

Original Article

Defensive and social aggression: repeatable but independent

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Behavioral traits that vary more between than within individuals are referred to as personality traits. When individuals interact with others, these interactions may form a social network and be described using social network measures. We suggest that these social interactions may reflect behavioral predispositions that themselves may be less variable within than between individuals. If so, the social attributes quantified using network statistics may themselves be personality traits. We have previously found that some social attributes of yellow-bellied marmot (*Marmota flaviventris*) may be heritable, suggesting that they are profitably viewed as reflecting individually distinctive social predispositions. Here, we asked the degree to which defensive aggression was independent of various measures of social aggression. We quantified defensive aggression when animals were live trapped and asked whether it was related to how socially tolerant marmots were. We found that although some of these social traits were repeatable, none were strongly correlated across contexts. Our results suggest that defensive aggression and social aggression are independent and thus not likely to constrain each other. *Key words*: aggression, defensive behavior, personality traits, social network, yellow-bellied marmots. [*Behav Ecol*]

INTRODUCTION

There is considerable interest in studying animal personality, typically defined as consistent, interindividual differences in behavior, and in its biological and ecological consequences (Gosling 2001; Réale et al. 2007; Sih et al. 2004; Sih et al. 2012). Personality traits are typically quantified by measuring behavioral differences in dimensions such as aggressiveness, boldness, or sociability; for example, many measures focus on responses to novelty or fearful situations (Réale et al. 2007). Personality traits may be correlated across contexts or between one another, forming behavioral syndromes, which importantly may then constrain optimal behavioral responses and selection on individual traits (Sih et al. 2004).

For many animals, personality influences and is influenced by the social environment (Stamps and Groothuis 2010). Traditional ways of quantifying personality differences in social responses include mirror-image stimulation (e.g., Svendsen and Armitage 1973), but real social environments are much more complex. Although studies of animal personality routinely quantify individual differences in social behavior, the recent integration of social network statistics in behavioral ecology has better equipped researchers to quantify the detailed structure of interactions and relationships among group members (i.e., the detailed social environment), and thus studying animal personality traits in a social network context is a promising but largely unexplored area (Krause et al. 2010). Links between personality traits and

social networks have been made in some studies of humans (Schaefer et al. 2006), and more recently in a limited number of animal groups (Pike et al. 2008; Croft et al. 2009; Schürch and Heg 2010; Godfrey et al. 2012). Recent studies have shown that these network statistics may be heritable (Fowler et al. 2009; Lea et al. 2010), which implies that there is a genetic mechanism for creating consistent between-individual differences. We suggest that measures of social network structure themselves thus offer novel ways to describe social environment and even personality traits. For example, the tendency to initiate social interactions is a personality trait that could be measured in a social network context. Social attractiveness, although not entirely a personality trait itself, is an important related concept that is a product of personality traits and social environment and can also be measured in social networks.

Personality traits may be contextually independent, or form a syndrome across contexts, and such syndromes may (or may not) vary across populations (Herczeg and Garamszegi 2012). For example, aggression toward conspecifics often forms a syndrome with boldness toward predators and higher activity levels (Sih et al. 2004; Pruitt et al. 2008; Pruitt et al. 2010), but the structure of an aggression behavioral syndrome may vary between populations based on selection (Wilson et al., 1994; Bell and Stamps 2004; Bell 2005; Bell & Sih 2007; Dingemanse et al. 2007; Doehrmann and Jenkins 2007). The nature of this variation can influence fitness and therefore ecological and evolutionary dynamics through demographic processes (Smith and Blumstein 2008; Sih et al. 2012). For example, more aggressive males may enhance their mating success, but their paternal care may suffer as a consequence. Male western bluebirds (*Sialia mexicana*) with higher levels of aggression during mate competition also guarded nests more intensely, a syndrome that resulted in a fitness trade-off; aggressive males

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provisioned females less during incubation and had lower fledgling rates (Duckworth 2006).

Aggressive syndromes are widespread, and in some cases include what we might call “defensive aggression” in response to a predator or novel or fearful situations (i.e., motor patterns seen in social aggression with conspecifics but directed at a predator or threatening situation). Defensive aggression might be related to social aggression in one of 2 ways. First, more aggressive individuals may also be more defensive toward a threat, which might be explained by a common and generally low threshold for aggressive behavior (Pruitt et al. 2008; Pruitt et al. 2010). Alternatively, we hypothesize that more defensive individuals may shun social interactions (or be avoided by others) and thus engage in fewer socially aggressive interactions. Either way, such a syndrome would suggest that the traits do not evolve independently, and that the trade-off itself must be studied, whereas lack of a syndrome would suggest that traits evolve independently or that they are plastic and could be subjected to different selective pressures in different environments (Bell 2004; Herczeg and Garamszegi 2012).

We asked if a potentially important ecological trait, aggression, was correlated across contexts. Specifically, we tested whether defensively aggressive yellow-bellied marmots (*Marmota flaviventris*) were more or less likely to engage in social aggression. We capitalized on a large dataset that has emerged from our long-term study of marmot biology, (Ozgul et al. 2010) and network dynamics (e.g., Blumstein et al. 2009; Wey and Blumstein 2012) in this system more recently, and quantified nonsocial defensive aggression in live-trapped subjects. Social aggression was quantified using network statistics. We used linear mixed-effects models to quantify the repeatability of traits and to test for a relationship between these 2 types of traits.

MATERIALS AND METHODS

We studied yellow-bellied marmots in and around the Rocky Mountain Biological Laboratory (RMBL), Gothic, Colorado, USA (lat 38°57'29"N; long 106°59'06"W). From 2002 to 2011 marmots were live trapped in Tomahawk traps baited with Omolene 100 horse feed (Ralston Purina, St. Louis, MO, USA). Individuals were transferred to cloth, conical handling bags and given unique ear tags, weighed, and marked with nontoxic fur dye for identification during observations.

Quantifying defensive aggression

From 2002 to 2011, we quantified the response of 1261 marmots (518 juvenile females, 595 juvenile males, 209 yearling females, 237 yearling males, 438 adult females, and 195 adult males; 479 individuals were trapped over multiple age categories). While in the trap, we scored marmots on a 0–1 (no/yes) scale on whether they alarm called, tooth chattered, struggled, bit the cage, walked immediately into the handling bag, or defecated. A priori, we expected that subjects that struggled and bit the cage were engaged in defensive aggression. Struggling and biting the cages are also motor patterns employed in defensive situations (personal observation). We also examined alarm calling and tooth chattering because marmots give alarm calls in response to predators and occasionally when pursued by an aggressive conspecific, and tooth chattering may precede alarm calling when animals are trapped (personal observation).

We used a Principle Component Analysis (varimax rotation, eigenvalues > 1) to reduce the number of measured variables into uncorrelated factors. Three factors, which together explained 62.8% of the variation, were identified: defensive

aggression (characterized by struggling or biting the cage), emitting alarm calls and not walking immediately into the bag, and defecation (Table 1). For the current study, we focused only on the first factor, which we define as defensive aggression. We used SPSS version 18.0 (SPSS Inc., Chicago, IL, USA) for the Principle Component Analysis and to obtain factor scores.

We define this as defensive aggression because it was elicited when subjects were “cornered” in a trap. A previous study found that individuals who struggled in the trap, bit at the cage, or alarm called had elevated fecal glucocorticoid metabolite levels 24h later, whereas those that did not struggle, bite the cage, or alarm call did not have elevated fecal glucocorticoid metabolite levels, suggesting that individuals that struggled were afraid (Smith et al. 2012). Thus, we could also profitably call this a “fearful” response. Nonetheless, because it used similar motor patterns (struggling and biting) that are seen in social aggression, we opted to refer to it as defensive aggression (see Discussion).

We averaged factor scores for each individual per year to generate one value each year. We used a linear mixed-effects model to estimate the repeatability of defensive aggression by modeling its variation with individual as a random effect.

Quantifying social aggression

From 2003 to 2008, marmots living in 4 permanent colonies (Bench-River, Marmot Meadow, Picnic, Town) were observed annually on most days between their emergence from hibernation (mid-April to mid-May) until early September (Lea et al. 2010). Subjects were observed with 10×40 binoculars and 10–40× spotting scopes from distances (typically 100–200 m) that did not otherwise influence their behavior. Observers noted every occurrence of bouts of aggressive behavior, along with the identity of the initiator and recipient (Lea et al. 2010). Only individuals that were observed 5 times in a year were included in social networks.

We constructed networks defined by the residents of each colony and the aggressive interactions among them in each year and calculated several measures of each individual’s involvement in aggressive interactions. Transient individuals (observed < 5 times) were excluded from analysis. Degree is defined as the number of other individuals with whom a focal individual interacts, and out-degree and in-degree are the number of other individuals to and from whom a focal individual initiates and receives interactions, respectively. Note that what we will refer to as degree, out-degree, and in-degree in the rest of the paper were actually valued measures, weighted by number of interactions, similar to the concept of “strength” used elsewhere (Barthélemy et al. 2005; Whitehead 2008), and were divided by network size to facilitate comparisons between individuals in different networks. We also calculated two other measures of

Table 1
Factor scores (Varimax rotation) based on the presence or absence of behaviors when yellow-bellied marmots were trapped

	Factor 1	Factor 2	Factor 3
Defecated	0.013	-0.04	0.914
Tooth chattered	0.087	0.7	0.312
Alarm called	-0.004	0.768	-0.113
Struggled	0.829	0.047	-0.072
Tried to bite	0.822	0.112	0.067
Walked immediately into bag	-0.175	-0.517	0.293
% Variance	27.43	18.46	16.91

aggressive interactions, expansiveness and attractiveness (as per Borgatti et al. 2002), which measure the tendency to initiate or receive aggression, respectively, relative to other individuals in a network. These measures were calculated based on unweighted networks and account for network density and levels of reciprocity, variables that can influence patterns of individual behavior (Holland and Leinhardt 1981). To calculate this, we dichotomized our main networks so that any subjects that interacted had a link.

Studying the relationship between defensive and social aggression

Our final dataset consisted of 291 individuals with measures of both defensive and social aggression (138 yearling females, 161 yearling males, 102 adult females, 60 adult males; 82 individuals were measured as both yearlings and adults). Measures of agonistic degree were square root transformed to normalize variance. We fitted linear mixed-effects models to identify the relationship between defensive aggression and each social network attribute. In all models, we included age, sex, and defensive aggression*age, defensive aggression*sex, and age*sex as fixed effects, because previous studies have shown that these are likely to be important factors. In the 3 models based on degree, we added two additional random effects to control for non-independence—colony and the interaction between year and colony. In all models, individual was also included as a random effect. We estimated the repeatability of agonistic degree by dividing the variance explained by the individual by the total variance explained by the model. The significance of repeatability was estimated with a log-likelihood test. We extracted *P* values and parameter estimates by Markov chain Monte Carlo sampling with 30 000 simulations using restricted maximum likelihoods. All models were fitted in R v. 2.14.0 (R Development Core Team 2011) using the lmer function in the lme4 package (Bates et al. 2011).

RESULTS

Individual accounted for significant amount of variation in both our measured dimensions of defensive aggression as well as in measures of agonistic degree but not aggressive expansiveness or aggressive attractiveness (Table 2). This significant repeatability suggests that there are consistent, interindividual differences in defensive aggression and degree measures.

After controlling for significant variation explained by age and sex (and sometimes their interaction), no significant variation in our network measures of social aggression was explained by our measure of defensive aggression (Table 3).

Table 2
Repeatability of defense/aggression and agonistic social network attributes

Trait	<i>r</i>	LRT	<i>P</i> value
Defensive aggression	0.304	31.026	<0.0001
Expansiveness	0.102	2.674	0.102
Attractiveness	0.086	1.500	0.221
Weighted standardized degree	0.216	31.967	<0.0001
Weighted standardized in-degree	0.195	19.765	<0.0001
Weighted standardized out-degree	0.177	9.470	<0.0001

The significance of repeatability was obtained by comparing linear mixed-effects models with and without individual as a random effect using likelihood ratio tests (LRT).

Table 3
Results from linear mixed-effects models explaining variation in measures of social aggression as a function of defensive aggression, after explaining variation accounted for by the fixed effects of age, sex, and their interactions

	Estimate	P-MCMC
Aggressive expansiveness		
(Intercept)	-0.003	0.817
Def Agg	-0.226	0.201
Age	-0.624	0.002
Sex	0.795	0.0001
Def Agg*Age	-0.428	0.275
Def Agg*Sex	0.225	0.491
Age*Sex	-0.655	0.015
Aggressive Attractiveness		
(Intercept)	-0.137	0.032
Def Agg	0.091	0.263
Age	0.359	0.0004
Sex	-0.080	0.455
Def Agg*Age	-0.018	0.807
Def Agg*Sex	-0.057	0.669
Age*Sex	-0.016	0.973
Aggressive weighted nDegree (sqrt transformed)		
(Intercept)	1.449	0.005
Def Agg	-0.094	0.233
Age	-0.069	0.350
Sex	0.308	0.020
Def Agg*Age	-0.100	0.445
Def Agg*Sex	0.226	0.084
Age*Sex	-0.243	0.159
Aggressive weighted nOutdegree (sqrt transformed)		
(Intercept)	1.019	0.009
Def Agg	-0.083	0.260
Age	-0.508	<0.0001
Sex	0.476	0.0002
Def Agg*Age	-0.074	0.534
Def Agg*Sex	0.038	0.689
Age*Sex	-0.210	0.214
Aggressive weighted nIndegree (sqrt transformed)		
(Intercept)	0.889	0.009
Def Agg	-0.036	0.764
Age	0.345	<0.0001
Sex	-0.083	0.453
Def Agg*Age	-0.105	0.277
Def Agg*Sex	0.148	0.273
Age*Sex	0.002	0.858

Adults and females are reference groups. Individual and two additional random effects were used to control for nonindependence—colony and the interaction between year and colony.

DISCUSSION

We found that two different types of aggressive behavior—what we refer to as defensive aggression, and some measures of social aggression—were each significantly repeatable. From this we conclude that these reflect personality differences among individual marmots. Interestingly, we found no evidence of an aggressive syndrome that would have been inferred if the two repeatable traits were themselves correlated.

The fact that defensive aggression was repeatable is supported from recent endocrinological results from our population of marmots that suggest that baseline glucocorticoid levels are significantly repeatable (Smith et al. 2012), a finding with a number of ramifications. We have previously discovered that glucocorticoid levels modulate both the probability of emitting alarm calls (Blumstein et al. 2006) and the acoustic structure of calls when emitted (Blumstein and Chi 2012) in the trap. We now know that “stressed” marmots struggle, bite, and alarm call, and this elevates glucocorticoid

levels (Smith et al. 2012). We interpret this struggling and biting as a form of trap-induced defensive aggression, and our measure of defensive aggression is itself repeatable.

Interestingly, measures of social aggression that were calculated from direct interactions (all 3 measures of agonistic degree) were repeatable, but not measures that, by incorporating network density and reciprocity, captured an individual's residual tendency to initiate or receive interactions (aggressive expansiveness or aggressive attractiveness). We cannot explain the discrepancy. It is possible that individuals with 0 interactions are left out of expansiveness/attractiveness measures, so these noninteractive individuals could contribute to this discrepancy, or that the residual effects are weaker. Nonetheless, our findings suggest that marmots have some control over their social interactions; some individuals are engaged in more types of agonistic social interactions than others.

Studies in other systems (e.g., fish—Ruzzante and Doyle, 1991, 1993; spiders—Pruitt et al. 2008; Pruitt et al. 2010; Pruitt et al. 2008, 2010; ants—Crosland 1990) have shown that individuals can have specific and repeatable social dispositions that may be correlated (phenotypically or genetically) with other traits—including antipredator behavior. In these papers, sociality was studied by quantifying aggregation tendencies, and other behaviors were studied in species-specific ways. By contrast, we used network statistics to quantify social tendencies. One strength of using social network statistics to quantify social tendencies is that each network statistic is well defined and, if consistently applied to other studies, could help us identify a more general understanding of personality and syndromes.

The fact that our measures of social aggression are repeatable is novel and important, because it suggests that social network traits may measure attributes of personality. Repeatability may set the upper limit of heritability (Boake 1989). Previous studies in humans (Fowler et al. 2009), and nonhumans (Lea et al. 2010), have reported significant heritable variation in social network traits. Patterns of within-individual repeatability (or plasticity) may vary in different populations or over time, and this is a future direction for research.

Given a repeatable measure of defensive aggression and a repeatable measure of social aggression, we expected that the two factors would be correlated and thus create an aggression syndrome. We found no evidence of such a syndrome, but Pruitt et al. 2008; Pruitt et al. 2010) have shown that some types of conspecific aggression are correlated with aggressive antipredator behavior. In our population of yellow-bellied marmots, however, these types of aggression are context specific. Although the outwardly expressed behaviors may be superficially similar (e.g., biting), “aggression” initiated in a fearful context (to a potential “predator”) is not the same as aggression initiated to another marmot. This also may suggest that the underlying proximate causation is different. Although glucocorticoid levels may modulate defensive aggression, a previous field study of fecal glucocorticoid metabolites found no obvious relationship between glucocorticoid levels and social attributes (Wey and Blumstein 2012). We do not understand what modulates social aggression in marmots, but experimental studies of meerkats (*Suricata suricata*—Madden and Clutton-Brock 2011), rats (*Rattus norvegicus*—Pedersen and Prange 1979), and humans (Zak et al. 2007) demonstrate that oxytocin may modulate a variety of prosocial behaviors. If indeed this is true for marmots, then the different proximate mechanisms modulating these different forms of aggressive behavior may explain the lack of an aggression syndrome.

In contrast to three-spined sticklebacks (*Gasterosteus aculeatus*—Huntingford 1976), funnel-web spiders (*Agelenopsis aperta*—Riechert and Hedrick 1993), rats (Benus et al. 1991),

and western bluebirds (Duckworth 2006) where an aggression syndrome has been identified, yellow-bellied marmot aggression in the two dimensions studied seems to be somewhat independent of each other. Thus defensive and social aggression can be individually optimized and are not likely to constrain each other. Further studies should investigate how these independent traits influence ecological and evolutionary dynamics. For example, agonistic interactions and group size as social integration (calculated as embeddedness) have been shown to influence dispersal (Blumstein et al. 2009). Ultimately, identifying the ecological, evolutionary, and proximate basis of behavioral syndromes may be particularly useful to developing a deeper understanding of the conditions and structure of syndromes (Stamps 1991; Sih et al. 2004).

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REFERENCES

- Barthélemy M, Barrat A, Pastor-Satorras R, Vespignani A. 2005. Characterization and modeling of weighted networks. *Physica A*. 346:34–43.
- Bates D, Maechler M, Bolker B 2011. lme4: Linear Mixed-effects models using Eigen and Eigen. [Internet] R package version 0.999375–42 [cited 2012 October 13]. Available from: <http://CRAN.R-project.org/package=lme4>.
- Bell AM. 2005. Behavioural differences between individuals and two populations of stickleback (*Gasterosteus aculeatus*). *J Evol Biol*. 18:464–473.
- Bell AM, Stamps JA 2004. The development of behavioral differences between individuals and populations of threespined stickleback. *Anim Behav*. 68:1339–1348.
- Bell AM, Sih A. 2007. Exposure to predation generates personality in threespined sticklebacks (*Gasterosteus aculeatus*). *Ecol Lett*. 10:828–834.
- Benus RF, Bohus B, Koolhaas JM, van Oortmerssen GA. 1991. Heritable variation for aggression as a reflection of individual coping strategies. *Experientia*. 47:1008–1019.
- Blumstein DT, Patton ML, Saltzman W. 2006. Faecal glucocorticoid metabolites and alarm calling in free-living yellow-bellied marmots. *Biol Lett*. 2:29–32.
- Blumstein DT, Wey TW, Tang K. 2009. A test of the social cohesion hypothesis: interactive female marmots remain at home. *Proc Biol Sci*. 276:3007–3012.
- Blumstein DT, Chi YY. 2012. Scared and less noisy: glucocorticoids are associated with alarm call entropy. *Biol Lett*. 8:89–192.
- Boake CRB. 1989. Repeatability: its role in evolutionary studies of mating behavior. *Evol Ecol*. 3:173–182.
- Borgatti SP, Everett MG, Freeman LC. 2002. Ucinet 6 for Windows: software for social network analysis. Cambridge, MA: Analytic Technologies.
- Croft DP, Krause J, Darden SK, Ramnarine IW, Faria JJ, James R. 2009. Behavioural trait assortment in a social network: patterns and implications. *Behav Ecol Sociobiol*. 63:1495–1503.
- Crosland MWJ. 1990. Variation in ant aggression and kin discrimination ability within and between colonies. *J Insect Behav*. 3:359–379.
- Dingemanse NJ, Wright J, Kazem AJ, Thomas DK, Hickling R, Dawnay N. 2007. Behavioural syndromes differ predictably between 12 populations of three-spined stickleback. *J Anim Ecol*. 76:1128–1138.
- Dochtermann NA, Jenkins SH. 2007. Behavioural syndromes in Merriam's kangaroo rats (*Dipodomys merriami*): a test of competing hypotheses. *Proc R Soc B*. 274:2342–2349.

- Duckworth RA. 2006. Behavioral correlations across breeding contexts provide a mechanism for a cost of aggression. *Behav Ecol*. 17:1011–1019.
- Fowler JH, Dawes CT, Christakis NA. 2009. Model of genetic variation in human social networks. *Proc Natl Acad Sci USA*. 106:1720–1724.
- Godfrey SS, Bradley JK, Sih A, Bull CM. 2012. Lovers and fighters in sleepy lizard land: where do aggressive males fit in a social network? *Anim Behav*. 83:209–215.
- Gosling SD. 2001. From mice to men: what can we learn about personality from animal research? *Psychol Bull*. 127:45–86.
- Herczeg G, Garamszegi LZ. 2012. Individual deviation from behavioural correlations: a simple approach to study the evolution of behavioural syndromes. *Behav Ecol Sociobiol*. 66:161–169.
- Holland P, Leinhardt J. 1981. An exponential family of probability distributions for directed graphs. *J Am Stat Assoc*. 76:33–36.
- Huntingford FA. 1976. The relationship between anti-predator behaviour and aggression among conspecifics in the three-spined stickleback, *Gasterosteus aculeatus*. *Anim Behav*. 24:245–260.
- Krause J, James R, Croft DP. 2010. Personality in the context of social networks. *Philos Trans R Soc Lond, B, Biol Sci*. 365:4099–4106.
- Lea AJ, Blumstein DT, Wey TW, Martin JG. 2010. Heritable victimization and the benefits of agonistic relationships. *Proc Natl Acad Sci USA*. 107:21587–21592.
- Madden JR, Clutton-Brock TH. 2011. Experimental peripheral administration of oxytocin elevates a suite of cooperative behaviours in a wild social mammal. *Proc Biol Sci*. 278:1189–1194.
- Ozgul A, Childs DZ, Oli MK, Armitage KB, Blumstein DT, Olson LE, Tuljapurkar S, Coulson T. 2010. Coupled dynamics of body mass and population growth in response to environmental change. *Nature*. 466:482–485.
- Pedersen CA, Prange Jr. AJ. 1979. Induction of maternal behavior in virgin rats after intracerebroventricular administration of oxytocin. *Proc Natl Acad Sci USA*. 76:1145–1148.
- Pike TW, Samanta M, Lindström J, Royle NJ. 2008. Behavioural phenotype affects social interactions in an animal network. *Proc Biol Sci*. 275:2515–2520.
- Pruitt JN, Riechert SE, Jones TC. 2008. Behavioural syndromes and their fitness consequences in a socially polymorphic spider, *Anelosimus studiosus*. *Anim Behav*. 76:871–879.
- Pruitt JN, Riechert SE, Iturralde G, Vega M, Fitzpatrick BM, Avilés L. 2010. Population differences in behaviour are explained by shared within-population trait correlations. *J Evol Biol*. 23:748–756.
- R Development Core Team. 2011. R: A language and environment for statistical computing [Internet]. Vienna (Austria): R Foundation for Statistical Computing [cited 2012 October 2013]. Available from: <http://www.R-project.org/>.
- Réale D, Reader SM, Sol D, McDougall PT, Dingemanse NJ. 2007. Integrating animal temperament within ecology and evolution. *Biol Rev Camb Philos Soc*. 82:291–318.
- Riechert SE, Hedrick AV. 1993. A test for correlations among fitness-linked behavioural traits in the spider *Agelenopsis aperta* (Aranea, Agelenidae). *Anim Behav*. 46:669–675.
- Ruzzante DE, Doyle RW. 1991. Rapid behavioral changes in medaka (*Oryzias latipes*) caused by selection for competitive and noncompetitive growth. *Evolution* 45:1936–1946.
- Ruzzante DE, Doyle RW. 1993. Evolution of social behavior in a resource-rich, structured environment: selection experiments with Medaka (*Oryzias latipes*). *Evolution* 47:456–470.
- Schaefer C, Geyer-Schulz A, Beringhaus S. 2006. Personality in social networks. A theoretical overview. In: Dreier T, Studer R, Weinhardt C, editors. Information management and market engineering. Karlsruhe, Germany: Univ. Karlsruhe Press. p. 197–206.
- Schürch R, Heg, D. 2010. Life history and behavioral type in the highly social cichlid *Neolamprologus pulcher*. *Behav Ecol*. 21:588–598.
- Sih A, Bell AM, Johnson JC, Ziemba RE. 2004. Behavioral syndromes: an integrative overview. *Q Rev Biol*. 79:241–277.
- Sih A, Cote J, Evans M, Fogarty S, Pruitt J. 2012. Ecological implications of behavioural syndromes. *Ecol Lett*. 15:278–289.
- Smith BR, Blumstein DT. 2008. Fitness consequences of personality: a meta-analysis. *Behav Ecol*. 19:448–455.
- Smith JE, Monclús R, Wantuck D, Florant GL, Blumstein DT. 2012. Fecal glucocorticoid metabolites in wild yellow-bellied marmots: Experimental validation, individual differences and ecological correlates. *Gen Comp Endocrinol*. 178:417–426.
- Stamps JA. 1991. Why evolutionary issues are reviving interest in proximate behavioral mechanisms. *Am Zool*. 31:338–348.
- Stamps J, Groothuis TG. 2010. The development of animal personality: relevance, concepts and perspectives. *Biol Rev Camb Philos Soc*. 85:301–325.
- Svendsen GE, Armitage KB. 1973. Mirror-image stimulation applied to field behavioral studies. *Ecology* 54:623–627.
- Wey TW, Blumstein, DT. 2012. Measuring social attributes and functional correlates of individual social variation in *Marmota flaviventris*. *Behav Ecol Sociobiol*. 66:1075–1085.
- Wilson DS, Clark AB, Coleman K, Dearstyne T. 1994. Shyness and boldness in humans and other animals. *Trends Ecol Evol*. 9:442–446.
- Whitehead H. 2008. Analyzing animal societies: quantitative methods for vertebrate social analysis. Chicago: University of Chicago Press.
- Zak PJ, Stanton AA, Ahmadi S. 2007. Oxytocin increases generosity in humans. *PLoS ONE*. 2:e1128.