

Fitness consequences of personality: a meta-analysis

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The study of nonhuman personality capitalizes on the fact that individuals of many species behave in predictable, variable, and quantifiable ways. Although a few empirical studies have examined the ultimate consequences of personality differences, there has been no synthesis of results. We conducted a formal meta-analysis of published studies reporting fitness consequences of single personality dimensions to identify general trends across species. We found bolder individuals had increased reproductive success, particularly in males, but incurred a survival cost, thus, supporting the hypothesis that variation in boldness was maintained due to a “trade-off” in fitness consequences across contexts. Potential mechanisms maintaining variation in exploration and aggression are not as clear. Exploration had a positive effect only on survival, whereas aggression had a positive effect on both reproductive success and, not significantly, on survival. Such results would suggest that selection is driving populations to become more explorative and aggressive. However, limitations in meta-analytic techniques preclude us from testing for the effects of fluctuating environmental conditions or other forms of selection on these dimensions. Results do, however, provide evidence for general relationships between personality and fitness, and we provide a framework for future studies to follow in the hopes of spurring more in-depth, long-term research into the evolutionary mechanisms maintaining variation in personality dimensions and overall behavioral syndromes. We conclude with a discussion on how understanding and managing personality traits may play a key role in the captive breeding and recovery programs of endangered species. *Key words:* behavioral syndrome, fitness, personality, reproductive success, survival. [*Behav Ecol*]

Although it has been recognized that individuals may adopt discrete alternative strategies (Gross 1996; Widemo 1998), other forms of continuous, individual variability have traditionally been viewed as statistical noise (Wilson 1998). Recently, however, behavioral ecologists have recognized that consistent behavioral differences between individuals may occur within single contexts or may be correlated across different contexts and, therefore, make up an overall personality trait (Gosling 2001) or behavioral syndrome (Sih, Bell, Johnson 2004; Sih, Bell, Johnson, Ziemba 2004; Bell 2007). Such variability in behavioral traits is hypothesized to have important ecological and evolutionary implications (Wilson et al. 1994; Réale et al. 2007). Traits may be variable and adaptive if individuals at the extreme ends of a distribution have higher fitness than phenotypically intermediate individuals (Wilson 1998). Selection for or against differing behavioral traits may also vary with the environment, thereby maintaining behavioral variation within populations (Réale and Festa-Bianchet 2003; Dingemanse et al. 2004).

Recent work has indeed found that fitness consequences for selected personality traits vary according to shifting environmental conditions such as predation pressure (Réale and Festa-Bianchet 2003), food availability (Dingemanse et al. 2004), and social condition (Both et al. 2005). Initial conclusions from such data may be that variation in traits is maintained because the long-term fitness of different behavioral phenotypes is equal. Such a mechanism would be similar to how frequency-dependent selection maintains alternate phenotypes within a population (i.e., the fitness of the most frequent phenotype is lower than the less frequent phenotype but overall they are equal: Gross [1996]; Dall et al. [2004]).

An alternative explanation may be that the fitness of personality dimensions varies depending on the context in which they are exhibited. A generally aggressive individual, for example, may be at an advantage when competing with conspecifics for mates and therefore have higher reproductive success, but such a personality attribute may be costly if this behavioral pattern is maintained in the antipredator context, thus lowering survival (Sih, Bell, Johnson, Ziemba 2004; Stamps 2007). A model based on this explanation has been developed to explain sexual cannibalism in the fishing spider *Dolomedes fimbriatus* (Arnqvist and Henriksson 1997). Juvenile females appear to have been selected for high levels of aggression to increase growth rate and adult fecundity. Aggression then “spills over” into adulthood and leads to maladaptive precopulatory sexual cannibalism. Such trade-offs across contexts could, therefore, lead to a single population of individuals that varies dramatically in aggression levels.

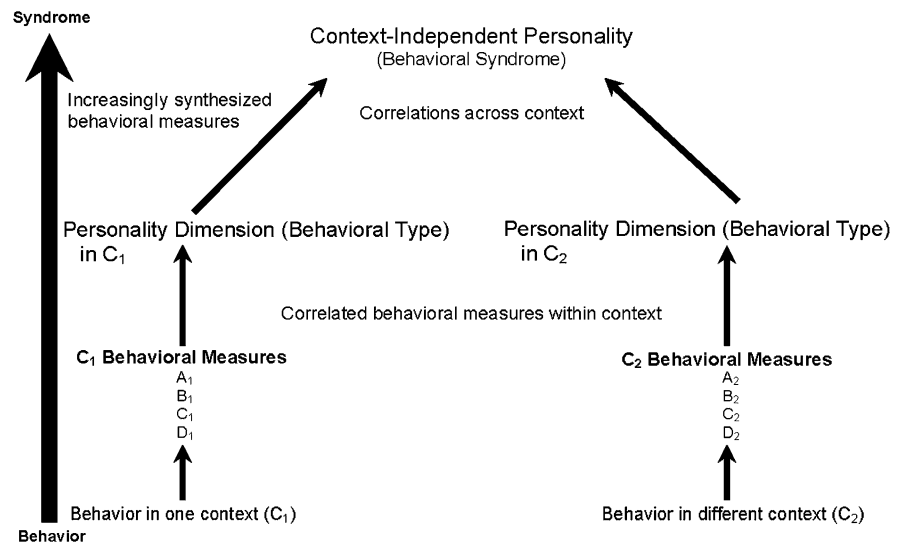
Unfortunately, few empirical studies have examined and compared the ultimate consequences of behavioral variability across species (for a review of select case studies see Dingemanse and Réale [2005]; Huntingford and Adams [2005]; McDougall et al. [2005]; Réale et al. [2007]) so the ecological and evolutionary implications of personality variation are unclear. In fact, lack of understanding of general links between personality traits and fitness across species has been implicated as one of the main reasons why personality has not been embraced by ecological theory and may explain why long-term studies on the effects of personality on fitness are relatively nonexistent (Réale et al. 2007). Although such long-term primary studies of multiple personality dimensions are needed to fully explain how the interaction of these traits affects fitness (Dingemanse and Réale 2005), a synthesis of the existing literature would be useful in identifying general trends across species to spur additional in-depth research and to provide direction and potentially fruitful lines of questions to this growing body of research.

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Figure 1

Hierarchical representation of behavioral measures. Observable behaviors (A, B, C, D) are measured in 2 different contexts (C_1 and C_2). Correlated behavioral measurements within a single context represent a personality dimension or behavioral type. Correlations across contexts represent context-independent personality or a behavioral syndrome.



We, therefore, conducted a formal meta-analysis of published data to examine the effects of single dimensions (Gosling 1998; Capitanio 1999) of animal personality (also termed behavioral types: from Sih, Bell, Johnson, Ziemba [2004]) on direct fitness correlates. We focused on single behavioral types measured in single contexts rather than overall, context-independent personalities, or behavioral syndromes (see Figure 1 for an illustrated description of these concepts), because we found only 1 study that examined the effect of a syndrome on fitness (Sih and Watters 2005). Due to the inconsistent use of terminology in nonhuman personality research in which similar behavioral traits have been defined differently or different traits defined the same across studies, we followed the general framework proposed by Réale et al. (2007) for interpreting temperament and personality studies. Our analyses examined the effects of the personality dimensions “boldness,” “exploration,” and “aggression” on the 2 direct fitness correlates of reproductive success and survival to identify fitness trends across species. We focused on these dimensions because various indices of these traits were measured in every publication identified in our literature search that fit our criteria for inclusion in the meta-analysis.

METHODS

Data collection

To obtain data, we first gathered relevant studies cited in Gosling (2001) and the related extended online bibliography (<http://homepage.psy.utexas.edu/HomePage/Faculty/Gosling/bibliography.htm>). We then searched the Web of Science database for all articles relating behavioral type or personality and fitness. Because numerous terms have been used to describe individual differences in behavioral patterns for non-human animals, we used the following search terms: personality, temperament, individual difference, aggression, aggressiveness, emotion, emotionality, bold, boldness, extravert, extraversion, coping style, behavioral trait, tameness, sociability, neophobia, impulsivity, behavioral axis, behavioral construct, exploration, fear, predator inspection, behavioral syndrome, behavioral phenotype, behavioral profile, behavioral strategy, and reactivity. The fitness-related search terms used were fitness, survival, breeding, reproductive success, mate choice, predation, fecundity, copulation, mortality, and reproduction. All combinations of behavioral type- and fitness-related search terms produced 9657 references. From

all the above searches, 31 publications met our criteria of correlating behavioral differences of individuals with reproductive success or survival. Every publication identified included some measure of boldness, exploration, and/or aggression. We, therefore, divided the data into studies measuring these 3 behavioral types.

The following data were extracted from each study for primary analyses and descriptive purposes: 1) year and author of publication; 2) study species; 3) condition (wild or captive/domestic); 4) personality dimension measured and whether the trait was categorical or continuous; 5) method used to measure personality (behavioral coding, rating, or naturalistic observation; see Gosling [2001]); 6) fitness trait measured and whether the trait was categorical or continuous; 7) sample size, sex, and age class; and 8) statistic and *P* value.

The 3 general methods used to quantify personality in the studies used in our analyses were coding of behaviors, rating of traits (Gosling 2001), and naturalistic observation. Most studies utilized coding of behaviors, which involved subjects that underwent various tests in which the context of the situation was manipulated and behavior was measured. Following Réale et al. (2007), behavioral tests involving response toward humans, confinement, novel objects, potential predators, and probability of being trapped were all interpreted as broadly describing a willingness to take risk, or “boldness” (Table 1). Behavioral tests involving the measurement of movement patterns in open fields or novel environments were interpreted as measures of “exploration” (Table 1). Behavioral tests involving a social contest between conspecifics in which agonistic behaviors were quantified, including mirror-image stimulation (Armitage 1986; Armitage and Van Vuren 2003), were interpreted as measures of “aggression” (Table 1). Two studies of zoo animals involved keepers rating subjects on various personality traits (Carlstead et al. 1999; Wielebnowski 1999). Although not included in the Réale et al. (2007) framework, rating by humans familiar with their subjects has been shown to be a reliable and valid method for assaying personality (see Gosling [2001] for a review) and was therefore included in our analyses following the interpretations of the studies’ authors (Table 1). Lastly, 3 studies involving naturalistic observations of agonistic behavior between conspecifics in noncaptive animals (Chism and Rogers 1997; McPhee and Quinn 1998; Natoli et al. 2005) were included in our analyses of aggression (Table 1).

Our sample of mammals, fish, arthropods, and birds included studies of male, female, and mixed-sex subjects, and

Table 1

Summary of data from each study used in the meta-analyses: boldness and reproductive success (a); boldness and survival (b); exploration and reproductive success (c); exploration and survival (d); aggression and reproductive success (e); aggression and survival (f)

Species	Condition/sex	Method	<i>N</i>	<i>r</i>	Source
(a)					
Bighorn sheep (<i>Ovis canadensis</i>)	Wild/female	Trappability and response to human handlers	38	0.33	Réale et al. (2000)
Guanaco (<i>Lama guanicoe</i>)	Wild/female	Response toward humans	160	-0.10	Sarno and Franklin (1999)
Mink (<i>Mustela vison</i>)	Captive/female	Novel object (stick test)	200	0.11	Korhonen et al. (2002)
Sable (<i>Martes zibellina</i>)	Captive/female	Novel object (stick test)	122	0.03	Korhonen et al. (2001)
Black rhinoceros (<i>Diceros bicornis</i>)	Captive/mixed	Rating of traits	24	0.09	Carlstead et al. (1999)
	Female		25	0	
	Male		23	0.17	
Cheetah (<i>Acinonyx jubatus</i>)	Captive/mixed	Rating of traits	44	0.61	Wielebnowski (1999)
	Female		25	0.56	
	Male		19	0.62	
Silver fox (<i>Vulpes vulpes</i>)	Captive/female	Novel object and response toward human	21	0	Korhonen and Niemelä (1996)
Domestic pig (<i>Sus scrofa</i>)	Domestic/female	Novel object and response toward human	24	0.24	Janczak et al. (2003)
Domestic pig (<i>Sus scrofa</i>)	Domestic/female	Response toward human	194	0.14	Hemsworth et al. (1999)
Merino sheep (<i>Ovis aries</i>)	Domestic/female	Response to confinement	39	-0.01	Murphy et al. (1994)
(b)					
Swift fox (<i>Vulpes velox</i>)	Wild/juvenile mixed	Novel object	16	-0.62	Bremner-Harrison et al. (2004)
Bighorn sheep (<i>Ovis canadensis</i>)	Wild/female	Trappability and response to human handlers	57	0.14	Réale and Festa-Bianchet (2003)
Pumpkinseed sunfish (<i>Lepomis gibbosus</i>)	Wild/juvenile mixed	Trappability	65	-0.29	Wilson et al. (1993)
Guppy (<i>Poecilia reticulata</i>)	Wild/male	Response to predator	60	-0.32	Dugatkin (1992)
Guppy (<i>Poecilia reticulata</i>)	Domestic/juvenile female	Response to predator	24	0.61	Godin and Davis (1995)
(c)					
Great tit (<i>Parus major</i>)	Wild/mixed	Novel environment	156	-0.004	Both et al. (2005)
	Female		156	-0.01	
	Male		156	0	
Great tit (<i>Parus major</i>)	Wild/female	Novel environment	11	0.13	Dingemanse et al. (2004)
Merino sheep (<i>Ovis aries</i>)	Domestic/female	Open field	39	0.04	Murphy et al. (1994)
(d)					
Great tit (<i>Parus major</i>)	Wild/mixed	Novel environment	53	0.03	Dingemanse et al. (2004)
	Female		58	0.03	
	Male		49	0.03	
Sibling vole (<i>Microtus rossiaemeridionalis</i>)	Wild/mixed	Distance moved following release	19	0.53	Banks et al. (2002)
Sprague-Dawley rat (<i>Rattus norvegicus</i>)	Domestic/male	Novel environment	28	0.40	Cavigelli and McClintock (2003)
(e)					
Fish spider (<i>Dolomedes triton</i>)	Wild/female	Latency to attack males in courtship trials	60	0.14	Johnson and Sih (2005)
Black field cricket (<i>Teleogryllus commodus</i>)	Wild/male	Paired contests	36	0.11	Shackleton et al. (2005)
Meadow vole (<i>Microtus pennsylvanicus</i>)	Wild/male	Paired contests	28	-0.14	Spritzer et al. (2005)
Yellow-bellied marmot (<i>Marmota flaviventris</i>)	Wild/mixed	Mirror-image stimulation	25	-0.19	Armitage and Van Vuren (2003)
	Female		22	-0.11	
	Male		27	-0.23	
Patas monkey (<i>Erythrocebus patas</i>)	Wild/male	Observation of agonistic behavior	5	-0.61	Chism and Rogers (1997)
Water strider (<i>Gerris remigis</i>)	Wild/female	Paired contests	18	0.41	Blanckenhorn (1991a)
Water strider (<i>Gerris remigis</i>)	Wild/female	Social contests	21	0.34	Blanckenhorn (1991b)
Yellow-bellied marmot (<i>Marmota flaviventris</i>)	Wild/female	Mirror-image stimulation	19	-0.09	Armitage (1986)
Deer mouse (<i>Peromyscus maniculatus</i>)	Wild/male	Paired contests	16	0.63	Dewsbury (1984)
Black rhinoceros (<i>Diceros bicornis</i>)	Captive/mixed	Rating of traits	24	-0.22	Carlstead et al. (1999)

Table 1, continued

Species	Condition/sex	Method	<i>N</i>	<i>r</i>	Source
	Female		25	0.09	
	Male		23	-0.50	
Cheetah (<i>Acinonyx jubatus</i>)	Captive/mixed	Rating of traits	44	0.06	Wielebnowski (1999)
Domestic cat (<i>Felis catus</i>)	Domestic/male	Observation of agonistic behavior	16	0.71	Natoli et al. (2005)
(f)					
Black field cricket (<i>Teleogryllus commodus</i>)	Wild/male	Paired contests	30	0.04	Shackleton et al. (2005)
Sockeye salmon (<i>Oncorhynchus nerka</i>)	Wild/female	Observation of agonistic behavior	40	0.35	McPhee and Quinn (1998)
Water strider (<i>Gerris remigis</i>)	Wild/female	Social contests	21	-0.24	Blanckenhorn (1991b)
House mouse (<i>Mus domesticus</i>)	Domestic/male	Paired contests	32	0.06	Lenington et al. (1996)

all but 3 studies (Wilson et al. 1993; Godin and Davis 1995; Bremner-Harrison et al. 2004) consisted solely of adults. Measures of reproductive success and survival varied from 1 breeding or predation event to total lifetime measurements.

Analyses

All conversions and analyses were done using Meta-Analysis Programs 5.3 (Ralf Schwarzer: http://web.fu-berlin.de/gesund/gesu_engl/meta_e.htm). We chose Pearson's product-moment correlation coefficient, r , as the measure of effect size for our studies (Rosenthal 1991). The r value is the magnitude of the effect of the measured behavioral type on the direct fitness correlate. When possible, coefficients were obtained from each study in the following order: 1) direct reporting of r , R^2 , or partial correlation; 2) other test statistics (F , U , t , χ^2) converted to r (Rosenthal 1991); 3) N and exact 1-tailed P values used to calculate r (reported 2-tailed P values were converted to 1-tailed by dividing by 2). To account for the use of 1-tailed P values by Meta-Analysis Programs 5.3, minus signs were given to probabilities in the opposite direction of our prediction. Thus, if a study found that bold individuals survived longer, the P value was given a positive sign; if survival was reduced, the P value was given a negative sign. The only deviation from the above methods was a study by Dingemanse et al. (2004), which fit models using information theory. Some results of this study could not be directly converted to effect sizes so we calculated values for the data points illustrated in Figure 2 (p. 850) and fitted linear regression models to obtain effect size estimates.

We attempted to contact authors for additional data when results did not report exact effect sizes or P values (e.g., they stated $P < 0.05$ or $P > 0.05$), and we obtained unpublished data for 2 studies (Armitage 1986; Dingemanse et al. 2004) that were used as r values. For other studies that included results which were not exact, P values were estimated to the nearest tenth or hundredth decimal place of the given value ($P < 0.25 = 0.2$; $P > 0.05 = 0.06$; $P > 0.1 = 0.2$) and results that reported nonsignificance with no P value were given P values of 0.5 ($r = 0.0$) (Rosenthal 1991). Only results where a direct comparison was made between a personality dimension and fitness correlate were included for analyses. Also, results were only included when it was clear from the publication that statistical tests had been used to examine the relationship. For example, if a paper stated that no relationship was obvious, but did not give the P value or test used, the result was not included. A summary of the data from each study used in the meta-analysis is shown in Table 1.

We performed a series of meta-analyses using the Schmidt-Hunter method (Hunter and Schmidt 1990) in which effect sizes from individual studies are weighted by their sample size to the proportion of total sample size. Most studies reported more than one result when comparing behavioral type to fitness. For these studies, each r value was converted to a Fisher's z_r . Fisher's z_r values were then averaged and converted back to r to give a single, overall r value for each study (Rosenthal 1991). The sample size for each result was also averaged to give a single overall N for each study (Schum et al. 2003). This technique is standard in meta-analysis and reduces the risk of treating nonindependent results as independent (Rosenthal 1991). Results of analyses were tested for significance using the Z -test (Rosenthal 1991). To address the "file drawer problem" (see Rosenthal 1991), we calculated the fail safe number for each weighted mean r . This value indicates the number of studies with effect sizes of 0 that would be needed to reduce the observed effect size to a nonsignificant level ($P > 0.05$). To test for homogeneity of results within each analysis, we calculated I^2 , which describes the percentage of variation (0–100%) across studies that is due to heterogeneity (Higgins et al. 2003).

We conducted a series of analyses. We first calculated effect sizes for entire data sets. To account for the fact that selection pressures may differ for wild animals as compared with domesticated animals or animals bred in captivity, we then subdivided the data sets into studies of captive or domestic animals versus wild animals. This grouping was based on the evolutionary origin of subjects and the environment in which fitness was tested. Studies were considered to be of wild animals when either:

- Subjects were born and reared from wild stock in the wild or
- Subjects were descended from wild stock, with no evidence of selective breeding, and fitness was assayed either in the wild or in seminatural environments in regard to the species in question.

When possible we also subdivided studies into groups of single age-sex classes to quantify gender differences in overall selection trends. We used cluster analysis to sort significantly heterogeneous results into homogeneous subsets. Clusters that were logically or taxonomically interpretable at the 5% level of significance were reanalyzed. We adopted Cohen's (1988) measures of effect size to interpret all results.

RESULTS

Do bolder individuals exhibit increased reproductive success and survival as compared with shyer ones?

Bolder individuals exhibited higher reproductive success than shyer ones, and the effect was homogeneous when cluster

Table 2

Effect size (r), standard deviation of effect size (SD), Z-score, percent of variation due to heterogeneity between studies (I^2), total number of studies (K), total combined sample size (N), and the number of studies averaging null results required to make the observed effect nonsignificant, $P > 0.05$ (fail-safe no.)

Personality dimension	Fitness factor	Breakdown	R	SD	Z	I^2 (%)	K	N	Fail-safe no.		
Boldness	Reproductive success	All	0.10	0.16	2.85**	64.2**	10	866	28		
		Exclude cheetahs	0.07	0.11	1.99*	14.2	9	822	5		
		Females	0.08	0.14	2.37**	45.2	10	848	17		
		Males (captive)	0.37	0.22	2.43**	63.1	2	42	3		
		Captive/domestic	0.13	0.14	3.35***	56.9*	8	668	24		
		Exclude cheetahs	0.10	0.06	2.39**	0	7	624	3		
	Females	0.11	0.11	2.81**	17.3	8	650	14			
	Wild (females)	-0.01	0.17	-0.19	81.9*	2	198	-2			
	Survival	All	-0.11	0.34	-1.69*	85.5***	5	222	-1		
		Mixed-sex Juveniles (wild)	-0.36	0.13	-3.28***	46.8	2	81	7		
		Wild	-0.20	0.24	-2.85**	74.2**	4	198	10		
		Fish only	-0.31	0.12	-3.48***	0	2	125	7		
Exploration		Reproductive success	All	0.01	0.03	0.18	0	3	206	-3	
			Females	0.005	0.04	0.07	0	3	206	-3	
	Wild		0.01	0.03	0.07	0	2	167	-2		
	Females		-0.004	0.04	-0.06	0	2	167	-2		
	Survival		All	0.23	0.21	2.27*	59.7	3	100	5	
			Males	0.16	0.18	1.42	59.2	2	77	0	
		Wild	0.16	0.22	1.36	73.7	2	72	0		
		Aggression	Reproductive success	All	0.10	0.27	1.79*	53.5*	12	312	2
				Females	0.13	0.16	1.61	0	6	165	0
				Males	0.01	0.40	0.07	77.3***	7	151	-7
	Captive/domestic			0.10	0.32	0.91	80.4**	3	84	-1	
	Exclude domestic cat			-0.04	0.13	-0.34	10.7	2	68	-2	
Males	-0.003			0.59	-0.02	93.7***	2	39	-2		
Survival	Wild		0.10	0.25	1.54	40.7	9	228	-3		
	Females		0.13	0.18	1.55	2.4	5	140	-1		
	Males		0.01	0.31	0.09	61.7*	5	112	-5		
	All		0.10	0.20	1.08	37.6	4	123	-3		
	Female (wild)		0.15	0.28	1.12	77.5*	2	61	-2		
	Male		0.05	0.01	0.40	0	2	62	-2		
Wild	0.11	0.23	1.06	57.5	3	91	-2				

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

analysis removed a single study of captive cheetahs (Table 2). There was no effect of boldness on reproductive success for wild animals, but a small, positive effect was found for captive/domestic animals. A sex difference also emerged as the effect of boldness on reproductive success was higher in males than in females but significant for both.

Alternatively, bolder individuals had a shorter life span than shyer ones and this effect held when looking only at mixed-sex juveniles and wild animals (Table 2). Studies of wild fish in particular, which cluster analysis grouped into a separate, homogeneous group, highlighted a moderate, negative effect of boldness on survival.

Do more exploratory individuals exhibit increased reproductive success and survival as compared with less exploratory ones?

There was no relationship between exploration and reproductive success for any of the analyses conducted (Table 2). A small, positive effect of exploration on survival was found for the entire data set, but this was not significant for males or for wild animals.

Do more aggressive individuals exhibit increased reproductive success and survival as compared with less aggressive ones?

Aggression had a small, positive effect on reproductive success, but the effect was not homogeneous across the entire

data set (Table 2). Cluster analysis created homogeneous groups of captive/domestic and wild individuals by removing 1 study and reanalysis highlighted a small, nonsignificant effect of aggression on reproductive success in wild animals, but there was no effect in captive/domestic animals. There was also a larger positive effect of aggression on reproductive success for females than for males, but the effect was not significant for either sex.

Aggression had a small positive effect on survival for the entire data set and wild animals, and had a larger effect in females than in males, but the effect was not significant in any of the analyses (Table 2).

DISCUSSION

Until now, there has been no attempt to synthesize the literature to quantify overall selection trends of personality. Such studies use varying methods and terms to measure and identify personality traits and are, therefore, not conducive for pooling results. The framework proposed by Réale et al. (2007) for studying temperament and personality in an ecological manner provides an interpretation that can be used across a variety of studies to look for general trends. Meta-analysis is the most widely used and accepted technique to conduct collective analyses of disparate studies to identify general patterns (Glass 1976; Rosenthal 1991). We, therefore, conducted a series of meta-analyses of existing studies using the Réale et al. (2007) interpretive framework to estimate the

average effect of personality traits on fitness. Although most of our analyses consisted of fewer than 10 studies, it is not uncommon in other fields, such as biomedicine where such techniques are more routinely used, for meta-analyses to include fewer than 10 studies (SanGiovanni et al. [2000]: $K = 4$; McNamara et al. [2001]: $K = 5$; Van Niel et al. [2002]: $K = 9$; Mehta et al. [2005]: $K = 7$; Gatta et al. [2007]: $K = 5$; Michalski et al. [2007]: $K = 3$). We hope that our synthesis highlights the need for additional studies to further understand this phenomenon and provides direction for future research.

One shortcoming of meta-analysis techniques is that they are limited by the assumptions of the included primary studies. As most of the studies we found assumed that there were linear relationships between personality traits and fitness (only 3 studies explored nonlinear relationships—Réale and Festa-Bianchet [2003]; Dingemanse et al. [2004]; Both et al. [2005]), we were only able to test for directional selection. Our analyses also focused solely on studies of unmanipulated behavioral variation in animals. We, therefore, excluded studies in which personality dimensions were altered artificially (Godin and Dugatkin 1996), hormonally (Foerster and Kempenaers 2004), or through selective breeding (Malmkvist et al. 1997). Our initial goal was to focus solely on studies of wild animals. Given the limited number of published studies quantifying the effect of boldness, exploration, or aggression on fitness in wild animals (19), we also included studies of captive/domestic animals in our analyses to increase sample size. We did, however, make the a priori decision to subdivide our data sets into studies of captive/domestic versus wild animals to account for varying selection pressures.

Our results suggest that the evolutionary mechanisms maintaining variation in boldness within populations may follow the trade-off hypothesis (Sih, Bell, Johnson, Ziemba 2004) in that individual fitness varies depending on the context of the situation. The general trend is that bolder individuals have greater reproductive success than shyer ones, particularly in males, but have shorter life spans. This last result is especially pronounced in wild fish, in which the tendency to inspect predators has often been used as an indicator of boldness (Godin and Dugatkin 1996; Dugatkin and Alfieri 2003). Thus, shy individuals may have reduced short-term reproductive success but live longer and, therefore, have the same overall fitness as bold individuals. Such a pattern is consistent with recent models proposed by Stamps (2007) and Wolf et al. (2007) explaining the evolution and maintenance of animal personalities. Additional morphological and environmental data are needed, however, to determine whether these general trends found across species are due to individual differences in growth rates (Stamps 2007), fluctuating resource availability affecting reproductive opportunities (Wolf et al. 2007), or a combination of both. Although we found no effect of boldness on reproductive success in wild animals, this may be explained by the fact that the 2 studies on wild animals were of females, which exhibited a smaller overall effect of boldness on reproduction than in males. Additional studies of wild animals, particularly males, therefore, need to be conducted to test the trade-off hypothesis and to examine whether there is differential selection on boldness in males and females.

The relationship between fitness and both exploration and aggression appear to be different. Exploration had no effect on reproductive success but had a small, positive effect on survival for all of the identified published studies. Aggression, however, had a small positive effect on both reproductive success and, nonsignificantly, on survival, with this relationship more prominent in females than in males. Such relationships would suggest directional selection with populations becom-

ing more explorative and aggressive. The lack of an effect between aggression and fitness in males may also indicate that selection is acting to stabilize the trait in this sex. It may be necessary, however, to account for the mating strategy for each species when explaining sex differences of personality traits on fitness. Sexual selection theory predicts that aggression should evolve through competition for mates and, therefore, one might expect aggression in males to have a stronger effect on fitness (Trivers 1972; Budaev 1999). Higher levels of female aggression, however, have been found in species in which females initiate courtship (Cole et al. 1980; Budaev et al. 1999). Thus, differences in mating behavior may play a role in shaping variation within the sexes. Variation may also be due to changing environmental conditions caused by temporal (Dingemanse et al. 2004), spatial (Wilson 1998), or frequency (Dall et al. 2004) fluctuations. Unfortunately, testing for such relationships is outside the scope of our analyses. Only 2 studies (Réale and Festa-Bianchet 2003; Dingemanse et al. 2004) tested fitness in populations across multiple years under varying environmental conditions, which precluded us from including yearly variation in our analyses. It is, therefore, imperative that long-term field studies are conducted that allow for nonlinear relationships in analyses to identify the type of selection (directional or stabilizing) acting on various personality traits within each sex.

Furthermore, to truly understand the ecological and evolutionary implications, as well as the function that variation in personality serves, future studies should focus on the fitness effects of multiple personality dimensions within populations and across species. We initially sought to explore this question in our analyses but we only found 1 study (Sih and Watters 2005), which examined the effect of a syndrome on fitness. Species often exhibit correlated suites of behaviors (Bell and Stamps 2004; Johnson and Sih 2005) and fitness effects on one trait could be due to selection on other, correlated traits. Only 4 studies (Sarno and Franklin 1999; Réale et al. 2000; Réale and Festa-Bianchet 2003; Both et al. 2005) controlled for life-history, morphological, or other personality traits when they measured the relationship between a particular personality trait and fitness. Thus, heterogeneous results in our analyses may be due to countering selection on correlated traits in some species. Even with such limitations to our synthesis, results do suggest that some general relationships exist between personality and fitness across species, and we hope this finding will spur further research to better understand the evolutionary mechanisms maintaining personality differences. To increase the consistency of future personality studies and allow more in-depth and powerful meta-analyses to be conducted, we suggest a framework in which both morphological measurements (e.g., body size, growth rate) and personality traits measured over multiple contexts (e.g., foraging, courtship/mating, antipredator [Johnson and Sih 2007]) are included in analyses to directly estimate the relationship between a specific personality trait and fitness, while controlling for potentially correlated traits. Direct fitness for species with short generation times should be quantified using measurements of lifetime reproductive success and total life span, whereas the fitness of species with long generation times should be quantified seasonally over multiple years, thus allowing for varying environmental conditions. Finally, if effect sizes are not given in analyses, we ask that editors require authors to report exact P values and sample sizes to increase the ability of future researchers to more accurately estimate effect size for use in subsequent meta-analyses.

Our results, particularly those between boldness and fitness, could have significant implications for captive breeding and recovery programs of endangered species. Data suggest that bold individuals in captivity have higher reproductive success,

but the relationship to survival is unclear because of lack of studies. Extended captivity may change selection pressures such that bolder individuals do not have reduced survival, which is the pattern found in studies with wild animals. Such a scenario may reduce variation in personality traits and select for traits that are maladaptive when animals are released back into the wild (McDougall et al. 2005). A study by McPhee (2003), indeed, found that oldfield mice, *Peromyscus polionotus subgriseus*, are less likely to seek refuge following exposure to a model predator the more generations they have been kept in captivity. There has, thus, been increasing interest in the idea of training animals to fear predators prior to release (Griffin et al. 2000) or to selectively release particular behavioral phenotypes (Bremner-Harrison et al. 2004) to counter these unintended consequences of captivity. Our results, however, suggest that releasing only shy animals, or training animals to be relatively shy in the presence of predators, may lead to a modest increase in survival but could have a negative impact on long-term reproductive success. Further research examining the relationship between personality and fitness, in both captive and wild animals, is therefore needed, as well as studies examining the flexibility of personality dimensions and behavioral syndromes to determine whether altering behavior in one context changes related behaviors in other contexts.

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REFERENCES

- Armitage KB. 1986. Individuality, social behavior, and reproductive success in yellow-bellied marmots. *Ecology*. 67:1186–1193.
- Armitage KB, Van Vuren DH. 2003. Individual differences and reproductive success in yellow-bellied marmots. *Ethol Ecol Evol*. 15: 207–233.
- Arnqvist G, Henriksson S. 1997. Sexual cannibalism in the fishing spider and a model for the evolution of sexual cannibalism based on genetic constraints. *Evol Ecol*. 11:255–273.
- Banks PB, Norrdahl K, Korpimäki E. 2002. Mobility decisions and the predation risks of reintroduction. *Biol Conserv*. 103:133–138.
- Bell AM. 2007. Future directions in behavioural syndromes research. *Proc R Soc Lond B Biol Sci*. 274:755–761.
- Bell AM, Stamps JA. 2004. Development of behavioural differences between individuals and populations of sticklebacks, *Gasterosteus aculeatus*. *Anim Behav*. 68:1339–1348.
- Blanckenhorn WU. 1991a. Fitness consequences of food-based territoriality in water striders, *Gerris remigis*. *Anim Behav*. 42:147–149.
- Blanckenhorn WU. 1991b. Fitness consequences of foraging success in water striders (*Gerris remigis*; Heteroptera: Gerridae). *Behav Ecol*. 2:46–55.
- Both C, Dingemanse NJ, Drent PJ, Tinbergen JM. 2005. Pairs of extreme avian personalities have highest reproductive success. *J Anim Ecol*. 74:667–674.
- Bremner-Harrison S, Prodohl PA, Elwood RW. 2004. Behavioural trait assessment as a release criterion: boldness predicts early death in a reintroduction programme of captive-bred swift fox (*Vulpes velox*). *Anim Conserv*. 7:313–320.
- Budaev SV. 1999. Sex differences in the Big Five personality factors: testing an evolutionary hypothesis. *Pers Individ Dif*. 26:801–813.
- Budaev SV, Zworykin DD, Moček AD. 1999. Individual differences in parental care and behaviour profile in the convict cichlid: a correlation study. *Anim Behav*. 58:195–202.
- Capitanio JP. 1999. Personality dimensions in adult rhesus macaques: prediction of behaviors across time and situation. *Am J Primatol*. 47:299–320.
- Carlstead K, Mellen J, Kleiman DG. 1999. Black rhinoceros (*Diceros bicornis*) in U.S. zoos: I. Individual behavior profiles and their relationship to breeding success. *Zoo Biol*. 18:17–34.
- Cavigelli SA, McClintock MK. 2003. Fear of novelty in infant rats predicts adult corticosterone dynamics and an early death. *Proc Natl Acad Sci USA*. 100:16131–16136.
- Chism J, Rogers W. 1997. Male competition, mating success and female choice in a seasonally breeding primate (*Erythrocebus patas*). *Ethology*. 103:109–126.
- Cohen J. 1988. *Statistical power analysis for the behavioral sciences*. 2nd ed. Hillsdale (NJ): Lawrence Erlbaum Associates.
- Cole HW, Figler MH, Parente FJ, Peeke HVS. 1980. The relationship between sex and aggression in convict cichlids (*Cichlasoma nigrofasciatum* Günther). *Behaviour*. 75:1–21.
- Dall SRX, Houston AI, McNamara JM. 2004. The behavioural ecology of personality: consistent individual differences from an adaptive perspective. *Ecol Lett*. 7:734–739.
- Dewsbury DA. 1984. Aggression, copulation, and differential reproduction of deer mice (*Peromyscus maniculatus*) in a semi-natural enclosure. *Behaviour*. 91:1–23.
- Dingemanse NJ, Both C, Drent PJ, Tinbergen JM. 2004. Fitness consequences of avian personalities in a fluctuating environment. *Proc R Soc Lond B Biol Sci*. 271:847–852.
- Dingemanse NJ, Réale D. 2005. Natural selection and animal personality. *Behaviour*. 142:1159–1184.
- Dugatkin LA. 1992. Tendency to inspect predators predicts mortality risk in the guppy (*Poecilia reticulata*). *Behav Ecol*. 3:124–127.
- Dugatkin LA, Alfieri MS. 2003. Boldness, behavioral inhibition and learning. *Ethol Ecol Evol*. 15:43–49.
- Foerster K, Kempenaers B. 2004. Experimentally elevated plasma levels of testosterone do not increase male reproductive success in blue tits. *Behav Ecol Sociobiol*. 56:482–490.
- Gatta L, Vaira D, Sorrenti G, Zucchini S, Sama C, Vakil N. 2007. Meta-analysis: the efficacy of proton pump inhibitors for laryngeal symptoms attributed to gastro-oesophageal reflux disease. *Aliment Pharmacol Ther*. 25:385–392.
- Glass GV. 1976. Primary, secondary, and meta-analysis of research. *Educ Res*. 5:3–8.
- Godin J-GJ, Davis SA. 1995. Who dares, benefits: predator approach behaviour in the guppy (*Poecilia reticulata*) deters predator pursuit. *Proc R Soc Lond B Biol Sci*. 259:193–200.
- Godin J-GJ, Dugatkin LA. 1996. Female mating preference for bold males in the guppy, *Poecilia reticulata*. *Proc Natl Acad Sci USA*. 93:10262–10267.
- Gosling SD. 1998. Personality dimensions in spotted hyenas (*Crocuta crocuta*). *J Comp Psychol*. 112:107–118.
- Gosling SD. 2001. From mice to men: what can we learn about personality from animal research? *Psychol Bull*. 127:45–86.
- Griffin AS, Blumstein DT, Evans CS. 2000. Training captive-bred or translocated animals to avoid predators. *Conserv Biol*. 14:1317–1326.
- Gross MR. 1996. Alternative reproductive strategies and tactics: diversity within sexes. *Trends Ecol Evol*. 11:92–98.
- Hemsworth PH, Pedersen V, Cox M, Cronin GM, Coleman GJ. 1999. A note on the relationship between the behavioural response of lactating sows to humans and the survival of their piglets. *Appl Anim Behav Sci*. 65:43–52.
- Higgins JPT, Thompson SG, Deeks JJ, Altman DG. 2003. Measuring inconsistency in meta-analysis. *Br Med J*. 327:557–560.
- Hunter JE, Schmidt FL. 1990. *Methods of meta-analysis: correcting error and bias in research findings*. Newbury Park (CA): Sage Publications.
- Huntingford F, Adams C. 2005. Behavioural syndromes in farmed fish: implications for production and welfare. *Behaviour*. 142:1207–1221.
- Janczak AM, Pedersen LJ, Rydmer L, Bakken M. 2003. Relation between early fear- and anxiety-related behaviour and maternal ability in sows. *Appl Anim Behav Sci*. 82:121–135.
- Johnson JC, Sih A. 2005. Precopulatory sexual cannibalism in fishing spiders (*Dolomedes triton*): a role for behavioral syndromes. *Behav Ecol Sociobiol*. 58:390–396.
- Johnson JC, Sih A. 2007. Fear, food, sex and parental care: a syndrome of boldness in the fishing spider, *Dolomedes triton*. *Anim Behav*. 74:1131–1138.

- Korhonen HT, Jauhiainen L, Rekilä T. 2002. Effect of temperament and behavioural reactions to the presence of a human during the pre-mating period on reproductive performance in farmed mink (*Mustela vison*). *Can J Anim Sci.* 82:275–282.
- Korhonen H, Niemelä P. 1996. Temperament and reproductive success in farmbred silver foxes housed with and without platforms. *J Anim Breed Genet.* 113:209–218.
- Korhonen H, Niemelä P, Siirilä P. 2001. Temperament and reproductive performance in farmed sable. *Agric Food Sci Finland.* 10: 91–98.
- Lenington S, Drickamer LC, Robinson AS, Erhart M. 1996. Genetic basis for male aggression and survivorship in wild house mice (*Mus domesticus*). *Aggress Behav.* 22:135–145.
- Malmkvist J, Houbak B, Hansen SW. 1997. Mating time and litter size in farm mink selected for confident or timid behaviour. *Anim Sci.* 65:521–525.
- McDougall PT, Réale D, Sol D, Reader SM. 2005. Wildlife conservation and animal temperament: causes and consequences of evolutionary change for captive, reintroduced, and wild populations. *Anim Conserv.* 9:39–48.
- McNamara B, Ray JL, Arthurs OJ, Boniface S. 2001. Transcranial magnetic stimulation for depression and other psychiatric disorders. *Psychol Med.* 31:1141–1146.
- McPhee ME. 2003. Generations in captivity increases behavioral variance: considerations for captive breeding and reintroduction programs. *Biol Conserv.* 115:71–77.
- McPhee MV, Quinn TP. 1998. Factors affecting the duration of nest defense and reproductive lifespan of female sockeye salmon, *Oncorhynchus nerka*. *Environ Biol Fish.* 51:369–375.
- Mehta SR, Cannon CP, Fox KAA, Wallentin L, Boden WE, Spacek R, Widimsky P, McCullough PA, Hunt D, Braunwald E, et al. 2005. Routine vs selective invasive strategies in patients with acute coronary syndromes: a collaborative meta-analysis of randomized trials. *J Am Med Assoc.* 293:2908–2917.
- Michalski CW, Kleff J, Wente MN, Diener MK, Büchler MW, Friess H. 2007. Systematic review and meta-analysis of standard and extended lymphadenectomy in pancreaticoduodenectomy for pancreatic cancer. *Br J Surg.* 94:265–273.
- Murphy PM, Purvis IW, Lindsay DR, Le Neindre P, Orgeur P, Poindron P. 1994. Measures of temperament are highly repeatable in Merino sheep and some are related to maternal behaviour. *Proc Aust Soc Anim Prod.* 20:247–250.
- Natoli E, Say L, Cafazzo S, Bonanni R, Schmid M, Pontier D. 2005. Bold attitude make urban feral domestic cats more vulnerable to feline immunodeficiency virus. *Neurosci Biobehav Rev.* 29: 151–157.
- Réale D, Festa-Bianchet M. 2003. Predator-induced natural selection on temperament in bighorn ewes. *Anim Behav.* 65:463–470.
- Réale D, Gallant BY, Leblanc M, Festa-Bianchet M. 2000. Consistency of temperament in bighorn ewes and correlates with behaviour and life history. *Anim Behav.* 60:589–597.
- Réale D, Reader SM, Sol D, McDougall PT, Dingemanse NJ. 2007. Integrating animal temperament within ecology and evolution. *Biol Rev.* 82:291–318.
- Rosenthal R. 1991. Meta-analytic procedures for social research. Rev. editor. Newbury Park (CA): Sage Publications.
- SanGiovanni JP, Parra-Cabrera S, Colditz GA, Berkey CS, Dwyer JT. 2000. Meta-analysis of dietary essential fatty acids and long-chain polyunsaturated fatty acids as they relate to visual resolution acuity in healthy preterm infants. *Pediatrics.* 105:1292–1298.
- Sarno RJ, Franklin WL. 1999. Maternal expenditure in the polygynous and monomorphic guanaco: suckling behavior, reproductive effort, yearly variation, and influence on juvenile survival. *Behav Ecol.* 10:41–47.
- Schum JL, Jorgensen RS, Verhaeghen P, Sauro M, Thibodeau R. 2003. Trait anger, anger expression, and ambulatory blood pressure: a meta-analytic review. *J Behav Med.* 26:395–415.
- Shackleton MA, Jennions MD, Hunt J. 2005. Fighting success and attractiveness as predictors of male mating success in the black field cricket, *Teleogryllus commodus*: the effectiveness of no-choice tests. *Behav Ecol Sociobiol.* 58:1–8.
- Sih A, Bell A, Johnson JC. 2004. Behavioral syndromes: an ecological and evolutionary overview. *Trends Ecol Evol.* 19:372–378.
- Sih A, Bell AM, Johnson JC, Ziemba RE. 2004. Behavioral syndromes: an integrative overview. *Q Rev Biol.* 79:241–277.
- Sih A, Watters JV. 2005. The mix matters: behavioural types and group dynamics in water striders. *Behaviour.* 142:1417–1431.
- Spritzer MD, Meikle DB, Solomon NG. 2005. Female choice based on male spatial ability and aggressiveness among meadow voles. *Anim Behav.* 69:1121–1130.
- Stamps JA. 2007. Growth-mortality tradeoffs and 'personality traits' in animals. *Ecol Lett.* 10:355–363.
- Trivers RL. 1972. Parental investment and sexual selection. In: Campbell BG, editor. *Sexual selection and the descent of man*. Chicago (IL): Aldine Press. p. 136–179.
- Van Niel CW, Feudtner C, Garrison MM, Christakis DA. 2002. *Lactobacillus* therapy for acute infectious diarrhea in children: a meta-analysis. *Pediatrics.* 109:678–684.
- Widemo F. 1998. Alternative reproductive strategies in the ruff, *Philomachus pugnax*: a mixed ESS? *Anim Behav.* 56:329–336.
- Wielebnowski NC. 1999. Behavioral differences as predictors of breeding status in captive cheetahs. *Zoo Biol.* 18:335–349.
- Wilson DS. 1998. Adaptive individual differences within single populations. *Philos Trans R Soc Lond B Biol Sci.* 353:199–205.
- Wilson DS, Clark AB, Coleman K, Dearstyne T. 1994. Shyness and boldness in humans and other animals. *Trends Ecol Evol.* 9:442–446.
- Wilson DS, Coleman K, Clark AB, Biederman L. 1993. Shy-bold continuum in pumpkinseed sunfish (*Lepomis gibbosus*): an ecological study of a psychological trait. *J Comp Psychol.* 107:250–260.
- Wolf M, van Doorn GS, Leimar O, Weissing FJ. 2007. Life-history trade-offs favour the evolution of animal personalities. *Nature.* 447:581–584.