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Social play predicts docility in juvenile ground squirrels

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Abstract

We evaluated the hypothesis that social play behavior influences the development of temperament in young animals, using docility as a measure of temperament. We observed the play behavior of juvenile Belding's ground squirrels (*Urocitellus beldingi*) during the developmental period in which play primarily occurs, and conducted behavioral tests measuring docility at the beginning and end of the play interval. Tests involved handling squirrels and recording their responses. Body mass was a reliable predictor of docility at the beginning of the play period. Rates of social play and maximum distances traveled from the natal burrow during the play interval were reliable predictors of change in docility across the play period. Juveniles who played at higher rates and traveled farther from the natal burrow tended to have greater decreases in docility over the play interval, supporting the idea that social play and other early-life experiences might influence the development of tendencies toward more active responses in this species. To gauge docility beyond the juvenile period, we conducted docility tests on females who weaned a litter during the study period, and on yearlings for whom play data were available from the previous year. Among females who weaned a litter during the study period, docility decreased significantly between gestation and emergence of young from the natal burrow. However, docility during gestation and lactation were reliable predictors of docility at litter emergence among reproductive females, suggesting that although docility may vary with reproductive state, individual squirrels may have their own distinct tendency toward docility. Rates of juvenile social play were a significant predictor of docility among yearling squirrels, raising the possibility that possible effects of social on the development of docility may be long term. We note that although we found a correlation between docility and play, we did not establish a causal relationship between them in this study.

Introduction

Play behavior is an important component of development in mammals, with young of nearly all mammalian species engaging in play (Bekoff and Byers 1998; Burghardt 2005). Play can be social, involving behavioral exchanges with conspecifics, or non-social, involving locomotion or interaction with objects in the environment (Burghardt, 2011). Specific play behaviors vary among species; however, Burghardt (2005) identified five unifying elements that define play across species. Play behaviors are 1) voluntary, 2) expressed repeatedly, 3) occur in healthy, unstressed individuals, 4) are not completely functional in the context in which they occur, and 5) when they resemble a functional behavior they are a modified version of it. Play behavior in early life can promote development of social competence, cognition, motor development, and adaptive regulation of emotions (Bekoff, 1972, 1988; da Silva et al., 1996; Byrd & Briner, 1999; van den Berg et al., 1999; Baarandse et al., 2013). Moreover, early play behavior has long-term influences on development of the brain (Pellis et al., 2010, 2014). The importance of play in mammalian development is suggested by its association with increased short- and long-term survival in some species (Fagen & Fagen, 2004, 2009; Cameron et al., 2008). In this work we studied a population of Belding's ground squirrels (*Urocitellus beldingi*) to evaluate the hypothesis that play behavior influences the development of temperament in young animals, using docility as a measure of temperament.

Play behavior can be both beneficial and costly for individuals. The adaptive benefits of engaging in play behavior vary among species and between sexes within a species (Olioff, & Stewart, 1978; Meder, 1990; Pederson et al., 1990; Pellis et al., 1996, 2014; Bekoff, & Byers, 1998; Nunes et al., 1999; Mastriperri, & Ross, 2004; Burghardt, 2005; Paukner, & Suomi, 2008; Auger, & Olesen, 2009). Adaptive functions of play include both short-term benefits during the juvenile period and long-term benefits, that extend into later life (Held, & Spinka, 2011; Blumstein et al., 2013; Nunes, 2014; Ahloy Dallaire, & Mason, 2017). Increased energetic costs are often associated with play behavior, as well as increased risk of predation when individuals at play become distracted or make themselves more noticeable to predators (Whishaw et al., 2001; Pellis et al., 2014). Extensive parental care in mammals can minimize these costs of having to adapt to the environment, allowing benefits of play to exceed potential costs, which may contribute to the prevalence of play among mammalian species (Burghardt, 2005; Pellis et al., 2014).

Individuals commonly exhibit behaviors that are consistent and repeatable over time and across situations. This tendency toward specific behavioral characteristics among individuals is commonly referred to as temperament or personality (Sih et. al, 2004; Reale et. al, 2007). Components of

temperament can include inclinations toward boldness in response to risks or threats, exploration of unfamiliar elements in the environment, or docile or active responses in specific situations (Cooper, 2009; Conrad et al., 2011; Herde and Eccard, 2013; Petelle et al., 2013; Vetter et al., 2016). Elements of temperament can be stable across an individual's lifespan, or can exhibit varying degrees of plasticity. For example, Petelle et al. (2013) observed in yellow-bellied marmots (*Marmota flaviventrus*) that tendencies toward boldness were consistent among individuals only when they were yearlings, whereas tendencies toward docility were consistent among individuals of all age classes. Further, they found that juvenile docility was a reliable predictor of docility later in life.

Špinka et al. (2001) proposed that play behavior might help to prepare young animals to successfully navigate unfamiliar, stressful situations. They suggested that play might improve motor coordination and shape the development of temperament so that young animals express greater motor control and emotional composure in novel situations. For example, diverse physical and social challenges during play might promote development of behavioral tendencies that are adaptive when encountering unexpected stimuli or events across diverse situations. Various studies with rats (*Rattus norvegicus*) have provided support for the idea that play helps prepares young animals for the unexpected (Pellis et al., 2014). Prior work with *U. beldingi* has also supported this idea. Juvenile squirrels who engaged in social play at higher rates and had longer play bout durations were able to escape more quickly from a novel testing arena, and also expressed greater tendencies toward boldness and exploration in a novel environment; suggesting a possible link between social play and the development of temperament in juvenile squirrels (Marks et al., 2017).

Environmental factors such as the prevalence of predators, abundance of resources, and local conspecific density might also influence temperament. Different temperaments can be favored in different environments. For example, in stable environments proactive individuals who respond quickly to environmental stimuli may have an advantage. By contrast, in unstable or unpredictable environments reactive individuals who gather information before acting may be favored by natural selection (Sih et al., 2004). Maternal influences on the development of temperament have been suggested to prepare offspring to be successful under prevailing environmental conditions (Storm & Lima, 2010; Kapheim et al. 2011; Dantzer et al. 2013). Environmental stresses experienced by mothers can directly affect the way that they raise their young, which in turn can affect the growth, metabolism, behavior, and immune and endocrine function of offspring (Weinstock, 2001; Hayward, & Wingfield, 2004; Mousseau, & Fox, 1998). Further, increased environmental stresses increase glucocorticoid levels in mothers, which then can be transferred to offspring during gestation or through milk transfer during

lactation. The transfer of glucocorticoids from mother to offspring can influence development of temperament in offspring (Petelle et al., 2017; Hinde et al., 2015; Weinstock, 2001). For example, in yellow-bellied marmots, older mothers with higher glucocorticoid levels tend to have offspring that are less docile (Petelle et al., 2017)

In this work, we evaluated the hypothesis that social play in juvenile *U. beldingi* influences the development of temperament. We also evaluated whether environmental factors such as population density shaped temperament. We used docility, the absence of action in a specific situation, as a measure of temperament. We observed the play behavior of juvenile *U. beldingi* and monitored local population density. Play behavior in juvenile *U. beldingi* occurs during a well-defined developmental period. Young *U. beldingi* remain underground in natal burrows during lactation, and first appear above ground when they are about four weeks old near the time of weaning. Juveniles engage in play behavior primarily during the two-week interval after they first emerge from the natal burrow (Nunes et al., 1999).

We conducted docility tests for juvenile *U. beldingi* at the beginning and toward the end of the play interval. Tests consisted of holding juveniles for 30 seconds and recording their responses. We predicted that if social play influences the development of docility, then social play should be correlated with changes in docility across the play period. We predicted that if population density influences the development of docility via maternal effects, then population density should be correlated with docility at juveniles' first emergence from the natal burrow. We further predicted that if population density influences the development of docility via direct effects on juveniles, then population density should be correlated with changes in docility during juveniles first two weeks above ground when they are first exposed to conspecifics in their natal areas.

Methods

From May through June 2016 and from June through August 2017 we studied a population of *U. beldingi* in a 25 hectare meadow at Tioga Pass (37° 55' N, 119° 15' W) in Mono County, California, United States. This species is diurnal and inhabits alpine and subalpine meadows in the western United States. Squirrels hibernate 8-9 months each year, with a 3-4 month active season in spring and summer (Jenkins, & Eshelman, 1984). Mating begins shortly after emergence from hibernation, and females bear at most one litter per year (Morton, & Gallup, 1975). Males do not begin breeding until two years old, whereas females may begin reproducing as yearlings (Jenkins, & Eshelman, 1984). Gestation lasts 24-25 days. Young remain underground in natal burrows during lactation and first emerge above ground at 25-28 days of age, near the time of weaning (Holekamp et al., 1984; Nunes et al., 1999). Reproductive

females defend maternal territories from which they aggressively evict intruders (Nunes et al., 2000). Play behavior occurs primarily during juveniles' first two weeks above ground, with > 97% of play interactions occurring between littermates (Nunes et al., 1999).

Squirrels were captured using Tomahawk live-traps (Tomahawk Live-Trap Company, Hazelhurst, Wisconsin, USA) baited with peanut butter. During trapping sessions we checked traps for captured squirrels every 30 minutes. Squirrels were fitted with numbered metal ear tags (National Band and Tag Company, Newport, Kentucky, USA) at their first capture for long-term identification. Ear tags of juveniles were painted different colors with nail polish prior to application to aid in identification of individuals during observations (Nunes et al., 2015). We also dyed the fur of squirrels with unique symbols using black hair dye (Clairol, Stamford, Connecticut, USA) to facilitate visual identification of individuals. We observed the territories of reproductive females daily to determine the dates that their litters first emerged from the natal burrow. Young were captured within two days of their first emergence during which time we were able to unambiguously assign offspring to mothers (Holekamp et al., 1984). Juveniles were weighed with spring balance scales (Avinet, Dryden, New York, USA) at their first capture and again 12-14 days after their first appearance above ground. Methods used in the study followed guidelines for wild mammals published by the American Society of Mammalogists (Sikes et al., 2016).

Behavioral Observations

In the summer of 2017, we observed the behavior of 90 juvenile *U. beldingi* from 19 litters. Juveniles were observed for an average of 484.7 ± 19.0 (SE) min per individual over an average of 6.1 ± 0.3 (SE) different days during their first 12 days above ground. Behavioral observations were conducted between 0700 and 1600 hours from elevated posts such as boulders and hillsides. During observations, all occurrences of social play were recorded. Rates of social play were calculated for individuals as the number of social play interactions per hour of observation. Specific play behaviors were defined (Table 1) following descriptions by Marks et al. (2017). The burrow entrances from which juveniles were first seen to emerge were marked with flags, and the maximum distances juveniles traveled from the burrow entrance were noted during observation sessions, and measured at the end of the session. During the summer of 2016 we observed the play behavior of 23 juvenile squirrels who were included in the study as yearlings in 2017, using methods described above. These squirrels were observed as juveniles for an average of 396 ± 16.2 (SE) min per individual over an average of 5.9 ± 0.2 (SE) different days during their first 12 days above ground.

Table 1.—Social play behavior of juvenile *U. beldingi*.

Behavior	Description
Wrestling	The juvenile faces another juvenile, typically in a ventrum-to-ventrum hold, and pecks at the other juvenile without inflicting bite wounds.
Tackling	The juvenile jumps or pounces on another juvenile, usually from a running start.
Boxing	The juvenile bats with the forepaws at another juvenile.
Chasing	The juvenile follows and pursues another juvenile for > 1 meter while both are running.
Mounting and play copulation	The juvenile climbs on the back of another juvenile and places its forepaws around the other juvenile, grasping in its mouth the other juvenile's neck, cheek, or back, and aligning its pelvis with other juvenile's pelvis; the juveniles typically both lie on their sides on the ground; intromission does not occur.

Behavioral Tests

Docility tests consisted of having a handler remove a squirrel from its trap and observing the squirrel's responses during the first 30 seconds of being handled. Squirrels were allowed to equilibrate in the trap for at least two minutes in a quiet area before the test began, after which time they were removed by the handler and held with handler's hand around the squirrel's chest and abdomen, with the squirrel's forelimbs free from the handler's grip. Squirrel responses during tests were recorded on video, and recordings were later viewed by observers to determine docility scores. Scores were calculated as the number of seconds during the 30 second test that squirrels were docile. Docility was defined as remaining motionless or the display slight movements such as turning the head or repositioning the paws. Squirrels were not considered be docile if they wriggled their bodies or otherwise struggled, used their forelimbs to push down on the handler's glove to try to lift their body free from the handler's grip, or bit the handler's glove. Recordings were scored by two observers, and the observers' scores were averaged. Docility tests were conducted before any other handling procedures such as ear-tagging, dye-marking, or weighing were performed to prevent the possibility of these procedures from influencing responses on tests.

Docility tests were conducted for juveniles at their first capture when they first emerged from the natal burrow. Juveniles were re-tested 12-14 days after their first appearance above ground. We regularly trapped adults and yearlings in the study area, and conducted docility tests at their first

capture. Reproductive females were re-tested after their young emerged from the natal burrow, within two days after the first appearance of young above ground.

Estimation of Local Population Density

We estimated the local population density experienced by reproductive females prior to the first emergence of their young from the natal burrow. We divided the study site into 18 sub-regions with natural borders such as creeks or stands of bushes or trees. Within each sub-region we recorded the number of individual squirrels observed in the region over a one-hour period on at least five different days. Individual squirrels could be distinguished from each other by their dye-marks (see above). Observations were made between 0800 and 1600 hours, with observations within a sub-region being made at different, non-overlapping times on different days. Areas of sub-regions were calculated using maps obtained from the United States Geological Survey. Densities were calculated for each observation day within each sub-region as the number of different squirrels observed per hectare, and densities were averaged across observation days.

In addition, we estimated the local population density experienced by mothers and juveniles after the juveniles' first emergence from the natal burrow. During behavioral observations of juveniles we recorded the number of different adults and yearlings seen within 25 meters of the juveniles' natal burrow. Juveniles and their mothers were rarely seen to venture more than 25 meters from the natal burrow during observation periods. Densities were calculated for each observation period as the number of different adults and yearlings observed per hectare, and densities were averaged across observation periods for each litter.

Statistical Analysis

Continuous variables evaluated in the study included scores on docility tests, changes in docility scores, body mass, local population density, rates of social play, and maximum distances juveniles traveled from the natal burrow during observation periods. Among these, rates of social play and distances from the natal burrow did not follow the normal distribution (Lilliefors test, $P < 0.05$). Values of these variables were log transformed to values that were normally distributed (transformed value = \ln [original value]). Correlations between variables were evaluated with Pearson's r . Data were compared between juvenile males and females using independent t -tests. Scores on docility tests for reproductive females prior to and after the first emergence of young from the natal burrow were compared using paired t -tests. Variances were pooled when assumptions of homoscedasticity were not met in t -tests. Multiple linear regression with forward stepping was used to evaluate whether body mass, local

population density, or mother's age were reliable predictors of juveniles' scores on docility tests at the time of emergence from the natal burrow. Multiple linear regression with forward stepping was also used to evaluate whether body mass, local population density, mother's age, rates of social play, or distances traveled from the natal burrow were reliable predictors of change in docility scores across the juvenile play interval. Variables found to be reliable predictors of initial docility scores or changes in docility scores were further analyzed with a mixed linear model, with the variables as fixed effects and litter as a random effect to account for any similarities among juveniles from the same litter. Assumptions of homoscedasticity were met in analyses using mixed linear models. Tukey's tests were used for pairwise comparisons after analyses with a mixed linear model. Linear regression was used to evaluate whether docility scores of reproductive females prior to emergence of young from the natal burrow were reliable predictors of docility scores after litter emergence. Linear regression was also used to evaluate whether rates of social play among juvenile squirrels were reliable predictors of their scores on docility tests as yearlings. Statistical tests were performed with Systat 13.1 (Systat Software, Inc., Chicago, Illinois, USA). Relationships indicated by statistical tests were considered significant when $P \leq 0.05$. For ease of interpretation, non-transformed values of variables are presented in graphs. Mean values are presented ± 1 SE.

Results

Initial Docility of Juveniles

The amount of time squirrels were docile during behavioral tests at first emergence from the natal burrow did not differ between juvenile males and females. We used multiple linear regression to determine whether any of the following variables were significant predictors of juveniles' scores on docility tests: body mass at first emergence, age of mothers, and local population density. Trapping data were available from prior years, allowing us to determine the age of mothers. None of the variables in this analysis were significantly correlated with any of the others ($-0.08 < r < 0.05$) and values did not differ between the sexes, so data were combined for juvenile males and females. Multiple linear regression indicated a significant relationship ($F_{1,149} = 8.13$, $P = 0.005$) between docility scores at emergence from the natal burrow and body mass ($t = 2.85$, $P = 0.005$).

We further evaluated the relationship between docility and body mass by dividing the range of body masses observed among the 151 juveniles in this analysis (34-110 grams) into equal thirds to assess juveniles with the lowest, intermediate, and greatest mass. A mixed linear model with body mass group as a fixed effect and litter as a random effect indicated that docility varied significantly with body mass (Fig. 1, $F_{2,117} = 4.19$, $P = 0.018$), with docility decreasing as body mass increased (Fig. 1)

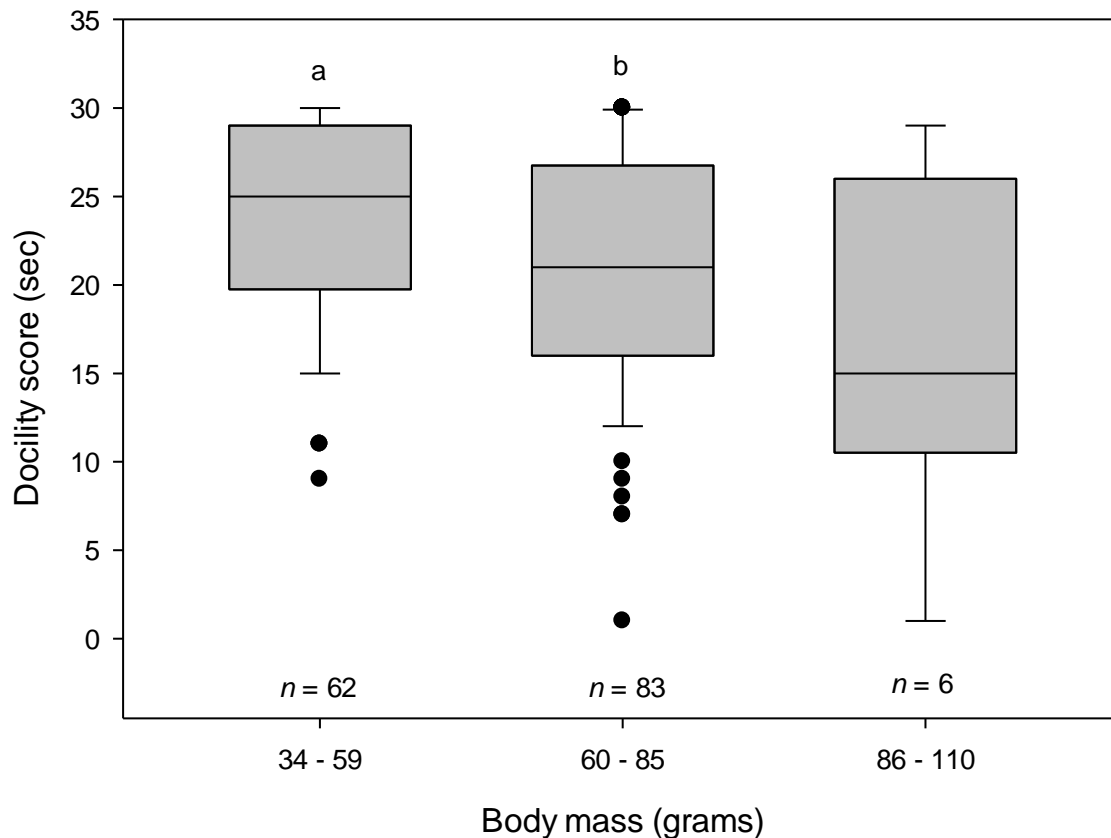


Figure 1. Box and whisker plot showing variation in scores on docility tests as a function of body mass in juvenile *Uroditellus beldingi*. Body mass was divided into lowest, middle, and highest thirds based on the overall range observed among juveniles in the study. Boxes delimit the 0.25 and 0.75 quantiles, horizontal lines indicated medians, whiskers extend to maximum and minimum values, and outliers are plotted as individual points. Letters indicate statistical differences at $P \leq 0.05$. Sample sizes are indicated on the graph.

Changes in Juvenile Docility

The amount of time juveniles were docile during behavioral tests decreased significantly between initial tests at first emergence from the natal burrow and re-tests near the end of the play period (22.3 ± 0.7 vs. 15.4 ± 0.7 sec, respectively, $t_{89} = 6.93$, $P < 0.001$). Changes in docility scores over the play interval, expressed as a proportion of the initial score, did not differ between juvenile males and females. We note that scores on initial tests were significantly correlated with scores on re-tests ($r = 0.34$, $P = 0.001$), but not with changes in docility over the play interval.

We used stepwise multiple linear regression to evaluate which of the following variables was a reliable predictor of change in docility across the play interval: average body mass during the play interval, age of mothers, local population density, rates of social play, and maximum distances from the natal burrow juveniles traveled during observation periods. None of the variables were significantly correlated with any others ($-0.20 < r < 0.24$). Moreover, none of these variables differed between the sexes, so data were combined for juvenile males and females. This analysis indicated an overall significant relationship ($F_{2,87} = 8.46$, $P < 0.001$) between changes in docility and both rates of social play ($t = 2.78$, $P = 0.007$) and the maximum distance from the natal burrow that juveniles were observed ($t = 2.28$, $P = 0.025$).

We further evaluated the relationship between changes in docility and these variables. We divided the range of social play rates observed for the 90 juveniles in this part of the study (0.4–7.3 interactions/hour) into equal thirds to assess juveniles who played at the lowest, intermediate, and highest rates. We similarly divided the range of maximum distances juveniles were observed from the natal burrow (4.8–34.5 meters) into equal thirds. A mixed linear model with social play groupings and distance groupings as a fixed effects and litter as a random effect indicated that changes in docility varied significantly with social play (Fig. 2A, $F_{2,67} = 6.74$, $P = 0.002$) as well as the distances juveniles traveled from the natal burrow during the play interval (Fig. 2A, $F_{2,67} = 4.08$, $P = 0.021$). In particular, decreases in docility across the play interval increased significantly as juveniles engaged in social play at higher rates and traveled greater distances from the natal burrow (Fig. 2).

Docility of Yearlings and Reproductive Females

We conducted docility tests for a total of 30 reproductive females both prior to and after the first emergence of their litters from the natal burrow. Among these females, 12 were first tested during gestation, and 18 were first tested during lactation. Docility scores increased significantly between the initial test and re-test for females first tested during gestation (Fig. 3, $t_{11} = 3.10$, $P = 0.010$), but not for those first tested during lactation. Linear regression indicated that scores on the initial docility tests were reliable predictors of scores on the re-tests for females first tested during gestation (Fig. 4A, $F_{1,10} = 11.99$, $P = 0.006$) as well as those first tested during lactation (Fig. 4B, $F_{1,16} = 15.49$, $P = 0.001$).

Juvenile play data from the previous year were available for 23 yearlings included in the study. Linear regression indicated that among these squirrels, rates of social play were reliable predictors of scores on docility tests (Fig. 5, $F_{1,21} = 5.13$, $P = 0.034$). In particular, squirrels who engaged in social play at higher rates as juveniles tended to be less docile as yearlings (Fig. 5).

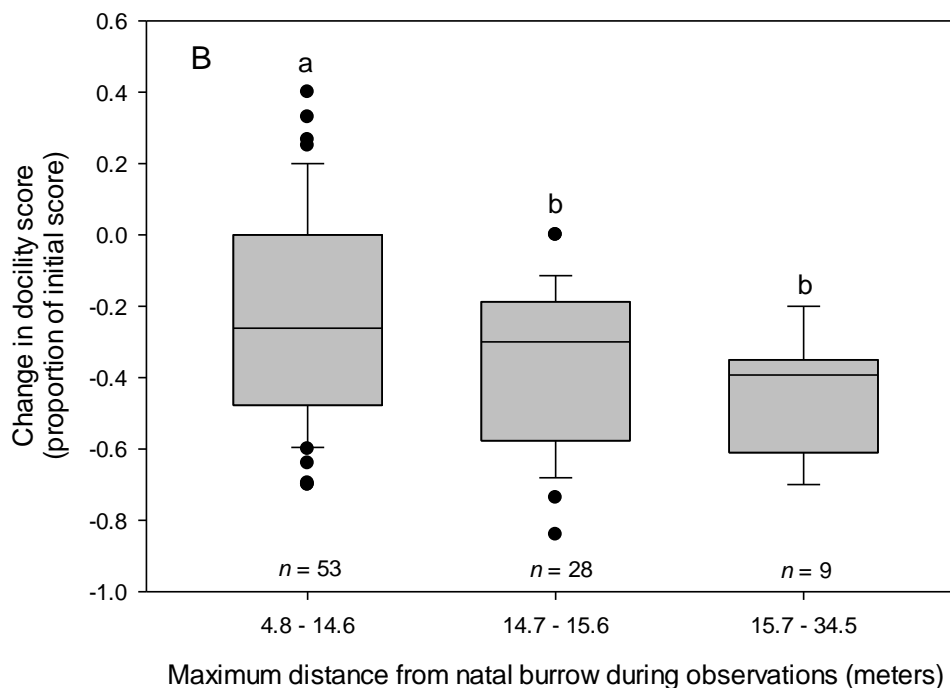
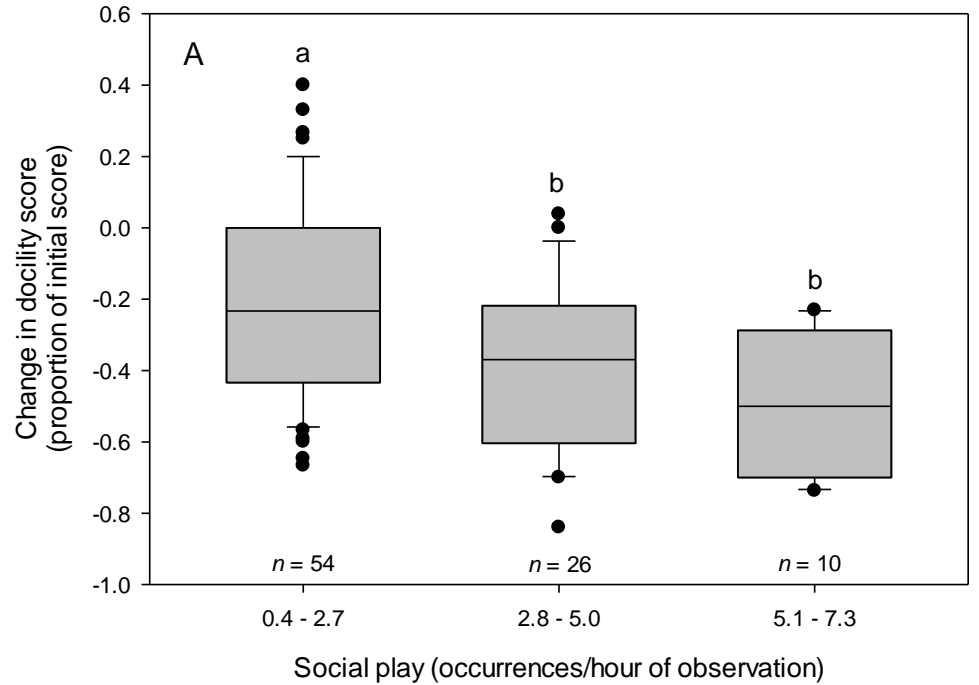


Figure 2. Box and whisker plots showing changes in docility scores across the play interval for juvenile *Uroditellus beldingi* as a function of A) rates of social play and B) maximum distances that juveniles travelled from their natal burrow during observations. Rates of play and distances were divided into lowest, middle, and highest thirds based on the overall ranges observed among juveniles in the study. Boxes delimit the 0.25 and 0.75 quantiles, horizontal lines indicated medians, whiskers extend to maximum and minimum values, and outliers are plotted as individual points. Letter indicate statistical differences at $P \leq 0.05$. Sample sizes are indicated on the graph.

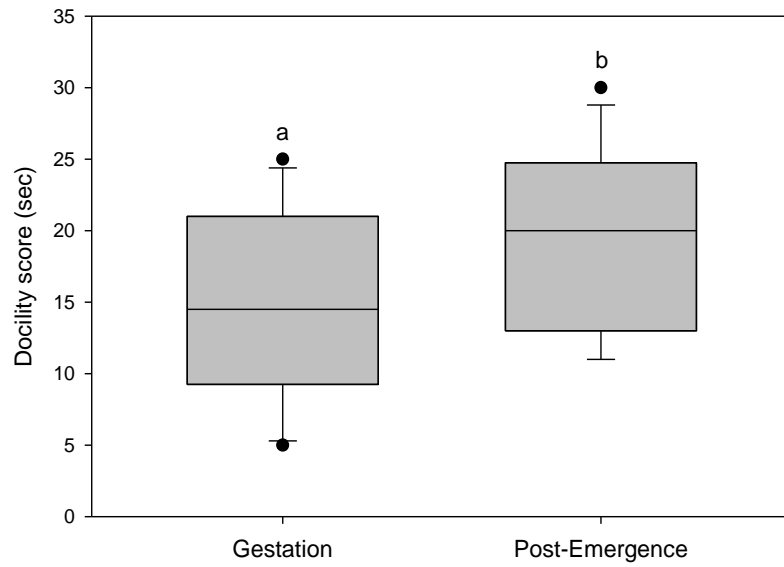


Figure 3. Box and whisker plots showing docility scores of 12 female *Urocitellus beldingi* during the reproductive cycle. Boxes delimit the 0.25 and 0.75 quantiles, horizontal lines indicated medians, whiskers extend to maximum and minimum values, and outliers are plotted as individual points. Letters indicate a significant difference between stages of the reproductive cycle at $P \leq 0.05$.

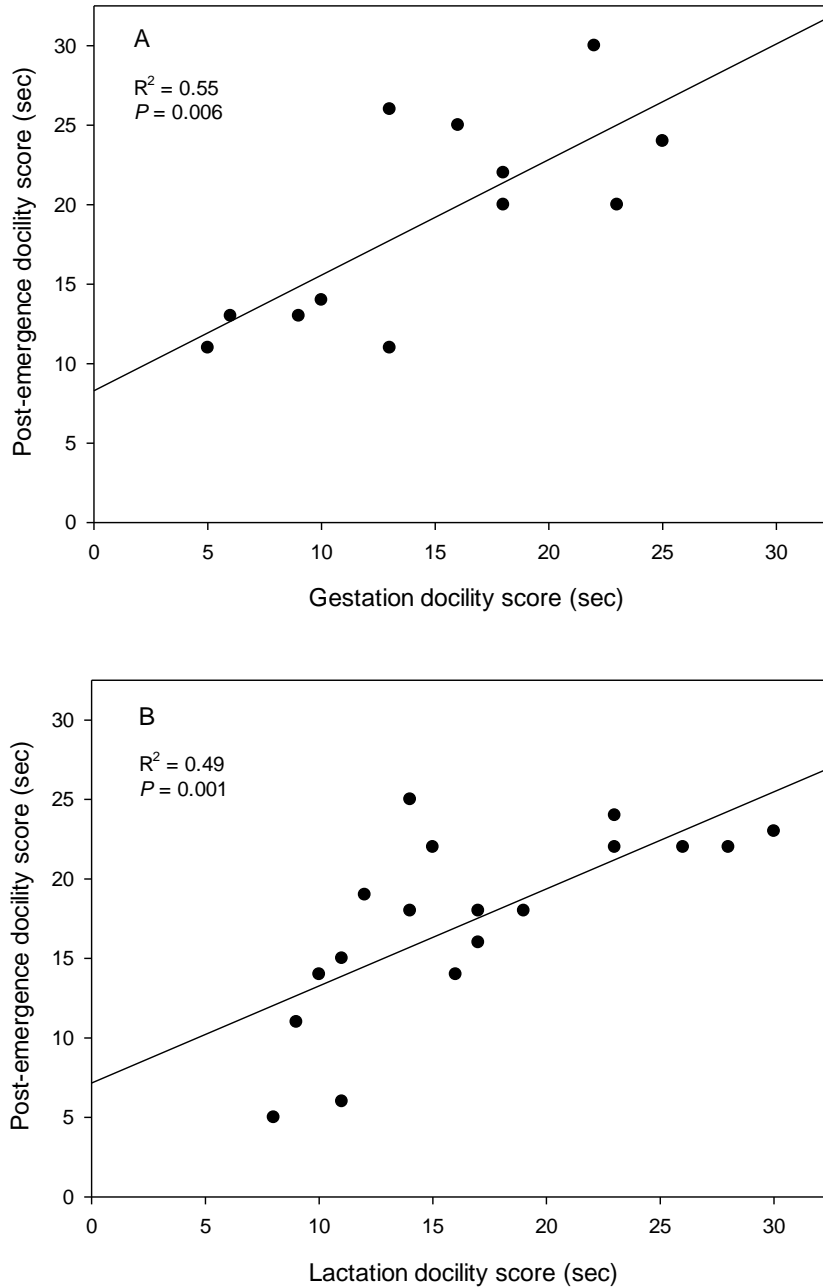


Figure 4. Regression plot showing the association between docility scores of reproductive female *Urocitellus beldingi* at the emergence of litters from the natal burrow and scored during A) gestation and B) lactation. Twelve females were sampled during gestation and at litter emergence, and 18 females were sampled during lactation and at litter emergence.

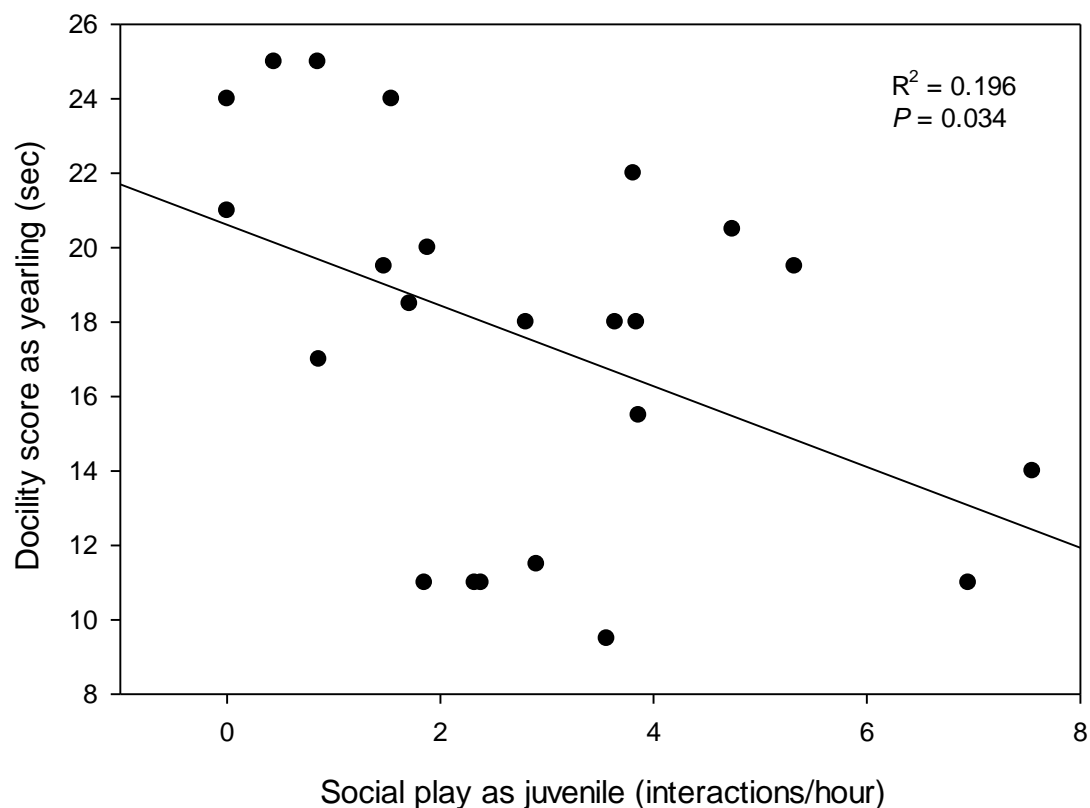


Figure 5. Regression plot showing the association between rates of social play as juveniles and scores on docility tests as yearlings for 23 *Urocitellus beldingi*.

Discussion

Both social play and distances traveled from the natal burrow were negatively correlated with docility among juvenile *U. beldingi* in our study during the two weeks after their first emergence from the natal burrow. Little is known about factors that influence the development of temperament; however, body mass has been shown to influence the developmental trajectory of tendencies toward boldness in European rabbits (*Oryctolagus cuniculus*; Rodel, & von Hulst, 2009; Rödel, & Monclús, 2011; Rodel et al., 2017). Our results suggest that in addition to body mass, early life experiences might also play an important role in the development of temperament in young animals.

Although, body mass was not a significant predictor of change in docility over the play interval among juvenile *U. beldingi* in our study, it was a reliable predictor of docility among juveniles at their first emergence from the natal burrow. One possibility is that body mass might have been an important determinant in the development of docility while young squirrels were still exclusively in the natal burrow, and other factors may have had a more prominent influence after juveniles emerged from the

natal burrow and were exposed to a greater array of interactions with conspecifics and the environment. Alternatively, body mass at emergence from the natal burrow might have reflected the expression of temperament during lactation. That is, less docile juveniles might have been more likely to seek nursing opportunities or been more successful at competing for milk, and thus might have been larger near the time of weaning (Rodel et al., 2017).

Surprisingly, population density was not associated with initial docility or changes in docility among juvenile *U. beldingi* in our study. Temperament can have important fitness consequences for individuals (Dingemanse et al., 2004; Both et al., 2005; Boon et al., 2007, 2008; Colchester, & Harrison, 2016), and different temperaments can be adaptive under different environmental conditions (Rasmussen, & Belk 2016; Vetter et al., 2016). Thus, natural selection should favor development of temperaments that are most suited for the prevailing environmental conditions. It is possible that other elements of temperament such as boldness are shaped more by environmental conditions during development than is docility. In marmots, docility is more consistent across the lifespan, whereas boldness is more malleable over time (Petelle et al., 2013). Adjusting boldness to environmental conditions might be more crucial than adjusting docility. Alternatively, population density in our study may have been too uniform over the study area to detect any possible density effects. Our study was conducted over a single active season in a continuous 25 hectare area, and differences in conditions throughout the study area may have been small and subtle.

We also failed to observe an association between the age of mothers and initial docility or changes in docility among juvenile *U. beldingi* in the study. Maternal age is correlated with various factors such as maternal behavior and litter size in *U. beldingi* (Sherman, & Morton 1984; Nunes et al., 2000). Maternal effects have an effect on the temperament of young in yellow-bellied marmots, and have been proposed as a mechanism for adjusting the temperament of offspring to prevailing environmental conditions (Petelle et al., 2017). We cannot rule out the possibility that maternal effects influenced the development of docility among juveniles in our study. As mentioned above, environmental conditions may have been similar enough throughout the study area so that any maternal effects on the development of docility were similar among juveniles in the study.

Social play of juvenile *U. beldingi* in this study was significantly correlated with their docility as yearlings. This correlation suggests that, as is the case with yellow-bellied marmots, docility in *U. beldingi* may be stable and repeatable across years (Petelle et al., 2013), and also suggests that effects of social play on the development of docility may be long-term. Play behavior has been shown to have a variety of adaptive benefits during the juvenile period (Bekoff, & Byers, 1998; Burghardt, 2005; Pellis et

al., 2014). However, less is known about the longer-term adaptive benefits of play behavior. Studies of meerkats (*Suricata suricatta*; Sharpe, & Cherry, 2003; Sharpe, 2005a, 2005b, 2005c) and chimpanzees (*Pan troglodytes schwinfurthi*; Heintz et al., 2017) did not reveal any associations between juvenile play and behavior later in life. However, studies of other species have indicated that play can have effects on behavior during adulthood as well as survival and reproductive success (Cameron et al., 2008; Fagen, & Fagen, 2009; Blumstein et al., 2013; Nunes, 2014; Ahloy Dallaire, & Mason, 2017). These discrepancies may reflect different trajectories in the evolution of play behavior among different species (Pellis et al. 2014).

Possible enduring effects of social play on behavior and temperament may be mediated by effects on the developing brain. In rats, social play experiences during early development are necessary for the establishment of competent social skills and the normal expression of social behavior in adulthood (Pellis et al., 2014). Juvenile play in rats has also been shown to modify development of areas in the frontal cortex associated with motor and social behavior as well as behavioral flexibility (Bell et al., 2009, 2010; Pellis et al., 2010; Himmler et al., 2013; Burlison et al., 2016).

We observed a significant increase in the docility of maternal *U. beldingi* between gestation and the emergence of their young from the natal burrow. This change in docility may reflect changes in aggressive behavior over the reproductive cycle of females. Maternal *U. beldingi* exhibit peak aggressive behavior during the gestational period when they are competing for space in which to establish a maternal territory; rates of aggression decrease significantly after gestation (Nunes et al., 1997, 2000). Thus, changes in tendencies toward docility may be reflected in aggressive behavior. Despite changes in docility across the reproductive cycle in female *U. beldingi*, docility during one phase of the reproductive cycle reliably predicted docility during another phase. This result suggests that the expression of docility can be influenced by factors such as reproductive state, but tendencies toward greater or lesser docility remain consistent among individual females.

Prior work with *U. beldingi* suggested that social play behavior may help prepare young animals to better deal with unfamiliar situations (Marks et al., 2017). Greater social play was correlated with increased exploration in an unfamiliar environment as well as quicker escape times from a novel testing arena. Although we did not specifically evaluate the relationship between temperament and preparation for the unexpected, our results are consistent with the idea that effects of social play on temperament might contribute to helping young animals deal with novel situations. Social play was associated with a shift from passive to active responses, which might benefit an individual when confronted with a new experience or challenge.

Results of this study indicate correlations between early life experiences and the development of temperament in juvenile *U. beldingi*. This work provides a foundation for possible future studies examining whether other elements of temperament such as boldness are associated with juvenile social play or other early-life experiences, as well as experimental studies evaluating causal links between social play and the development of temperament.

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