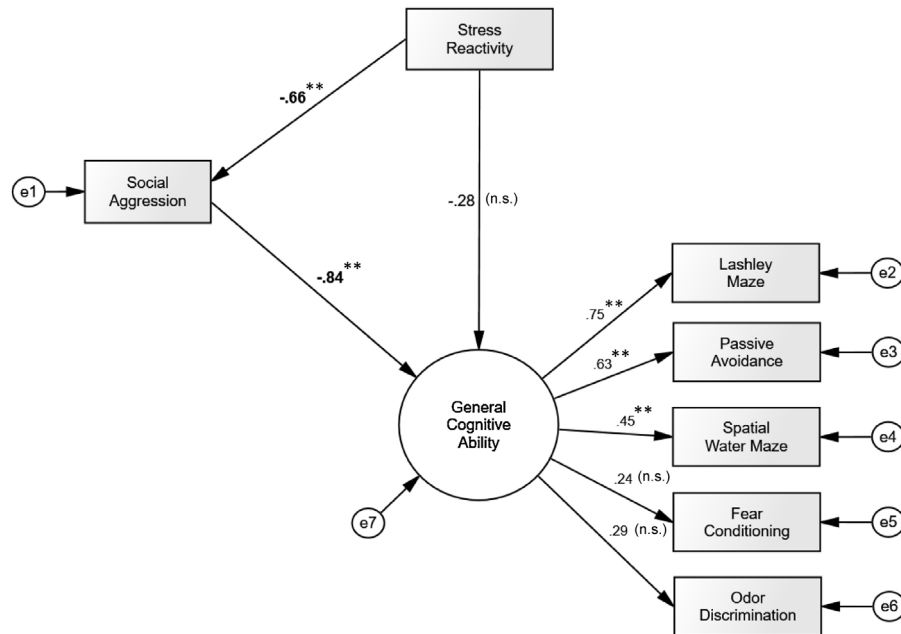


Fig. 2. SEM results of our first Stress Reactivity Model (S1). The model overall had an excellent fit to the data. Arrows going out of the latent factor represent factor loadings. Circles with an “e” represent error. The arrow from Social Aggression (a measure of social dominance) to General Cognitive Ability represents a regression weight, which was significant. The arrow from Stress Reactivity (measured by corticosterone levels after a mild stressor) to Social Aggression represents a regression weight, which was significant. The arrow from Stress Reactivity to General Cognitive Ability represents a regression weight, which was not significant. All parameters shown are standardized.

*p < 0.05.
 ** p < 0.01.

S1 and S2. As seen in Fig. 2, S1 states that stress reactivity (corticosterone levels) influences the variation in both social aggression and general cognitive ability, while social aggression itself influences general cognitive ability. As seen in Fig. 3, S2 assumes that stress reactivity (corticosterone levels) influences the variation in both the urination in the center area of a novel field and general

cognitive ability, and urination in the center area influences general cognitive ability. Both stress reactivity models were informed by the results from the Dominance Model and prior expectations we had on the relationship between intelligence, dominance, and stress reactivity. Evolutionarily, stress reactivity might have been a compensatory mechanism regulating both low tendencies for dom-

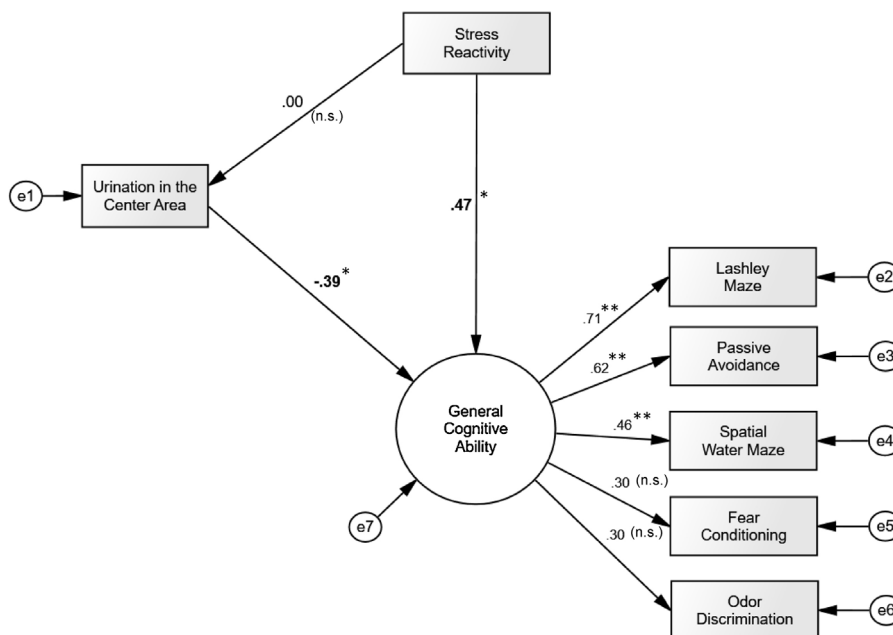


Fig. 3. SEM results of our second Stress Reactivity Model (S2). The model overall had an excellent fit to the data. Arrows going out of the latent factor represent factor loadings. Circles with an “e” represent error. The arrow from Urination in the Center Area (a measure of social dominance) to General Cognitive Ability represents a regression weight, which was significant. The arrow from Stress Reactivity (measured by corticosterone levels after a mild stressor) to Urination in the Center Area represents a regression weight, which was not significant. The arrow from Stress Reactivity to General Cognitive Ability represents a regression weight, which was significant. All parameters shown are standardized.

*p < 0.05.
**p < 0.01.

Table 1
Factor loadings and variance explained by the first factor (General Cognitive Ability) extracted from the five learning tasks using an exploratory factor analysis. n = 64.

Learning Task	General Cognitive Ability
Lashley Maze	0.68
Passive Avoidance	0.63
Spatial Water Maze	0.62
Fear Conditioning	0.26
Odor Discrimination	0.29
Eigenvalue	1.39
Proportion of common variance	27.9%

inance and higher intelligence. Finally, in both S1 and S2 models we tested for potentially indirect effects between stress reactivity and general cognitive ability related to our measures of social dominance. We tested this using the PRODCLIN algorithm developed by MacKinnon et al. (2007). This algorithm tests mediational effects without some of the problems inherent in other methods (such as inflated rates of Type I error), and is considered especially fit for use with SEM (MacKinnon et al., 2002).

To assess our three main models (D1, S1, and S2), we used the maximum likelihood estimation in AMOS 23. We tested model fit by using two absolute indices – Model Chi-Square and RMSEA – that describe how the model represents the observed data, and where lower values mean better fit (hence, they are also referred to as test of “badness-of-fit”). For the Model Chi-Square (χ^2_M), the null hypothesis is the model itself, so failing to reject it (i.e., a small Model Chi-Square) indicates a good fit (with alpha here set at 0.05) (Kline, 2011). Following a similar reasoning, RMSEA values of 0.06 and below are considered good (Hu and Bentler, 1999). In addition to these three absolute indices, we also assessed model fit with two incremental indices – TLI and CFI – that describe how well the model fits in comparison to a baseline model where all variables are uncorrelated and without latent variables, and where higher values mean better fit (“goodness-of-fit” in the literal sense) (Kline,

Table 2
Means, standard deviations, and correlations among scores of General Cognitive Ability (standardized scores extracted from the first factor of the exploratory factor analysis from the five learning tasks; higher values indicate higher general cognitive ability), body weight (grams), social aggression (rank from 0 to 4; higher values indicate more dominance), urination in the center area (in%; higher values indicate more dominance), and stress reactivity (measured by level of corticosterone after a mild stressor, in ng/ml; higher values indicate more stress reactivity).

	1	2	3	4	5
1. General Cognitive Ability	–				
2. Body weight (g)	–0.13	–			
3. Social aggression (rank 0–4)	–0.55 ^b	0.01	–		
4. Urination in the center area (%)	–0.35 ^b	0.01	0.34 ^b	–	
5. Stress reactivity (ng/ml)	0.38 ^a	0.06	–0.68 ^b	0.03	–
Mean	–	36.50	2	37.18	96.16
Standard Deviation	–	6.26	1.1	18.13	30.41

^a p < 0.05.
^b p < 0.01.

2011). TLI and CFI indicate an adequate model fit at values of 0.95 or above (Hu and Bentler, 1999). We chose these tests due to their statistical relevance and frequent use (Kline, 2011; MacKinnon et al., 2007; Schreiber et al., 2006). For testing the significance of individual parameters (regression paths and correlations), we chose an alpha value of 0.05.

3. Results

3.1. Exploratory factor analysis of learning tasks

As seen in Table 1, the exploratory factory analysis revealed that performance loaded moderately and consistently on the first factor, which we have interpreted as “general cognitive ability” (Table 1). We then used the exploratory factor analysis to assign a factor score to each animal. (A factor score is analogous to each animal’s average Z- score for the five learning tasks, where the Z-score for each

task is weighted by that task's relative loading on the relevant factor.) These scores were normally distributed, with a non-significant Shapiro-Wilk test for a null of normality ($W=0.99$, $p=0.742$), as well as with skewness and kurtosis within normal values (-0.18 and -0.16 , respectively).

3.2. Correlations among general cognitive ability and other variables

Social aggression was assessed by observing pairs of weight-matched mice during direct social interactions in a confined environment. Animals were classified as either "winners" or "losers" in each of four confrontations (where after the first and subsequent rounds, winners were paired with winners from the previous round, and losers were paired with losers). From the total sample of 64 animals, five animals received scores of "0" (indicative of no wins in four bouts) and five received scores of "4" (indicative of four wins in four bouts). Eighteen animals each received scores of "1", "2", or "3". For the urination test of dominance (conducted prior to tests of aggressive confrontation), we measured the urination in the center area of an open field where each mouse was allowed to explore for 6 h. As described in Methods, a higher proportion of urination in the center of the open field represents a higher tendency for dominance. Similar to the measure of social aggression, individual animals exhibited widely different patterns of urination in the open field, with urination in the center area of the field ranging from 0 to 96% across individuals.

After the completion of all behavioral tests, corticosterone levels were measured in the mice after exposing them to a mild environmental stressor (confinement on a small elevated platform). We have previously found that corticosterone levels rose from an average of 32 ng/ml at rest to 105 ng/ml after this mild stress. This intermediate corticosterone response was also observed here, where the average corticosterone level after stress exposure was 96.2 ng/ml (± 30.41 SD). It is noted that after exposure to a more intense stressor, such as submersion in a pool of cold water, corticosterone levels are typically 2–3 times higher.

The means, standard deviations, and correlations among scores of General Cognitive Ability (factor scores extracted from the first factor of the exploratory factor analysis from the five learning tasks), and the measured variables of body weight, social aggression, urination in the center of an open field (an index of dominance/submission), and stress reactivity (measured by level of corticosterone after a mild stressor) are provided in Table 2. For the purpose of the present analysis, two of the reported correlations are particularly relevant. Specifically, General Cognitive Ability was inversely related to both of our measures of dominance (social aggression, $r(30)=-0.55$, $p<0.01$; urination in the center of a novel field, $r(30)=-0.35$, $p<0.05$), i.e., social submission was associated with superior general cognitive performance.

3.3. SEM analysis: dominance model

Structural equation modeling analysis of our Dominance Model indicated that the model has an excellent fit to the data ($\chi^2=13.92$, $df=19$, $p=0.788$; $RMSEA<0.001$; $TLI=1.153$; $CFI=1.000$). The factor loadings for the construct Social Dominance and the construct General Cognitive Ability on their corresponding observed variables can be seen in Fig. 1. All indicators significantly loaded onto their latent variables ($p<0.05$), with the exception of Fear Conditioning, which was close to significance ($p=0.087$). Also illustrated in Fig. 1 is the regression path from Social Dominance to General Cognitive Ability, which was significant ($\beta=-0.90$, $p=0.007$), and the correlation between Social Dominance and Weight, which was not significant ($r=0.09$, $p=0.561$). Based on these results, it appears that independent of prior experience with social hierarchies, ani-

mals' tendencies to occupy particular positions in dominance hierarchies is related to their general cognitive abilities such that social submission is predictive of generally superior cognitive performance.

To test our Dominance Model against other possibilities, we generated two alternative models: D2) a model in which Social Dominance is unrelated to GCA, and D3) a model in which Weight is not correlated with Social Dominance. Because our main model can be considered a nested model within either the D2 and the D3 models, we used the Chi-square difference to test if these alternative models could explain the data more parsimoniously. The D2 model was significantly worse than our main model, $\chi^2(1, N=64)=24.059$, $p<0.001$. This means that the additional parameter (the influence of social dominance on general cognitive ability) contained in our main model is indeed important. The D3 model, however, was not statistically different than our main model, $\chi^2(1, N=64)=0.316$, $p=0.574$. Because the D3 model is more parsimonious (fewer parameters) than our main model, the non-significance suggests that Weight as measured in this study has no explanatory value.

3.4. SEM analysis: stress reactivity model

Structural equation modeling analysis of our first Stress Reactivity Model, S1, indicated that the model has an excellent fit to the data ($\chi^2=11.46$, $df=13$, $p=0.572$; $RMSEA<0.001$; $TLI=1.058$; $CFI=1.000$). Fig. 2 shows the regression path from Social Aggression to General Cognitive Ability, which was significant ($\beta=-0.84$, $p<0.001$). This reinforces our finding in the Dominance Model showing that submissiveness is associated with superior cognitive ability. Fig. 2 also shows the regression path from Stress Reactivity to Social Aggression, which was significant ($\beta=-0.66$, $p<0.001$), and the regression path from Stress Reactivity to General Cognitive Ability, which was not significant ($\beta=-0.28$, $p=0.214$). Even though the direct path from Stress Reactivity to General Cognitive Ability was not significant, there could be a partial mediation effect via Social Aggression. By using the PRODCLIN program to test for mediation, we found that the results yield a lower and upper 95% confidence limit of 0.007 and 0.023. Since these values do not include zero, this suggests the existence of a mediation effect.

Structural equation modeling analysis of our second Stress Reactivity Model, S2, indicated that the model, similar to S1, also has an excellent fit to the data ($\chi^2=12.27$, $df=13$, $p=0.506$; $RMSEA<0.001$; $TLI=1.058$; $CFI=1.000$). Fig. 2 shows the regression path from Urination in the Center Area to General Cognitive Ability, which was significant ($\beta=-0.39$, $p=0.010$). This, once again, reinforces our finding in the Dominance Model showing that submissiveness leads to superior cognitive ability. Fig. 3 also shows the regression path from Stress Reactivity to Urination in the Center Area, which was not significant ($\beta=-0.003$, $p=0.986$), and the regression path from Stress Reactivity to General Cognitive Ability, which was significant ($\beta=0.47$, $p=0.011$). Given the significant path from Stress Reactivity to General Cognitive Ability, there could also be a partial mediation effect via Urination in the Center Area. By using the PRODCLIN program to test for mediation, we found that the results yield a lower and upper 95% confidence limit of -0.003 and 0.003. Since these values include zero, we can say there is no mediation effect.

4. Discussion

Here we found a link between social submissiveness and superior cognitive performance in mice with no experience in adult dominance hierarchies. To better understand the full implications

of this main finding, it is worth first exploring our specific results below.

Similar to our previous work, there was positive correlation of each mouse's rate of acquisition across all learning tasks. A general cognitive ability factor accounted for 28% of the common variance in mice's performance (Table 1), which is equivalent to accounting for 38% of the total variance (from a Principal Component Analysis). That result is similar to what we have found in that past, where the cognitive ability factor explained 32% to 48% of the total variance across tests in a learning battery (for review, see Matzel et al., 2013).

The SEM analyses determined that body weight was neither correlated with social submission nor relevant for its link with general cognitive ability. In mammals, variables which contribute to physical "stature", in particular, body weight, usually contribute to the establishment of dominance hierarchies (Clarke and Faulkes, 2006; Sapolsky, 2005), so it may seem surprising that we did not observe such relationship here. However, here we matched the mice for body weight during the test of social interactions. This forced pairing would attenuate any potential effect that weight might have on the social aggression test, though the urination test (our other test of social dominance) had no such limitation. Regardless, our results suggest that body weight is not a *necessary* determinant of the establishment of dominance or of the tendency for dominant/submissive behavior.

It is worth noting again that the mice in our study were genetically diverse and had no experience in dominance hierarchies from a time beginning prior to adolescence. This suggests that the link between social submission and general cognitive ability is not driven by behavioral plasticity (in response to prior aggressive interactions), but instead comes from innate (possibly genetic) tendencies. Less dominant animals might have evolved compensatory cognitive strategies to facilitate their survival within the group. This conclusion is consistent with a general theme that has been advanced in recent years among evolutionary biologists and psychologist (Holekamp, 2007; Kamil, 2004; McNally et al., 2012), but for which direct experimental support has been limited, although a similar trade-off between learning ability and fitness (larval competition) has been previously observed in *Drosophila* (Mery and Kawecki, 2003) and wild birds (Cole and Quinn, 2012). Mery & Kawecki suggested an interpretation of their results with *Drosophila* that is antithetical to ours, namely, that better cognitive abilities have costs that render the beneficiaries of improved cognition less fit. Of course we cannot distinguish between these possibilities, although it is true that the development and maintenance of the neural architecture that supports learning and memory storage is associated with high energetic costs (Johnston, 1982; Laughlin, 2001). It is entirely possible that cognitive abilities are both compensatory and simultaneously mitigate fitness. In any case, either of these interpretations must be considered with caution. It is still possible that environmental factors other than experience with dominance hierarchies, such as variations in maternal care or the early physiological environment, may have influenced the phenotype of the mice in the current study. Due to these possibilities, the tendency for social submission might be genetic, environmental, or a combination of the two. Thus the role of evolved compensatory strategies should be taken only as a possible scenario that will require further investigation.

Regarding the directionality of the relationship between the tendency for social submission and general cognitive ability, our Dominance Model was structured based on an assumption that social dominance influences general cognitive ability. This assumption reflects the idea that animals that tended to be submissive developed compensatory mechanisms (e.g., higher intelligence) as an alternative strategy for success. However, the causal relationship might be reversed. A model with general cognitive ability influencing innate tendency for social dominance fitted the data here

well, and was statistically equivalent to our main model. Therefore, the directionality of this relationship is uncertain, though it is harder for us to imagine how high intelligence could have guided the evolution of the tendency for submissiveness, although as noted above, the costs (e.g., metabolic energy) associated with cognitive processes could potentially render the beneficiaries of improved cognition less fit.

Additionally, our results suggest that elevated stress reactivity might be a common factor leading to both social submissiveness and superior cognitive performance. The mediation analysis of our S1 Model showed that stress reactivity has an indirect effect on general cognitive ability via social aggression, even though it lacks a direct effect. For the S2 Model, however, all of the effect of stress reactivity on general cognitive ability was direct. Relationships between social dominance and stress reactivity have been previously reported by (Politch and Leshner, 1997), and Blanchard et al. observed that animals' victories in paired social interactions were inversely related to corticosterone elevations in response to mild environmental stress (Blanchard et al., 2006), i.e., heightened corticosterone responses were associated with submissive tendencies. However, it is important to note that in our models tested here, stress reactivity only influenced our measure of social dominance in the social aggression test, but not in the urination test. We also observed here an effect of stress reactivity (corticosterone response) and animals' factor scores indicative of general cognitive ability, such that better general cognitive ability was associated with higher stress reactivity. This contrasts with prior work in our laboratory, which has suggested that stress reactivity (at least within this moderate range) is unlikely to causally impact general cognitive performance (Matzel et al., 2006). Taken together, these results suggest that variations in stress reactivity may in some instances be related to variations in general cognitive ability, but that stress reactivity in itself is not sufficient to account for these variations.

In both human and animal populations, the imposition of subordination often has deleterious effects on cognitive function (Colas-Zelin et al., 2012; Fitchett et al., 2005; Ladd et al., 1997). This observation has important ramifications in educational settings (Baumeister et al., 2002), where among humans, the formation of dominance hierarchies are quite common (Sutton and Keogh, 2000). However, the present results suggest that *predispositions* toward subordination may be co-expressed with a higher capacity for cognitive performance. Thus absent the *imposition* of subordination, normally submissive individuals may be better prepared for cognitive/academic achievement.

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