

Functional relationships between early play behavior and adult dominance roles in yellow-bellied marmots (*Marmota flaviventris*)

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Abstract

Play has been defined as apparently functionless behavior, yet since play is costly, it must have some function (or functions) to outweigh its costs. We provide the strongest evidence for a long-standing, but poorly supported hypothesis: that early play is practice for later dominance relationships. We calculated the relative dominance rank by observing the directional outcome of playful interactions in both pup and yearling yellow-bellied marmots (*Marmota flaviventris*) using the Clutton-Brock index. We found that these play rank relationships were highly correlated with later dominance ranks calculated from agonistic interactions, which leads us to suggest that while play may have multiple functions, one of them can be to establish later dominance relationships in a minimally costly way.

Introduction

Play is defined as “apparently functionless behavior” (Bekoff and Byers 1981) but it must have benefits to overcome any costs associated with it (Harcourt 1991). Despite over a century of study, the functional significance of play behavior is not readily known and there are both many non-mutually-exclusive hypotheses (Burghardt 2005), and considerable variation in play between species (Fagen 1981). The widely suggested “practice hypothesis” asserts that play provides younger individuals the opportunity to practice and refine skills needed later in adulthood (Groos 1898). Support for this hypothesis is provided by examples of play increasing motor functions (and Nunes et al. 2004). However, few attempts have been made to directly quantify the effects of early play behavior and its subsequent effect on adulthood dominance.

There have been 6 studies that have tried to directly evaluate the practice hypothesis by viewing play as practice for later dominance. Support is equivocal. Though limited with a

relative small sample size, baboons and wolves have been shown to exhibit no correlation between aggressive behavior and social play (Mancini & Palgai 2009; Cordoni 2009). However, even with longer study periods and more individuals, support is mixed between studies conducted on meerkats and hyenas (Sharpe 2005; Tanner et al. 2007) Lastly, the consequence of play on subsequent dominance in dogs appears inconclusive as well (Trisko 2011; Pal 2010).

We studied the relationship between early play behavior and adult dominance in a wild population of yellow-bellied marmots (*Marmota flaviventris*). Yellow-bellied marmots are particularly well suited for a study of the relationship between early play and later dominance for the following reasons. First, they are facultatively social rodents that live in a variety of group sizes; some with overlapping generations (Blumstein & Armitage 1999). Second, they play during the first two years of their life (Jamieson & Armitage 1987; Nowicki & Armitage 1979), as both pups (<1 year old) and yearlings (1 year old), which presents a unique opportunity to test two complementary hypotheses (see below). Third, our population has been studied since 1962, which enables us to draw upon a wealth of information about their long-term social interactions as well as an extensive observational dataset (Armitage 2010). Fourth, marmots are easily trapped and marked in the field, which allows for non-dispersing individuals to be repeatedly identified in the wild throughout their entire lives.

If the practice hypothesis of play behavior explains a function of marmot play, we predict that dominance ranks calculated from asymmetric play behavior early in life should influence an individual's subsequent dominance rank calculated from agonistic behavior in adulthood. We tested this two ways. First, we asked whether dominance ranks calculated from affiliative play behavior as pups predicts relative dominance ranks based on agonistic outcomes as yearlings.

Second, we asked whether dominance ranks calculated from all observed play (as both pups and yearlings), predicted relative dominance rank later in life.

Methods

Subjects and Data Collection

From 2002 to 2011, we monitored wild yellow-bellied marmots from different colonies located around the Rocky Mountain Biological Laboratory (RMBL) in Gunnison County, Colorado (38°57'29"N, 106°59'06"W, elevation ~2890 m). All subjects were individually recognized and part of a long-term study initiated in 1962 (Armitage 2010). During the active season, we regularly trapped marmots in Tomahawk live traps set around burrow entrances on a bi-weekly schedule with minimal disturbance to the animals (Smith et al. 2012). Upon capture, we transferred each marmot into a canvas, handling bag where we weighed, sexed, and collected samples (feces, blood). Marmots were individually marked with uniquely numbered ear tags and Nyanzol cattle dye at first capture. Marmots were classified into three discrete life history stages, each separated by annual periods of hibernation: pups (<1 year old), yearlings (1 year old) and adults (sexually-mature animals, ≥ 2 years old).

From April to September, observers monitored each colony site during times of peak activity in the mornings (0700 h to 1000 h) and afternoons (1600 h to 1900 h) on most days using spotting scopes from a distance (20-150 m) without influencing the behavior of the subjects. At each observation session for a given colony site, we recorded all individuals that were present and the duration of that sampling period. We used all-occurrence sampling to record the initiator and recipient of each social exchange (Altmann 1974). Affiliative play behavior included all accounts of play biting, boxing, chasing, grabbing, slapping, pushing,

pouncing, mounting, and wrestling. Directionality of affiliative play was determined by who was displaced at the end of an interaction. Agonistic interactions were all accounts of aggression and displacements for which the initiator directed aggression towards or actively displaced its recipient. Either way quantified, we created pair-wise matrices of “wins and losses” that were subsequently used for dominance calculations. Matrices were created for each colony-year for a total of 110 matrices, of which 64 were play and 56 were agonistic.

Analyses

We calculated dominance from either affiliative or agonistic matrices using the Clutton-Brock index, a method that calculates dominance based on an individual’s relative number of wins or losses and is particularly tolerant of missing pair-wise interactions and weights wins highly (Clutton-Brock et al. 1979; Bayley et al. 2006; Bang et al. 2010). To account for variation in group size, we transformed actual ranks to relative ranks where the highest ranking individual within a colony-year was set to 1 and the lowest ranking individual was set to 0 (Huang et al. 2011).

With these dominance ranks, we asked whether an individual’s relative rank based on play outcomes as a pup predicted its relative rank based on agonistic outcomes as a yearling, and we also asked whether the rank calculated from all observed play (both as pups and yearlings) predicted its relative rank based on agonistic outcomes as an adult in subsequent years. We fitted linear mixed effects models using R (R 2.12.2, R Development Core Team, 2011) in which the random effects of “colony” and “year” were added to the model to control for variation in behaviors attributed to site and annual variation, respectively.

RESULTS

We recorded a total of 27,493 social interactions involving 803 marmots ($N = 429$ males and 374 females). Of these, 4,020 and 8,556 events were agonistic and playful, respectively. On average, each of individuals was observed in a total of 67 ± 4 social interactions across this study, including 17 ± 2 agonistic ($N = 250$ male and 212 females) and 28 ± 2 playful interactions ($N = 344$ males and 274 females). Assignments of clear winners and losses were possible for 4,910 interactions ($N = 2,817$ play and 2,093 agonistic outcomes) involving a total of 509 individuals ($N = 282$ males and 227 females). On average, each individual was involved in 19.3 ± 1.1 social interactions with clear outcomes ($N = 13.0 \pm 0.9$ play and 10.8 ± 0.8 agonistic outcomes). Ultimately, relative ranks for each colony-year therefore totaled 971 rank assignments based on play (2002 to 2010, $N = 222$ males and 179 females) and 803 rank assignments based on agonistic interactions (2003 to 2011, $N = 217$ males and 190 females). Data reported here were collected during 9,157 hours of observation at 7 main colony sites: 1) Bench, 2) Boulder, 4) Marmot meadow, 5) Picnic, 6) River and 7) Town. A total of 775 matched relative ranks based on play early in life and agonistic outcomes later in life involved 279 participants ($N = 152$ male and 127 females).

Overall, the relative agonistic dominance rank of an individual marmot ($N = 152$ males and 127 females) based on fight outcomes later in life was predicted by that individual's relative rank based on the outcomes of play interactions early in life (Relative rank based on play: Estimate $\pm$ S.E. = 0.136 ± 0.048 , $t = 2.819$, $P = 0.005$; Table 1A). This was the case after controlling for the effects of sex; males were generally socially dominant to females (Sex: 0.064 ± 0.029 , $t = 2.195$, $P = 0.028$). Relative dominance ranks based on agonistic interactions increased as the difference in years between ranks based on early play and later agonistic interactions passed (Years between measures: 0.037 ± 0.008 , $t = 4.976$, $P < 0.00001$). Moreover,

because adults were socially dominant to yearlings, agonistic ranks measured for yearlings were lower than those of adults (Yearling stage: -0.137 ± 0.028 , $t = -4.965$, $P < 0.00001$).

Finally, the individuals with high late season body mass as immature individuals at the time play was recorded were generally of higher social rank later in life than were those individuals of low body mass, although this finding was not statistically significant (Mass: 0.00002 ± 0.00001 , $t = 1.916$, $P = 0.056$). None of the two-way interaction terms improved the fit of the model (reducing its AIC value) and were therefore excluded from the final model (see Table 1A-C for details).

Given our findings that relative dominance measures change over the life course, we next investigated these patterns to understand the precise nature of these ontogenetic shifts and to assess the extent to which the effects of early ranks based on play outcomes persisted into adulthood. Specifically, two subsequent analyses focused on subsets of the data for which agonistic dominance was measured for: 1) yearlings ($N = 148$ males, 122 females) and 2) adults ($N = 36$ males, 72 females).

First, as for the overall data set, the model explaining agonistic ranks for yearlings revealed that the relative rank of pups based on the outcome of play positively predicted the relative dominance rank based on agonistic interactions of yearlings (Play rank: 0.180 ± 0.053 , $t = 3.406$, $P < 0.001$) after accounting yearling males generally being social dominant to yearling females in agonistic interactions (0.090 ± 0.031 , $t = 2.926$, $P = 0.004$, Fig. 1A and Table 1B). However, late season body mass for pups, however, failed to predict relative dominance ranks of yearlings (-0.000009 ± 0.00005 , $t = -0.186$, $P = 0.853$, Table 1B).

Interestingly, the effects of early ranks based on play attenuated across the life course such that they failed to the relative agonistic rank for adults, although this relationship remained

positive (Play rank of immature individuals: 0.074 ± 0.079 , $t = 0.936$, $P = 0.350$, Fig. 1B, Table C). Sex was no longer was a significant predictor of adult dominance rank (Sex: 0.021 ± 0.052 , $t = 0.395$, $P = 0.693$, Table 1C). Instead, the absolute age of individuals predicted agonistic dominance, with older adults being socially dominant to younger ones (Age: 0.039 ± 0.007 , $t = 5.271$, $P < 0.000001$). This effect of age as the main determinant of dominance rank in adults persisted after accounting for the effects of the life history stage at which play was recorded, with trends remaining for yearlings generally being socially subordinate to adults (-0.087 ± 0.072 , $t = -1.203$, $P = 0.230$) and heavier immature animals tending to be more socially dominant as adults than were lighter immature animals (0.00005 ± 0.00004 , $t = 1.240$, $P = 0.216$).

Table 1. Independent variables predicting the relative dominance rank of yellow-bellied marmots based on agonistic interactions.

A) Full data set: Early play of pups and yearlings predicts dominance in subsequent years

	Estimate $\pm$ S.E.	t-value	P-value
(Intercept)	0.336 $\pm$ 0.047	7.222	< 0.00001
# of years between play & agonistic measures of rank	0.037 $\pm$ 0.008	4.976	< 0.00001
Life history stage when dominance recorded (yearling)	-0.137 $\pm$ 0.028	-4.965	< 0.00001
Relative rank based on outcomes of play	0.136 $\pm$ 0.048	2.819	0.005
Sex (male)	0.064 $\pm$ 0.029	2.195	0.028
Body mass for season in which play recorded	0.00002 $\pm$ 0.00001	1.916	0.056

Data on early play of pups and yearlings (2002-2010) and later dominance (2003-2011) ranks based on 775 measures on 277 individuals ($N = 281$ and 494 measures, respectively, on 152 males and 127 females) at seven colony sites. The following interaction terms failed to improve the fit of our model: Sex*Play rank: 0.143 ± 0.097 , $t = 1.477$, $P = 0.140$; Sex*Life history stage: 0.078 ± 0.044 , $t = 1.794$, $P = 0.073$; Sex*Body mass: -0.00002 ± 0.00002 , $t = -0.969$, $P = 0.333$; Sex * # of Years: -0.028 ± 0.016 , $t = -1.713$, $P = 0.090$; Play rank*Life history stage: 0.111 ± 0.074 , $t = 1.503$, $P = 0.134$; Play rank*Sex: 0.143 ± 0.097 , $t = 1.477$, $P = 0.140$; Play rank*Mass: -0.00002 ± 0.00004 , $t = -0.403$, $P = 0.687$; Play rank* # of Years: -0.008 ± 0.025 , -0.318 , 0.751 ; Life history stage*Mass: -0.00003 ± 0.00005 , $t = -0.620$, $P = 0.535$. Including random effect of the individual improved the fit of the model (Likelihood ratio test: $\chi^2 = 52.7$, $df = 1$, $P < 0.00001$), explaining 32.8 % of the variation in the relative dominance rank of yearling or adult marmots; neither year, colony or valley improved the model (Likelihood ratio tests: $df = 1$ for each, $P = 1.000$).

B) Reduced data set: Play outcomes for pups predicts relative dominance rank of yearlings

	Estimate $\pm$ S.E.	t-value	P-value
(Intercept)	0.243 $\pm$ 0.069	3.540	0.0005
Relative rank based on outcomes of play	0.180 $\pm$ 0.053	3.406	0.0008
Sex (male)	0.090 $\pm$ 0.031	2.926	0.004
Body mass for season in which play recorded	-0.000009 $\pm$ 0.00005	-0.186	0.853

Data on pup play (2002-2010) and yearling dominance (2003-2011) ranks are based on 270 individual marmots ($N = 148$ males and 122 females) at seven colony sites. The following interaction terms failed to improve the fit of our model: Sex*Play rank: 0.082 ± 0.106 , $t = 0.773$, $P = 0.438$, Sex*Mass: -0.0002 ± 0.0001 , $t = -1.638$, $P = 0.103$, Play rank*Mass: 0.00005 ± 0.0001 , 0.348 , $P = 0.728$). Random effects of year and colony failed to improve the fit of the model (Likelihood ratio tests: $df = 1$ and $P = 1.000$ for both).

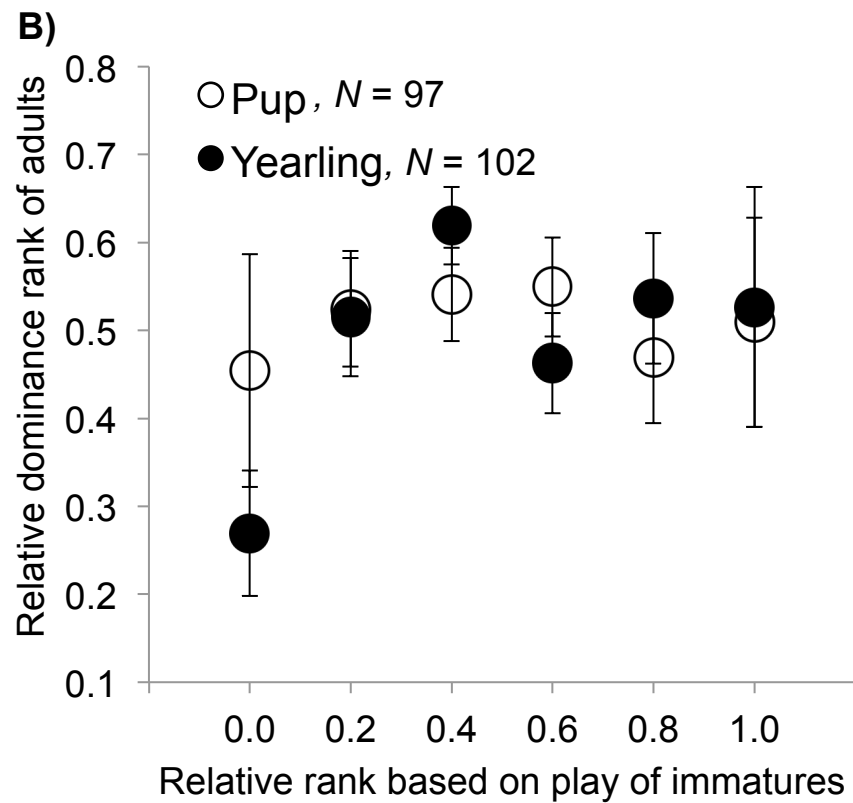
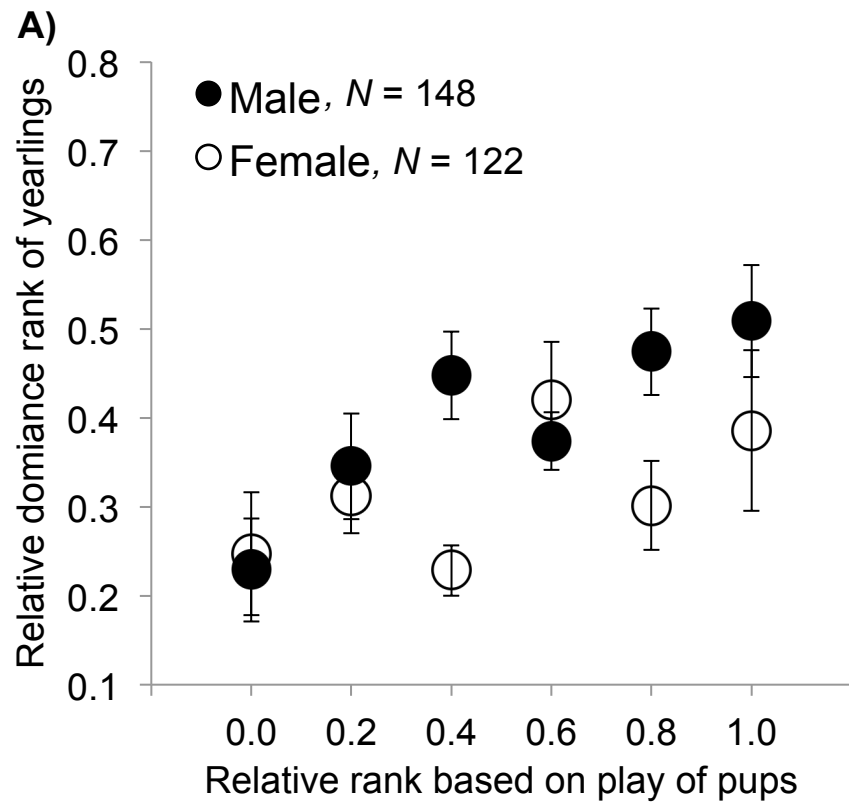
C) Reduced data set: Limited effects of early play on relative dominance of adults

	Estimate $\pm$ S.E.	t-value	P-value
(Intercept)	0.335 $\pm$ 0.072	4.665	< 0.000001
Age as an adult when dominance measured	0.039 $\pm$ 0.007	5.271	< 0.000001
Life history stage when play recorded (yearling)	-0.087 $\pm$ 0.072	-1.203	0.230
Relative rank based on outcomes of play	0.074 $\pm$ 0.079	0.936	0.350
Body mass for season in which play recorded	0.00005 $\pm$ 0.00004	1.240	0.216
Sex (male)	0.021 $\pm$ 0.052	0.395	0.693

Data on early play of pups and yearlings (2002-2010) and later dominance (2003-2011) ranks of adults based on 505 measures on 108 individuals ($N = 133$ and 372 measures, respectively, on 36 males and 72 females) at seven colony sites. Excluded interaction terms were: Sex*Life history: $-0.013 \pm 4.436e-02$, $t = -0.300$, $P = 0.764$; Sex*Age: -0.028 ± 0.021 , $t = -1.346$, $P = 0.179$; Sex*Mass: -0.000004 ± 0.00002 , $t = -0.177$, $P = 0.860$; Sex*Play rank: 0.158 ± 0.167 , $t = 0.946$, $P = 0.345$; Life history stage*Age: 0.003 ± 0.012 , $t = 0.253$, $P = 0.800$; Life history stage*Mass: 0.000008 ± 0.00006 , $t = 0.142$, $P = 0.887$; Life history stage*Play rank: 0.024 ± 0.073 , $t = 0.326$, $P = 0.745$; Age*Mass: 0.000002 ± 0.00007 , $t = 0.325$, $P = 0.745$; Age*Play rank: 0.034 ± 0.030 , $t = 1.134$, $P = 0.257$; Mass*Play rank: 0.00002 ± 0.00004 , $t = 0.392$, $P = 0.695$. Including random effect of the individual improved the fit of the model (Likelihood ratio test: $\chi^2 = 91.3$, $df = 1$, $P < 0.00001$), explaining 51.6 % of the variation in the relative dominance rank of adult marmots; neither year, colony, or valley effects improved the model (Likelihood ratio tests: $df = 1$ and $P = 1.000$ for both).

Figure Legends

Figure 1. Relationships between the mean $\pm$ S.E. relative ranks based on the outcomes of **A)** play as pups and later agonistic (dominance) interactions as yearlings ($N = 148$ males, shown as filled-in circles; 122 females, shown as open circles) and **B)** play as immature (pups or yearlings) and agonistic interactions for those same individuals as 2 year old adults ($N = 32$ males and 67 females as pups ($N = 97$) and yearlings ($N = 102$). Ranks for adults are pooled because we detected no sex difference (see text). Relative ranks based on play are shown separately for pups (open circles) and yearlings (filled-in circles) to account for differences between life history stages. Because dominance ranks increased as during between as age od adults increased, data shown here are limited to the first year of adulthood.



Discussion

The ultimate function, or functions, of play has been an age-old question in ethology (Spinka et al. 2001). The “practice hypothesis” attributes the function of play as a means for younger individuals to refine and develop skills that will be needed in adulthood. Therefore, play is expected to have reproductive consequences, with individuals who play more as pups having the skill advantage to outcompete their peers (Groos 1898).

We have shown the strongest correlative evidence of any study conducted that early play behavior does have a functional consequence on adult dominance social ranks later in life. However, the degree to which play behaviors successfully predicted social rank in adulthood varied depending on the life history stage at which play was measured. Though play is most strongly correlated to dominance in the pup to yearling transition, no matter how we look at it, the effect of play on later dominance is still there. Marmots are somewhat unique in that yearlings, in addition to pups, may play (Nowicki & Armitage 1979). Since yearlings are generally subordinate to adults, this phenomenon created a situation in which play behavior measured as yearlings resulted in higher dominance relative ranks as first year adults as compared to play behavior measured as pups.

This unique yearling stage represents an important life history decision for individual marmots as to whether they should disperse or stay at their native burrow. Since nearly all males, but only about half of females disperse (Armitage 1991), having a higher dominance ranking would allow individuals to possibly counter the effects of reproductive suppression (Armitage 2003). Therefore, early play behavior represents a low-cost method to establish dominance in later life, particularly since individual marmots rarely become injured while playing. Rather than risk injury with agonistic interactions in adulthood, individuals can simply play more as

juveniles. This conclusion is further bolstered by other possible functions of play as well (e.g., Nunes et al. 2004). If early play behavior does confer a subsequent dominance benefit in addition to all of its other supported function, than it certainly represents a key phenomenon universal to many animals during ontogeny.

However, the effects of play do weaken over time, such that early play behavior shows a stronger correlation with yearling dominance than adult dominance. The effects of play become increasingly weaker in older adults as well. Though older adults may not benefit directly from play behavior they engaged in as pups, play behavior may have still helped set the trajectory of their younger adult years to where they are today.

In evaluating our study with previous results, our larger sample size may be better suited to finding the weaker effects of play on later life dominance. Since the sum of an individual's play behavior is not as strongly correlated with just a single life history transition, previous studies may not have had the observational data to uncover these effects. However, even with a large sample size, we may have skewed results by evaluating play outcomes in a similar manner as agonistic outcomes. A key, defining characteristic of play in marmots is that it is often reciprocated (Nowicki & Armitage 1979). In observing marmots, it becomes apparent that sometimes the individual who was actually displaced during the play event may not have actually been the loser. However, this distinction needed to be made in order to quantify a winner or loser from a playful interaction. With a large enough sample size, we do not think that this effect played a significant role within our results.

Although we have shown one demonstrable function of play, there are possibly still many others. In uncovering this enigma, we are beginning to gain a deeper appreciation as to the consequence of early juvenile behavior and their consequences later in life.

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