



Published in final edited form as:

Behav Genet. 2013 March ; 43(2): 151–160. doi:10.1007/s10519-012-9577-3.

COMPETITIVE ABILITY IN MALE HOUSE MICE (*Mus musculus*): GENETIC INFLUENCES

Christopher B. Cunningham, James S. Ruff, Kevin Chase, Wayne K. Potts, and David R. Carrier

Department of Biology, University of Utah, Salt Lake City, UT

Abstract

Conspecifics of many animal species physically compete to gain reproductive resources and thus fitness. Despite the importance of competitive ability across the animal kingdom, specific traits that influence or underpin competitive ability are poorly characterized. Here, we investigate whether there are genetic influences on competitive ability within male house mice. Additionally, we examined if litter demographics (litter size and litter sex ratio) influence competitive ability. We phenotyped two generations for a male's ability to possess a reproductive resource--a prime nesting site--using semi-natural enclosures with mixed sex groupings. We used the animal model coupled with an extensive pedigree to estimate several genetic parameters. Competitive ability was found to be highly heritable, but only displayed a moderate genetic correlation to body mass. Interestingly, litter sex ratio had a weak negative influence on competitive ability. Litter size had no significant influence on competitive ability. Our study also highlights how much remains unknown about the proximal causes of competitive ability.

Keywords

Heritability; Genetic Correlation; Life-History Evolution; Male-Male Competition; Sexual Selection

Introduction

Darwin (1871) was one of the first to recognize the importance of physical conflict to anatomical, behavioral, and life history traits. In many species, it is the cumulative outcome of multiple physical agonistic interactions that leads to differential access to reproductive resources (Dewsbury 1982; Kaufmann 1983; Hand 1986; Ellis 1995). Across the animal kingdom, this differential access directly translates into fitness differences biased towards highly competitive individuals (Dewsbury 1982; Ellis 1995). The importance of physical competition among conspecific is also attested to by its ubiquity (Dewsbury 1982; Kaufmann 1983; Ellis 1995; Emlen 2008), its costliness (Briffa and Sneddon 2007; Emlen 2008), and highlights the need to understand more about its physiological, behavioral, and evolutionary basis.

Here, we investigate the possible influences of both genetic (additive genetic variance, genetic correlations) and demographic (litter size, litter sex-ratio) components on competitive ability, while controlling for the influence of body mass. To this end, we used two generations of mice grouped into multi-male/single female populations and placed into semi-natural enclosures. Competitive ability, or the capacity of an individual to gain

resources through consistently winning agonistic encounters, was assessed by two well-established indicators of competitive ability--possession of a preferred nesting site and wounding--over three days. Additionally, we used two competition rounds within each generation to more extensively phenotype individuals, with the winners and losers of the first round being grouped separately during the second round.

House mice (*Mus musculus*) were selected as our model species for several reasons. First, competitive ability plays a critical role in male, and likely female, reproductive success (e.g., De Fries and McClearn 1970; Dewsbury 1982; Wolff 1985; Hurst 1987; Ellis 1995; Carroll et al. 2004). Second, the *Mus* social system is based on polygynous deme formation (Crowcroft 1955; Oakeshott 1974; Wolff 1985; Hurst 1987; Hayashi 1993; Drickamer 2001), which are established quickly through intense physical competition, even in semi-natural enclosures (Oakeshott 1974; Drickamer 2001). This makes house mice amenable to laboratory investigations of naturalistic behaviors. Finally, numerous aspects of the house mouse mating and social system are broadly representative of many mammalian species, which increases the likelihood results from this study can be more broadly applied.

Our first aim was to estimate the influence of genetic factors on competitive ability. It has been suggested that competitive ability cannot evolve (i.e., has no genetic influences) because it is a trait derived from the interaction of multiple individuals (e.g., Barrette 1987; Barrette 1993). However, there now exists a large amount of theoretical and empirical evidence that demonstrates the ability of socially expressed traits to have a genetic basis, including competitive ability (Dewsbury 1990; Moore 1993; Moore et al. 2002). For example, a quantitative genetic model of social traits was developed by Moore et al. (1997) and extend to specifically address social dominance (Moore et al. 2002). The model's predictions have now been supported by many studies, empirically establishing the ability of socially expressed traits to evolve (e.g., Moore et al. 2002; Satori and Mantovani 2012).

Our second aim was to examine the influence of two demographic factors on competitive ability; litter size and litter sex ratio. Litter size is negatively correlated with weaning weight in house mice (Krackow 1993). Weaning weight is positively correlated with adult body weight, which is positively correlated with competitive ability within house mice (Krackow 1993). For these reasons, we predicted that increasing litter size negatively influences competitive ability.

Litter sex ratio could influence male competitive ability through multiple, non-exclusive mechanisms. One of the most likely mechanisms is a pre-natal influence mediated through differences in *in utero* positioning, which causes many well-established phenotypic effects (e.g., vom Saal and Bronson 1980; vom Saal et al. 1983; Zielinski et al. 1992). Post-natal competition for maternal care against predominately brothers may lead to a different phenotype than competition against mainly sisters. This might be mediated by something as straight forward as weight difference between the sexes as a litter matures towards weaning. To try to tease these two possibilities apart, we used several different measures of litter sex composition; sex ratio, number of male siblings, number of female siblings, and assessed if an interaction between litter size and litter sex ratio existed.

Because individuals during the second round of competition are grouped based on success in the first round, we had a unique opportunity to assess if potentially casual factors have differing levels of influences based on the level of social competition. Therefore, we assessed the influence of our traits on multiple divisions of our data set, where applicable. For example, does the additive genetic variation change substantially if the first round data alone is used vs. data from the entire study? Generally, the data was assessed across the

entire study, using first round data alone (when males were randomized), and using second round data from winner and losers separately.

Materials and methods

Experimental Design Overview

Mixed sex groupings (4 males, 1 female) of house mice were placed into semi-natural enclosures for three days to assess the competitive ability of the male mice in the presence of reproductive resources (a preferred nesting site and a sexually mature female). Following this competition round, a second competition round was completed with the same protocol for groupings of three males and one female. In this second round, males were grouped based on their win/loss experience in the first round. Winners of the first round were grouped randomly together and first round losers were randomly grouped with other first round losers. This protocol was repeated to assess the male progeny from individuals who successfully bred into the second generation.

Test population, breeding protocol, and animal husbandry

An established colony of house mice at the Department of Biology, University of Utah, provided the original breeders for this study. The original founders of this population were wild caught mice and the colony had been maintained with a circular breeding program for 11 generations at the time of the study. Our study's population had an average coefficient of relationship of 0.0839, which is comparable to estimates from a wild population (Sutherland et al. 2005). The coefficient of relationship is a measure of consanguinity between two individuals given their pedigree (Wright 1921). Here, we calculated all the pairwise coefficient of relationships between mice using the 13-generation pedigree for this population and averaged these measures to give a summary descriptor of our population. Mice from this population have already been used in many behavioral studies including inbreeding depression (Meagher et al. 2000; Ilmonen et al. 2008), the interplay of disease resistance and sexual attractiveness (Zala et al. 2008), and fitness consequences of infectious and genetic disease (e.g., Carroll et al. 2004; Zala et al. 2008).

All males of the first generation that completed both competition round were used to sire the second generation. Males were randomly mated to the sisters of other competing males. Siblings and cousins were not mated to avoid inbreeding, which has serious impacts on house mouse fitness (Meagher et al. 2000; Ilmonen et al. 2008).

Our colony males regularly display post-weaning aggression when group housed. To help remove the possible confounding effects from intra-litter competitive networks, males were singly housed. Individual housing also removed the effects from differential number of littermates, which would have been present if males were caged with family groups. Males were housed individually starting at weaning; females were housed with sisters. Although unlikely in nature for extended periods, solitary housing is preferable to the alternative in this case. Additionally, males are likely solitary after dispersal. This solitary period ends with a male gaining a territory or being accepted as a subordinate in an established territory. Solitary housing has also been shown to increase aggression (Crawley 2007), which is an effect likely present in our population. However, we have direct evidence to show that aggression has a minimal influence on competitive ability in this population (Cunningham et al. 2012). Animals were housed in standard polycarbonate (15 × 30 × 15 cm) colony cages with Cellsorb (Fangmen Specialties) for bedding under a 12:12h light:dark cycle. Tekland 2018 rodent chow (Harlan Laboratories) and water were available *ad libitum*. Mice were also provided nesting material (paper towels). All protocols were approved by the IACUC, University of Utah.

Preparation Procedures

Randomly selected females were used to encourage competition in each competition arena. These females were singly housed for two weeks previous to the beginning of each competition round (Kuse and De Fries 1976). These females were not used in subsequent breedings. Passive integrated transponders were placed into all males of the second generation to speed the identification of the preferred territory owner using a hand-held receiver.

Mice of generation one (g1) were eight months and generation two (g2) mice were five months old at the beginning of their respective first competition round. Full bodily maturity is hard to predict for any population of mice. However, other wild-derived colonies display skeletal growth and are not sexually mature until at least 90 days (Knudsen 1962). Although they are sexually mature, mice (females and males) from our colony show body mass growth for one year. Females of some wild, commensal-derived colonies reach sexual maturity at 59 ± 24 days; therefore, it is likely one needs to wait > 3 months to ensure the vast majority of females are sexually mature (Miller et al. 2002). Also, males disperse from natal litters when they are ~ 3 months of age (Gerlach 1996). For these reasons, our mice were not tested before 4 months of age. Several logistical challenges caused the delay in the testing of g1 (i.e., the remote doors were difficult to get working, see below). Importantly, these ages are within the young adults life stage for laboratory maintained, wild-derived colonies (Miller et al. 2002; Garratt et al. 2011). Additionally, if an interaction between genotypes and age existed such that different genotypes “peaked” in competitive ability at different ages, then we would likely lose the signal from causal factors.

Our competitors were sexually inexperienced entering the first competition round. We believe that dispersing males are not sexually experienced as they attempt to gain a territory, but are not aware of any studies directly addressing this point. We purposely chose this state for several reasons. First, territorial males increase aggression directed towards male offspring while they mature (Gerlach 1990; Gerlach 1996; Rusu et al. 2008). Second, mice avoid inbreeding when possible (Krackow and Matuschak 1991). For these reasons, we kept our males sexually inexperienced as they entered the first competition round. We intentionally did not control for possible differences in sexual experience during the second round. This was for two main reasons. First, males that are competing over a territory likely have differing sexual histories. Second, mating causes several large hormonal shifts (Ely and Henry 1978; Phelps et al. 1998), which might complicate our ability to detect effects based solely on difference in competitive ability.

Competition Arenas

Arena design was based on the established “phenotron model system”. This system originally helped discover MHC-based mating and nesting preferences in wild mice (Potts et al. 1991; Ruff et al. 2012). Acrylic sheeting was used to construct the arenas; dimensions $140 \times 30 \times 15$ cm. The design utilizes the preference of house mice to establish territories with secluded nest sites offering protection from infanticidal conspecifics and predators (Wolff 1985; Hurst 1987; Manning et al. 1995). Therefore, each arena was divided into two chambers: 1) a preferred nesting site and 2) a larger suboptimal communal area. The preferred nesting site had opaque walls and ceiling, food and water, and nesting material (paper towels); dimensions $15 \times 30 \times 15$ cm. The larger communal area had transparent walls and ceiling, shared food and water, and no nesting material.

Remotely operated, sliding electric doors permitted us to restrict access to the preferred site before entering the study area to enable identification of the male inhabiting the preferred site concretely. This was necessary because during preliminary trials all mice regardless of

competitive ability retreated to the preferred nesting site as investigators approached the arenas. This made it extremely difficult to observe which male occupied the preferred territory before human disturbance and was the impetus for a solution to separate physically the two areas to ensure the identification of the preferred territory holding male.

Testing Procedures

Eighty males from g1 and 48 males from g2 began the competition. We completely phenotyped 117 males. Some males were not analyzed for methodical reasons. For example, three males were grouped in the second competition round and a multiple of three was not always available. Therefore, some males that completed round one did not complete round two and were not completely phenotyped.

At the start of each competition round, four males and one female were randomly grouped into an arena. Siblings (male or female) were never grouped together. This is a density of ten males/m², which is roughly 1.5–2.5× the density reported for commensal populations and wild-derived colonies in large enclosures with self-regulated growth (Lidicker 1976; Berry 1991). This is also about 4× a male biased sex ratio reported from commensal populations (Gomez et al. 2008). All mice were inspected to ensure that they had not developed conspicuous abnormalities or injuries. All mice were then weighed, ear punched (for identification), and placed within the arenas. Mice were reweighed at the end of the competition round. Six weeks of recovery were allowed between rounds. During a second competition round, males that won the first round were placed with other winning males and first round losers with other losers. Because some males were removed from the first competition round, only three males and one female were grouped in the second competition round. Mice that had competed against each other in the first round were excluded from being opponents during the second round of competition.

Group composition for the first competition round with g2 was dictated by an individual sire's competitive ability. One male from a two-time winning sire, two males from different single winning sires, and one male from a zero-winning sire were randomly grouped into an arena with one female. Competition rounds for g2 mice were completed using the same protocol as the g1 mice.

Males were not randomized for the second competition round for several reasons. First, it would have disregarded the winner/loser effects that cause large changes in hormonal (e.g., Louch and Higginbotham 1967; Barkley and Goldman 1977; Ely and Henry 1978; Oyegbile and Marler 2005), gene expression (Fuxjager et al. 2010), and behavioral measures in mice and other rodents (e.g., Desjardins et al. 1973; Ely and Henry 1978). Second, our experiment was designed to emphasize competitive ability. No new information would have been gained in knowing that a first-round winner beat a first-round loser in the second round. Third, although the two competition rounds were not independent of each other, randomizing males during the second round would not have resolved the non-independence problem. Moreover, competing males in a third round would likely not have changed the results qualitatively. Our conclusion is mainly due to the use of the animal model, which incorporates the entire pedigree in estimating heritability. Even if we had competed males for a third round, it is likely there still would have been a non-random distribution of 3-time winning and 3-time losing families. Finally, by grouping males in the second round based on their first round performance, we increased the likelihood of finding traits that modestly influenced competitive ability. This is because our protocol reduces the variation of strongly influential traits between competitors in the second round. For example, body mass influences competitive ability in many animal species. If first round winners were larger than average, then in the second round we would see less variation in the distribution of body mass in winner arenas. This reduction in the disparity of a causal trait between opponents would

increase our ability to find influences from other less influential factors. We therefore feel our two round tournament that grouped males in the second round by their win/loss result in the first round is advantageous because it allowed very accurate phenotyping of an individual's competitive ability and increased our ability to detect moderately influential traits.

Competition rounds lasted three days, which was determined to be the optimum length to observe differences in competitive ability while keeping the duress to males at a minimum. At least six observations determined which male occupied the preferred site most over the three days. One observation per day was during the night resting period. Mice that appeared seriously stressed were removed immediately. We used multiple qualitative criteria to decide if males should be removed from a competition round. First, males were assessed for visible wounds (especially on the abdomen) or limping. Next, males were assessed for general appearance (e.g., pelage condition, sunken in abdomen, body mass loss, etc.). Finally, males were evaluated for their reaction to human presence (e.g., was the male aware of the investigator's presence as a normal mouse is, was it responsive, did it react to a short tap on the acrylic, etc.). Males that were removed due to apparent stress were excluded from the second competition round.

Scoring Regimes for a Single Round and Across the Study

We used two, well established measures of competitive ability to score males as winners or losers within each arena; possession of the preferred territory and wounding. Possession of a preferred territory is evidence that a male is highly competitive and is used commonly as a measure of competitive ability, even in the absence of direct behavioral observations (e.g., De Fries and McClearn 1970; Kuse and De Fries 1976; Potts et al. 1991; Meagher et al. 2000; Ilmonen et al. 2008). Lack of wounding and good body condition are also traditional measures of competitive ability (De Fries and McClearn 1970; Oakeshott 1974; Kuse and De Fries 1976; Benton et al. 1980). Wounding was scored separately for the hind flank and tail regions. Wounding was scored none (0 marks), slight (1–5 marks), moderate (6–10 marks), and extensive (> 10 marks). Wounding data was not scored in the first round of the first generation with the above metric; rather a more qualitative scale was used to indicate the degree of wounding over the entire body (extensive, moderate, some, absent). General body condition was scored as weight loss between the beginning and end of a competition round and was reliably associated with winning within an arena ($r = 0.38$, $p \ll 0.001$). Winners were established by grading the disparity of these measures between all of the competing males.

Competitive ability was quantified as the number of rounds each male won. For example, males that won both rounds were given a score of 2. We considered this a ranked variable. As such they can be analyzed with a linear mixed model if the distribution is not too skewed, which we assessed before analysis (Wilson et al. 2009). Additionally, we also scored males as two round winners (2), winner/loser (1.25), loser/winner (0.75), and zero winners (0) in a preliminary data analysis to assess the influence of our scoring system. The results were qualitatively similar (i.e., highly significant, moderate values for additive genetic variation).

Statistical Analyses

Heritability was estimated using the “Animal Model”, which utilizes pedigree information and a linear mixed model to partition variance into causal components (e.g., genetic, environmental) (Wilson et al. 2009). Using all available relationships greatly increases power to estimate additive genetic variance (Wilson et al. 2009); however, we note that our sample size is relatively small and thus constrains our ability to utilize more comprehensive

quantitative genetic methods (Wilson et al. 2009). We also assessed the genetic correlation between body mass and competitive ability to estimate the amount of shared genetic controls of the two traits. The heritability of competitive ability, the heritability of body mass entering the competition trials (also served as a positive control), and the genetic correlation (r_G) between body mass and competitive ability was estimated with the “MCMCglmm” package (Hadfield 2010) of R. In our models, we used a Poisson distribution for competitive ability and a normal distribution for body mass. These distributions were chosen based on statistical likelihood. Models were run through one million iterations. Additionally, we estimated the heritability of winning the first round alone with a binomial distribution and the protocol above. Other factors, like litter size and sex ratio, were included in preliminary models, but never approached significance and therefore were not included in the final model.

Competitive ability was regressed against each male's natal litter size and litter sex ratio. In addition, to validate all our assumptions, adult body mass was correlated (Spearman's rank method (ρ)) with weaning weight and litter size with weaning weight. Weaning weight was only available from g2. Litter sex ratio was scored as a percentage (# of males / # of progeny). It was also correlated with competitive ability. The interaction between litter size and litter sex ratio was assessed with a linear regression.

Previously, order of placement, ear punched, and relative age have been shown not to be confounding factors and so were not included into any analysis (Cunningham et al. 2012).

All analyses were conducted in R (R-Development-Core-Team 2011).

Results

Descriptive Results of Contest Outcomes

The preferred nesting site was occupied by the eventual winner of each round at different rates and with differing degrees of exclusivity. Some males were found to occupy exclusively the preferred nesting site from the first observation onward; some contests had multiple males occupy the nesting site for at least one observation. In contests where multiple males occupied the preferred site, wounding usually showed a large disparity between the competitive males. Some winning males allowed another male to continually co-habitate in the preferred nesting site; however, in these cases there was a clear and sizable disparity in superficial wounding and general body condition between the cohabitators. Possession of the preferred nesting site and wounding/general body condition together never produced an ambiguous winner. See Fig. 1 for the distributions of these measures.

Heritability of Competitive Ability

Competitive ability had a high narrow sense heritability, $h^2 = 0.58$ (95% CI s: 0.23–0.92; $p < 0.01$; $n=117$; Table 1). Using data from the first round only, produced similar qualitative results, $h^2 = 0.51$ (95% CI s: 0.16–0.8; $p < 0.01$; Table 1).

Body Mass: Heritability and Co-Variation with Competitive Ability

Body mass was heritable, $h^2 = 0.82$ ($p < 0.001$; $n = 117$; Table 1). There was a genetic correlation between competitive ability and body mass of 0.66 (95% CI s: 0.016–0.88; $p = 0.05$; Table 1).

Demographic Factors: Influences of Litter Size and Litter Sex Ratio

Weaning weight was significantly correlated with adult body size, as expected ($\rho = 0.65$, $p < 0.001$; $n = 46$). However, weaning weight was not correlated with litter size ($\rho = 0.17$, $p = 0.27$).

Competitive ability was not influenced by litter size across the study (slope = -0.015 , $p = 0.74$; $\rho = 0.1$, $p = 0.27$). Litter size was also not associated with competitive ability if the data is broken down by round and win/loss groupings (Round 1: slope = 0.11 , $p = 0.37$; Round 2: winners- slope = -0.26 , $p = 0.20$; losers- slope = 0.15 , $p = 0.35$).

Litter sex-ratio negatively influenced competitive ability, (slope = -0.68 , $p = 0.02$; $\rho = -0.18$, $p = 0.053$; Fig. 2); however, it was not a significant factor when included in the heritability model. Competitive ability from round one alone is significantly negatively associated with litter sex ratio (slope = -2.78 , $p = 0.02$). Litter sex ratio was not associated with winning in the second round (winners: slope = -2.09 , $p = 0.42$; losers: slope = -0.73 , $p = 0.55$). Number of male siblings was not correlated with competitive ability ($\rho = -0.07$, $p = 0.45$), but number of sisters was ($\rho = 0.19$, $p = 0.042$).

There was no interaction between natal litter size and sex ratio ($p = 0.14$).

Discussion

We performed an experiment to estimate the genetic influences on competitive ability of male house mice using semi-natural enclosures and mixed sex groupings. We also estimated the influence of litter size and litter sex ratio on competitive ability. Competitive ability displayed large additive genetic variation, using all of the data and data from the first round alone (Table 1). The moderate genetic correlation between body mass and competitive ability demonstrates the two traits have a substantial amounts of non-overlapping genetic controls (Table 1). Litter size was not correlated with competitive ability and there was no interaction between litter size and litter sex ratio. Litter sex ratio modestly influenced competition ability (Fig. 2). Interestingly, there was a stronger relationship between the number of sisters and competitive ability than with the number of brothers. The results being qualitatively similar across all analyses suggest robustness to our conclusions. Taken with results from other studies, we suggest that competitive ability has a complex multi-trait foundation.

Given the reproductive advantages of occupying the top of a social hierarchy, it is not surprising that competitive ability is often similar in parents and offspring. Here, we found a high heritability for competitive ability (Table 1). The heritability of competitive ability has also been estimated in six other species: a cockroach (Moore 1990), paradise fish (Francis 1984), Japanese quail (Nol et al. 1996), chickens (Craig et al. 1965), cattle (Satori and Mantovani 2012), and deer mice (Dewsbury 1990). Consistent with our results, competitive ability was found to be heritable in all of the studies. Our result is also consistent with current quantitative genetic models of social traits (Moore 1993; 1997; Moore et al. 2002; McGlothlin et al. 2010). Significant additive genetic variation in competitive ability suggests the possibility of counter-selecting pressures from other life-history traits (e.g., locomotor efficiency), which might help maintain genetic variation despite this trait being closely linked to fitness (Falconer and Mackay 1996; Pasi and Carrier 2003). Alternatively, indirect genetic effects could have led to the high heritability (Moore et al. 1997).

Litter sex ratio was significantly, negatively correlated with competitive ability depending on the subset of the data that was tested (Fig. 2). Effects from litter sex ratio can be caused by pre- or post-natal influences. The most likely pre-natal influence would be from *in utero*

hormonal environment. Here, as the proportion of male progeny increased, males from that litter demonstrated lower competitive ability. This is an opposite effect than previously found in female mice (Zielinski et al. 1992). Alternatively, the effect could be equally well described as the proportions of female progeny increased, males from those litters demonstrated increased competitive ability. It could also be that litter sex-ratio effects are mediated through post-natal interactions with siblings. It is possible that as a litter becomes male biased there is more competition for maternal care. We assessed whether the number of male or female siblings better correlated with competitive ability. Only the number of female siblings significantly correlated with competitive ability. This suggests that the litter sex-ratio effect is mediated more through sisters than brothers. On the surface this lends support to a post-natal interpretation of our results. While our data suggests a possible trait underpinning variation in male competitive ability, an explicit experiment addressing this hypothesis is needed.

Litter size did not have a detectable relationship with competitive ability. This result is surprising given the high metabolic demands large litters place on the nursing mother (Konig et al. 1988). Although, given the moderate effect that body size has on competitive ability, finding no link between the two variables seems plausible (Cunningham et al. 2012). It is possible that dams were able to compensate for large litters because of the high quality *ad libitum* food and water. The non-significant positive trend between litter size and weaning weight supports this possibility. Additionally, it is known that mice can control their own body mass after weaning, which may also provide an explanation for the lack of a relationship between litter size and competitive ability (Bult and Lynch 1997).

Our results here and elsewhere (Cunningham et al. 2012) suggest that many factors underpin competitive ability. While our results here do not help elucidate which other characters are important in physical conflict, several traits have been correlated with competitive ability or increasing physical conflict. For example, short legs are expected to improve fighting performance and a negative correlation between hind-limb length and body size sexual dimorphism exists in apes (Carrier 2007). Larger musculature, in a dog breed bred for fighting, was found distally in the limbs compared to a running breed, which is expected to allow high force and power production used for agility, balance, and opponent manipulation (Pasi and Carrier 2003). In two species of lizards, bite force rather than size was the best correlate with the winners of encounters and reproductive fitness (Huyghe et al. 2005; Lappin and Husak 2005). A study on green anoles has suggested that different traits promote high competitive ability at different developmental stages in green anoles (Lailvaux et al. 2004). Competitive ability has been linked to pheromone composition in a species of cockroach (Moore et al. 1997). Behavioral traits have also been linked to competitive ability. Aggression has been widely suggested to play a role in competitive ability in several species of rodents (Blanchard et al. 1992; Rolland et al. 2003); however, we have direct evidence that aggression plays no role in competitive ability in this population (Cunningham et al. 2012). Epigenetics can play an important role in shaping offspring phenotypes based on social experiences of their parents, specifically social defeats (Dietz et al. 2011); it is possible that epigenetic effects played an important role here by helping to generate similar phenotypes between parents and offspring. Collectively, these observations plus our findings here suggest that a complex suite of traits likely determines competitive ability.

Acknowledgments

We would like to thank Fred Adler, Elizabeth Cashdan, Terry Dial, Gordon Lark, Allen Moore, Nadja Schilling, and Jon Seger for insightful discussions. We would also like to thank Terry Dial and Daryl McLaren who helped with data collection and Linda Morrison who maintained the mouse population's pedigree. This work was primarily funded through the University of Utah Funding Incentive Seed Grant Program to DR Carrier. Additional funding was provided through NSF grants to DR Carrier (IOS 08-17782) and WK Potts (DEB 09-18969) and an NIH grant

to WK Potts (RO1- GM039578). CB Cunningham and JS Ruff were supported by NSF GK-12 Educational Outreach Fellowships (DGE 08-41233).

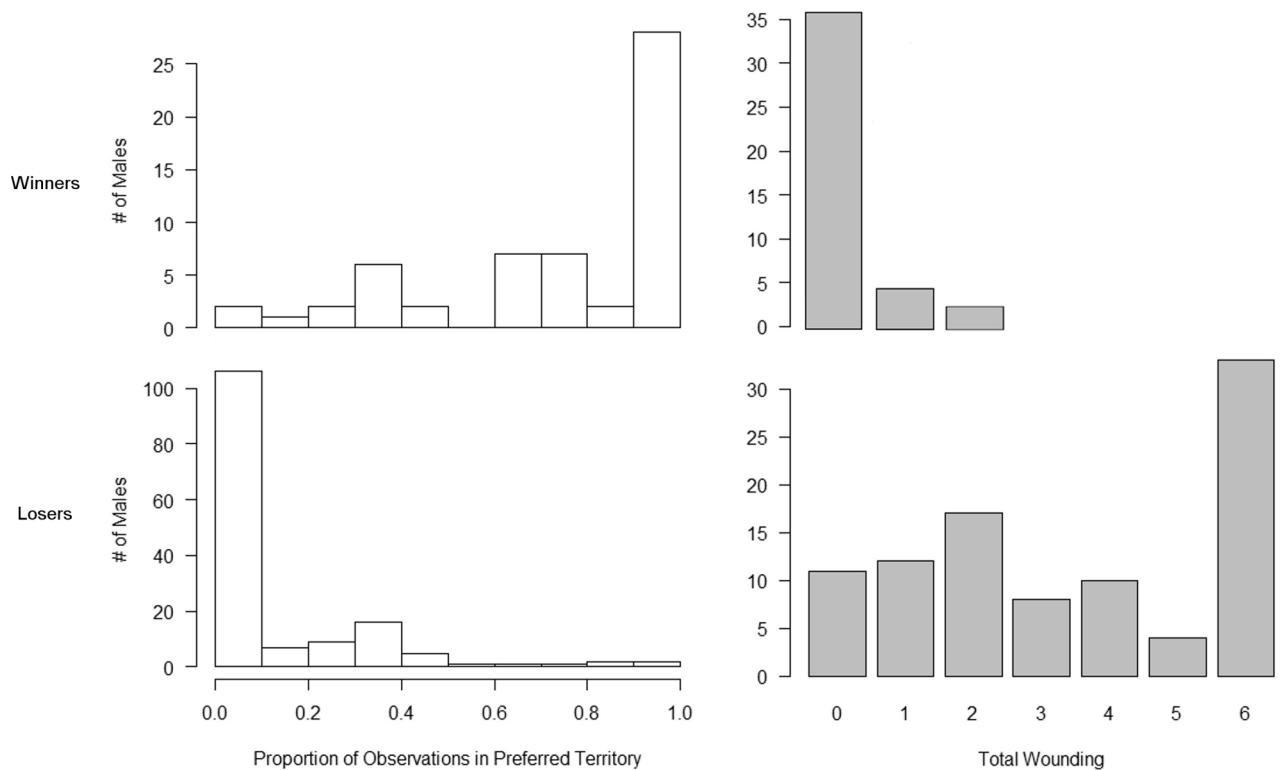
References

- Barkley M, Goldman B. A quantitative study of serum testosterone, sex accessory organ growth, and the development of intermale aggression in the mouse. *Hormones and Behavior*. 1977; 8:208–218. [PubMed: 558957]
- Barrette C. Dominance cannot be inherited. *Trends in Ecology & Evolution*. 1987; 2:251. [PubMed: 21227861]
- Barrette C. The “inheritance of dominance”, or of an aptitude to dominate? *Animal Behaviour*. 1993; 46:591–593.
- Benton D, Dalrymple-Alford J, Brain F. Comparisons of measures of dominance in the laboratory mouse. *Animal Behaviour*. 1980; 28:1274–1279.
- Berry, RJ. House Mouse *Mus domesticus*. In: Corbet, GB.; Harris, S., editors. *Handbook of British Mammals*. Blackwell Scientific; Oxford: 1991. p. 239-247.
- Blanchard RJ, Flores T, Magee W, Weiss S, Blanchard DC. Pregrouping aggression and defense scores influences alcohol consumption for dominant and subordinate rats in visible burrow systems. *Aggressive Behavior*. 1992; 18:459–467.
- Briffa M, Sneddon LU. Physiological constraints on contest behaviour. *Functional Ecology*. 2007; 21:627–637.
- Bult A, Lynch CB. Nesting and fitness: Lifetime reproductive success in house mice bidirectionally selected for thymoregulatory nest-building behavior. *Behavior Genetics*. 1997; 27:231–240. [PubMed: 9210794]
- Carrier DR. The short legs of great apes: evidence for aggressive behavior in Australopiths. *Evolution*. 2007; 61:596–605. [PubMed: 17348922]
- Carroll LS, Meagher S, Morrison L, Penn D, Potts WK. Fitness effects of a selfish gene are revealed in an ecological context. *Evolution*. 2004; 58:1318–1328. [PubMed: 15266980]
- Craig JV, Ortman LL, Guhl AM. Genetic selection for social dominance ability in chickens. *Animal Behaviour*. 1965; 13:114–131.
- Crawley, JN. What’s wrong with my mouse? Behavioral phenotyping of transgenic and knockout mice. Wiley; Hoboken, NJ: 2007.
- Crowcroft P. Territoriality in wild mice, *Mus musculus* L. *Journal of Mammalogy*. 1955; 36:299–301.
- Cunningham CB, Ruff JS, Chase K, Potts WK, Carrier DR. Competitive ability in male house mice (*Mus musculus*): The influence of body mass under differing levels of social competition. 2012 In review.
- Cunningham, CB.; Ruff, JS.; Edmunds, T.; Chase, K.; Carrier, DR. Competitive ability and aggression are different phenomena in male house mice. 2012. In review
- Darwin, C. *The Descent of Man and Selection in Relation to Sex*. Murray; London: 1871.
- De Fries J, McClearn G. Social dominance and darwinian fitness in the laboratory mouse. *American Naturalist*. 1970; 104:408–411.
- Desjardins C, Maruniak JA, Bronson FH. Social rank in house mice: differentiation revealed by ultraviolet visualization of urinary marking patterns. *Science*. 1973; 182:939–941. [PubMed: 4745598]
- Dewsbury DA. Dominance rank, copulatory behavior, and differential reproduction. *Quarterly Review of Biology*. 1982; 57:135–159.
- Dewsbury DA. Fathers and sons: genetic factors and social dominance in deer mice, *Peromyscus maniculatus*. *Animal Behaviour*. 1990; 39:284–289.
- Dietz DM, LaPlant Q, Watts EL, Hodes GE, Russo SJ, Feng J, Oosting RS, Vialou V, Nestler E. Paternal transmission of stress-induced pathologies. *Biological Psychiatry*. 2011; 70:408–414. [PubMed: 21679926]
- Drickamer LC. Urine marking and social dominance in male house mice (*Mus musculus domesticus*). *Behavioural Processes*. 2001; 53:113–120. [PubMed: 11254998]

- Ellis L. Dominance and reproductive success among nonhuman animals: a cross-species comparison. *Ethology and Sociobiology*. 1995; 16:257–333.
- Ely DL, Henry JP. Neuroendocrine response patterns in dominant and subordinate mice. *Hormones and Behavior*. 1978; 10:156–169. [PubMed: 29002]
- Emlen D. The evolution of animal weapons. *Annual Review of Ecology, Evolution, and Systematics*. 2008; 39:387–413.
- Falconer, D.; Mackay, T. *Introduction to Quantitative Genetics*. Longman Publishing Group; 1996.
- Francis RC. The effects of bidirectional selection for social dominance on agonistic behavior and sex ratios in the paradise fish (*Macropodus opercularis*). *Behaviour*. 1984; 90:25–45.
- Fuxjager MJ, Forbes-Lorman RM, Coss DJ, Auger CJ, Auger AP, Marler CA. Winning territorial disputes selectively enhances androgen sensitivity in neural pathways related to motivation and social aggression. *Proceedings of the National Academy of Science*. 2010; 107:12393–12398.
- Garratt M, Stockley P, Armstrong SD, Beynon RJ, Hurst J. The scent of senescence: sexual signalling and female preference in house mice. *Journal of Evolutionary Biology*. 2011; 24:2398–2409. [PubMed: 21848973]
- Gerlach G. Dispersal mechanisms in a captive wild house mouse population (*Mus musculus* Ruddy). *Biological Journal of the Linnean Society*. 1990; 41:271–277.
- Gerlach G. Emigration mechanisms in feral house mice- a laboratory investigation of the influence of social structure, population density, and aggression. *Behavioral Ecology and Sociobiology*. 1996; 39:159–170.
- Gomez MD, Priotto J, Provencal MC, Steinmann A, Castillo E, Polop JJ. A population study of house mice (*Mus musculus*) inhabiting different habitats in an Argentine urban area. *International Biodeterioration & Biodegradation*. 2008; 62:270–273.
- Hadfield J. MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. *Journal of Statistical Software*. 2010; (33):1–22.
- Hand J. Resolution of social conflicts: dominance, egalitarianism, spheres of dominance, and game theory. *Quarterly Review of Biology*. 1986; 61:201–220.
- Hayashi S. Development and diversity of social structure in male mice. *Journal of Ethology*. 1993; 11:77–82.
- Hurst J. Behavioural variation in wild house mice *Mus domesticus* Ruddy: a quantitative assessment of female social organization. *Animal Behaviour*. 1987; 35:1846–1857.
- Huyghe K, Vanhooydonck B, Scheers H, Molica-Borja M, Van Damme R. Morphology performance and fighting capacity in male lizards, *Gallotia galloti*. *Functional Ecology*. 2005; 19:800–807.
- Ilmonen P, Penn DJ, Damjanovich K, Clarke J, Lamborn D, Morrison L, Ghotbi L, Potts WK. Experimental infection magnifies inbreeding depression in house mice. *Journal of Evolutionary Biology*. 2008; 21:834–841. [PubMed: 18312317]
- Kaufmann J. On the definitions and functions of dominance and territoriality. *Biological Review*. 1983; 58:1–20.
- Knudsen B. Growth and reproduction of house mice at three different temperatures. *Oikos*. 1962; 13:1–14.
- Konig B, Riester J, Markl H. Maternal care in house mice (*Mus musculus*): II. The energy cost of lactation as a function of litter size. *Journal of Zoology*. 1988; 216:195–210.
- Krackow S. The effect of weaning weight on offspring fitness in wild house mice (*Mus musculus domesticus*): A preliminary study. *Ethology*. 1993; 95:76–82.
- Krackow S, Matuschak B. Mate choice for non-siblings in wild house mice: evidence from a choice test and a reproductive test. *Ethology*. 1991; 88:99–108.
- Kuse A, De Fries J. Social dominance and Darwinian fitness in laboratory mice: an alternative test. *Behavioral Biology*. 1976; 16:113–116. [PubMed: 943157]
- Lailvaux SP, Herrel A, VanHooydonck B, Meyers JJ, Irschick DJ. Performance capacity, fighting tactics and the evolution of life-stage male morphs in the green anole lizard (*Anolis carolinensis*). *Proceedings of the Royal Society of London: B*. 2004; 271:2501–2508.

- Lappin AK, Husak JF. Weapon performance, not size, determines mating success and potential reproductive output in the collared lizard (*Crotaphytus collaris*). *American Naturalist*. 2005; 166:426–436.
- Lidicker WZ. Social Behaviour and density regulation in house mice living in large enclosures. *Journal of Animal Ecology*. 1976; 45:677–697.
- Louch CD, Higginbotham M. The relation between social rank and plasma corticosterone levels in mice. *General and Comparative Endocrinology*. 1967; 8:441–444. [PubMed: 6068098]
- Manning C, Wakeland E, Dewsbury DA, Potts WK. Communal nesting and communal nursing in housemice, *Mus musculus domesticus*. *Animal Behaviour*. 1995; 50:741–751.
- McGlothlin JW, Moore AJ, Wolf JB, Brodie ED III. Interacting phenotypes and the evolutionary process. III. Social evolution. *Evolution*. 2010; 64:2558–2574. [PubMed: 20394666]
- Meagher S, Penn D, Potts WK. Male-male competition magnifies inbreeding depression in wild house mice. *Proceedings of the National Academy of Science*. 2000; 97:3324–3329.
- Miller RA, Harper JM, Dysko RC, Durkee SJ, Austad SN. Longer life spans and delayed maturation in wild-derived mice. *Experimental Biology and Medicine*. 2002; 227:500–508. [PubMed: 12094015]
- Moore A. Towards an evolutionary view of social dominance. *Animal Behaviour*. 1993; 46:594–596.
- Moore AJ. The inheritance of social dominance, mating behaviour and attractiveness to mates in male *Nauphoeta cinerea*. *Animal Behaviour*. 1990; 39:388–397.
- Moore AJ, Brodie ED III, Wolff JB. Interacting phenotypes and the evolutionary process: I. Direct and indirect genetic effects of social interactions. *Evolution*. 1997; 51:1352–1362.
- Moore AJ, Haynes KF, Preziosi RF, Moore PJ. The evolution of interacting phenotypes: genetics and evolution of social dominance. *The American Naturalist*. 2002; 160:S186–S197.
- Moore PJ, Reagan-Wallin NL, Haynes KF, Moore AJ. Odour conveys status on cockroaches. *Nature*. 1997; 389:25. [PubMed: 9288961]
- Nol E, Cheng K, Nichols C. Heritability and phenotypic correlations of behaviour and dominance rank of Japanese quail. *Animal Behaviour*. 1996; 52:813–820.
- Oakeshott JG. Social dominance, aggressiveness, and mating success among male house mice (*Mus musculus*). *Oecologia*. 1974; 15:143–158.
- Oyegbile TO, Marler CA. Winning fights elevates testosterone levels in California mice and enhances future ability to win fights. *Hormones and Behavior*. 2005; 48:259–267. [PubMed: 15979073]
- Pasi B, Carrier DR. Functional trade-offs in the limbs of dogs selected for running vs. fighting. *Journal of Evolutionary Biology*. 2003; 16:324–332. [PubMed: 14635871]
- Phelps SM, Lydon JP, O'Malley BW, Crews D. Regulation of male sexual behavior by progesterone receptor, sexual experience, and androgen. *Hormones and Behavior*. 1998; 34:294–302. [PubMed: 9878278]
- Potts WK, Manning C, Wakeland E. Mating patterns in semi-natural populations of mice influenced by MHC genotype. *Nature*. 1991; 352:619–621. [PubMed: 1865924]
- R-Development-Core-Team. R: A language and environment for statistical computing. R Foundation for Statistical Computing; Vienna, Austria: 2011.
- Rolland C, MacDonald D, de Fraipont M, Berdoy M. Free female choice in house mice: Leaving best for last. *Behaviour*. 2003; 140:1371–1388.
- Ruff, JS.; Nelson, AC.; Kubinak, JL.; Potts, WK. MHC signaling during social communication. In: Lopez-Larrea, C., editor. *Self and Nonself*. Landes Bioscience; Austin, TX: 2012.
- Rusu AS, Krackow S, Jedelsky PL, Stopka P, Konig B. A qualitative investigation of major urinary proteins in relation to the onset of aggressive behavior and dispersive motivation in male wild house mice (*Mus musculus domesticus*). *Journal of Ethology*. 2008; 26:127–135.
- Satori C, Mantovani R. Indirect genetic effects and the genetic bases of social dominance: evidence from cattle. *Heredity*. 2012:1–7.
- Sutherland D, Spencer P, Singleton G, Taylor A. Kin interactions and changing social structure during a population outbreak of feral house mice. *Molecular Ecology*. 2005; 14:2803–2814. [PubMed: 16029479]

- vom Saal F, Bronson FH. Sexual characteristics of adult female mice are correlated with their blood testosterone levels during prenatal development. *Science*. 1980; 208:597–599. [PubMed: 7367881]
- vom Saal F, Grant WM, McMullen CW, Laves KS. High fetal estrogen concentrations: correlations with increased adult sexual activity and decreased aggression in male mice. *Science*. 1983; 220:1306–1309. [PubMed: 6857252]
- Wilson A, Reale D, Clements M, Morrissey M, Postma E, Walling C, Kruuk L, Nussey D. An ecologist's guide to the animal model. *Journal of Animal Ecology*. 2009; 79:13–26. [PubMed: 20409158]
- Wilson B, Nicholas F, James J, Thomson P. Comparison of genetic parameters obtained from an ordinal canine hip phenotype data set by linear or ordinal analysis. *Proceedings of the Association for the Advancement of Animal Breeding and Genetics*. 2009; 18:450–453.
- Wolff JO. Mating behavior and female choice: the relation to social structure in wild caught house mice (*Mus musculus*) housed in semi-natural environment. *Journal of Zoology (London)*. 1985; 207:43–51.
- Wright S. Coefficients of inbreeding and relationship. *The American Naturalist*. 1921; 56:330–338.
- Zala S, Potts WK, Penn D. Exposing males to female scent increases the cost of controlling *Salmonella* infection in wild house mice. *Behavioral Ecology and Sociobiology*. 2008; 62:895–900.
- Zielinski W, vom Saal F, Vandenberg J. The effect of intrauterine position on the survival, reproduction, and home range size of female house mice (*Mus musculus*). *Behavioral Ecology and Sociobiology*. 1992; 30:185–191.

**Fig. 1.**

Graph represents the distribution of observations of preferred territory occupation and wounding between arena winners and losers. Data in the first column are the proportion of observations that an individual male occupied the preferred territory from the total observations when there was a male present in the preferred territory. Please note the large difference in the scale of the Y-axis. Data in the second column are wounding values converted to numeric scores. The four levels (0 wounds=0, 1–5 wounds=1, 6–10 wounds=2, >10 wounds= 3) from the two areas (hind flanks and tail) that were scored separately were summed together, giving scores between zero and six.

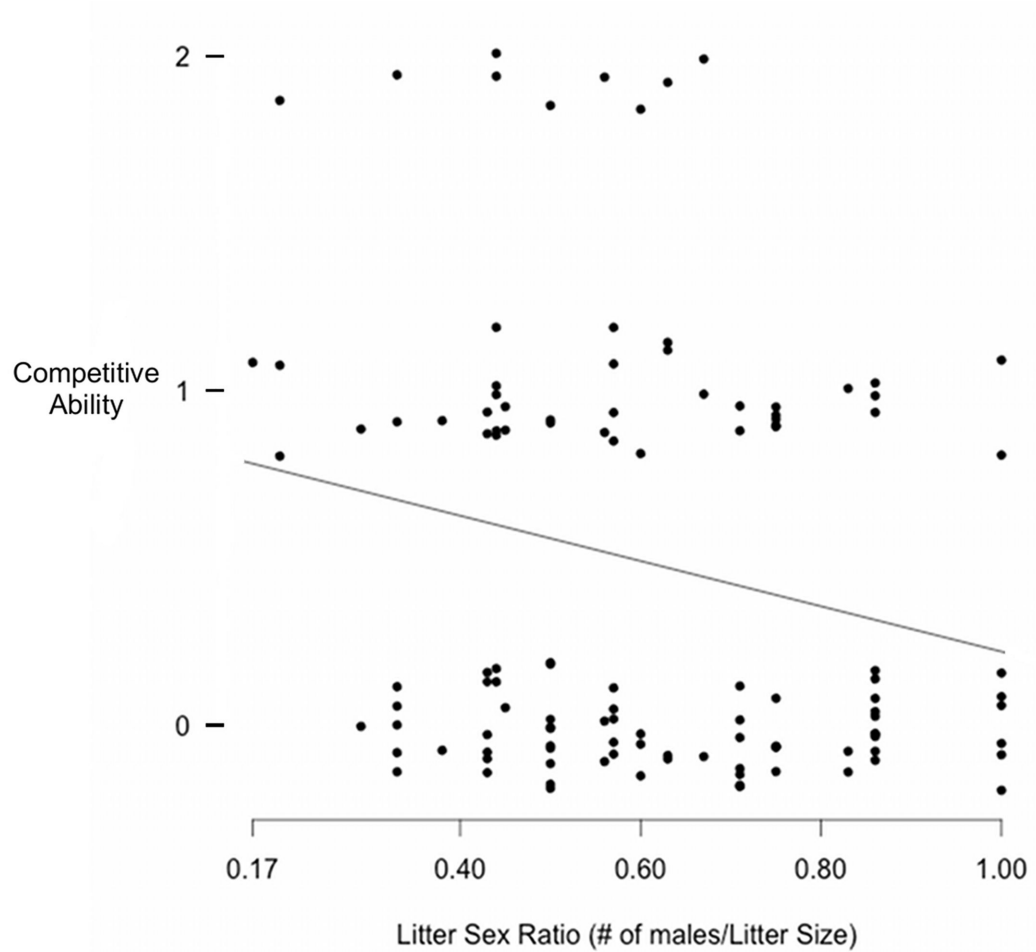


Fig. 2.

Graph represents the overall relationship between litter sex ratio and competitive ability. Scatter plot of Litter sex ratio (# of males/# of progeny) *versus* Competitive ability (# of competition rounds won) (slope = -0.68 , $p = 0.02$; $\rho = -0.18$, $p = 0.053$). Random noise was added to the y-values to help visualize the data.

Table I

Quantitative Genetics of Competitive Ability.

Trait	Magnitude	95% CI	n	p
<u>Animal Model: Body Mass $\propto V_A$</u>				
V_A/V_P	0.827	(.45–0.947)	117	<0.01
<u>Animal Model: CA $\propto V_A$</u>				
V_A/V_P	0.58	(0.23–0.92)	117	<0.01
<u>Animal Model: CA $\propto V_A$ (1st Round Data Only)</u>				
V_A/V_P	0.51	(0.16–0.80)	117	<0.01
<u>Genetic Correlation: CA \propto Body Mass</u>				
BM	0.66	(0.016–0.889)	117	0.05

Estimates were generated using the Animal Model, see methods for details.

CI= Confidence Intervals, n= Sample Size, V_A = Additive Genetic Variance, V_P = Total Phenotypic Variance, CA= Competitive Ability, BM= Body Mass.