ELSEVIER

Evolution and Human Behavior 30 (2009) 190–200

Evolution and Human Behavior

Human prosociality from an evolutionary perspective: variation and correlations at a city-wide scale☆

David Sloan Wilson[a,b,*], Daniel Tumminelli O'Brien[a], Artura Sesma[c]

[a]Department of Biology, Binghamton University (State University of New York), Binghamton, NY 13902-6000, USA
[b]Department of Anthropology, Binghamton University (State University of New York), Binghamton, NY 13902-6000, USA
[c]Search Institute, Minneapolis, MN 55413, USA

Initial receipt 23 June 2008; final revision received 27 December 2008

Abstract

Prosociality is a fundamental theme in all branches of the human behavioral sciences. Evolutionary theory sets an even broader stage by examining prosociality in all species, including the distinctive human capacity to cooperate in large groups of unrelated individuals. We use evolutionary theory to investigate human prosociality at the scale of a small city (Binghamton, NY), based on survey data and a direct measure of prosocial behavior. In a survey of public school students (Grades 6–12), individual prosociality correlates strongly with social support, which is a basic requirement for prosociality to succeed as a behavioral strategy in Darwinian terms. The most prosocial individuals receive social support from multiple sources (e.g., family, school, neighborhood, religion and extracurricular activities). Neighborhood social support is significant as a group-level variable in addition to an individual-level variable. The median income of a neighborhood does not directly influence individual prosociality, but only indirectly through forms of social support. Variation in neighborhood quality, as measured by the survey, corresponds to the likelihood that a stamped addressed letter dropped on the sidewalk of a given neighborhood will be mailed. We discuss the results in relation to evolutionary theory, the experimental economics literature and the social capital literature in an effort to integrate the study of human prosociality across disciplines.

Keywords: Altruism; Community-based research; Evolutionary theory; Experimental economics; Prosociality; Selfishness; Social capital

The two faces of human social behavior — selfishness and altruism — have long presented the human behavioral sciences with a paradox. Daily life is replete with examples of selfishness, from students who insist that the dog ate their homework to CEOs who plunder entire companies for their own gain. Yet, people also perform acts of kindness, from lending cups of sugar to dying for their country. Is altruism just a disguised or enlightened form of selfishness, or does it require a separate explanation?

This question has been asked in all branches of the human behavioral sciences (e.g., social psychology, sociology, political science, economics, anthropology). Evolutionary theory broadens the scope by examining the evolution of altruism and selfishness in *all* species (Sober & Wilson, 1998). When these terms are defined at the behavioral level, then selfishness is *locally advantageous*; almost by definition, selfish individuals survive and reproduce better than the altruists with whom they interact. However, altruism can still succeed as a behavioral strategy to the degree that altruists confine their interactions to each other and avoid interacting with selfish individuals. In this case, a population structure develops in which groups composed primarily of altruists contribute more to the total gene pool than groups composed primarily of selfish individuals. The groups need not have discrete boundaries and the segregation need not be complete, but only sufficient for the collective advantages of altruism to outweigh its vulnerability to exploitation from within.

All evolutionary theories of social behavior reflect this basic dynamic, including the coefficient of relatedness in inclusive fitness theory, the phenotypic matching that occurs when conditional strategies such as tit-for-tat adopt the behavior of their partner in game theory models, and the

☆ Funded in part by a grant from the Institute for Research on Unlimited Love.

* Corresponding author. Department of Biology, Binghamton University (State University of New York), Binghamton, NY 13902-6000, USA.
E-mail address: dwilson@binghamton.edu (D.S. Wilson).

1090-5138/$ – see front matter © 2009 Elsevier Inc. All rights reserved.
doi:10.1016/j.evolhumbehav.2008.12.002

within- vs. between-group components of multilevel selection theory (see Wilson & Wilson, 2007 for a recent review). Together, these theories provide a satisfying explanation for selfishness and altruism in nonhuman species, from microbes that overexploit their resources in a "tragedy of the commons" situation (e.g., Kerr, Neuhauser, Bohannan, & Dean, 2006) to insect colonies that truly qualify as "superorganisms" (e.g., Seeley, 1995; Wilson & Holldobler, 2009).

The same theoretical framework can be used to study human altruism and selfishness. It can even go beyond the study of human genetic evolution to include faster processes of human behavioral change. Game theorists refer to a "replicator dynamic" as any process whereby the most successful behavioral strategy increases in frequency through time, which can include such things as learning and imitation in addition to genetic evolution (Bowles, 2003; Gintis, 2000). Any replicator dynamic counts as an evolutionary process, vastly expanding the relevance of evolutionary theory to contemporary human affairs.

Even though evolutionary theory can be used to study altruism in humans and nonhumans alike, it is also clear that humans represent a very special case. Our hunter–gatherer ancestors cooperated far more within their groups than any other primate species (Bingham, 1999; Boehm, 1999). Cumulative cultural evolution has expanded the scale of human societies to many millions of genetically unrelated individuals. One key ingredient for this kind of ultrasociality appears to be low-cost social control (Boyd & Richerson, 1992). If selfishness can be quickly detected, communicated and punished without imposing too large a cost on the punishers (a form of second-order altruism), then selection for behaviors with collective benefits can dominate selection for within-group selfishness. Another key ingredient appears to be social transmission processes that create *behavioral* variation among groups without requiring *genetic* variation among groups (Richerson & Boyd, 2005). When this happens, genetic inheritance mechanisms are replaced by cultural inheritance mechanisms.

The field of experimental economics has been especially influential during the last decade in revealing human social preferences and how they interact to promote either altruism or selfishness at the behavioral level, depending upon the circumstances. In experimental games that include altruism and selfishness as behavioral options, most people are moderately altruistic but quickly "turn selfish" to protect themselves in the presence of other selfish individuals. When punishment is added as a behavioral option, some individuals will punish selfishness, even at their own expense. Punishment takes the altruism out of first-order altruism by making it disadvantageous to cheat, but punishment itself counts as a form of altruism (what economists call a second-order public goods problem) to the extent that it provides collective benefits at personal cost (Fehr & Fischbacher, 2003, 2005). Gossip, reputation, friendship, establishing norms by previous discussion, repeated interactions and manipulating elements of the physical environment all contribute to the suppression of selfishness within groups and promotion of behaviors that deliver collective benefits. Experimental economists are increasingly turning to evolutionary theory to explain how these particular social preferences arose by genetic and cultural evolution (e.g., Gintis, Bowles, Boyd, & Fehr, 2005; Hammerstein, 2003). Although most experimental economics games are performed in the laboratory, they are also starting to be performed in field situations (e.g., Carpenter & Cardenas, 2008; Carpenter, Harrison, & List, 2005), including an important worldwide comparison of small-scale traditional societies (Henrich et al., 2004). These field-oriented studies are comparable to field studies of nonhuman species in evolutionary biology, which are required to understand the relationship between organisms and their environment and provide the starting point for more controlled experiments.

The literature on social capital provides another rich source of information on human altruism and selfishness (e.g., Halpern, 2004; Putnam, 2000; Sampson, McAdam, MacIndoe, & Weffer-Elizondo, 2005). Social capital can be broadly defined as the benefits of investing in social relationships, similar to financial capital and human capital (investing in individual capacities such as education). An extensive literature shows that human welfare depends heavily on social capital and also that social capital varies widely among human social environments. This literature has the virtue of being primarily field based and therefore documenting human altruism and selfishness as it takes place in the real world. However, it has not yet been integrated with evolutionary theory or the recent experimental economics literature.

In this article, we describe a study of human altruism and selfishness in everyday American life at a city-wide scale. Our study resembles the social capital literature in documenting variation among the neighborhoods of a city, but our approach is guided by evolutionary theory, including the recent experimental economics literature. We think that much can be gained by integrating across disciplines to achieve a single coherent framework for basic and applied research on human altruism and selfishness.

We begin by describing individual differences in altruism and selfishness, as measured by a survey given to public school students in Grades 6–12. Then we show how altruism correlates with various aspects of the social environment, including family, neighborhood, school, religion and extracurricular activities. Finally, we validate and extend the survey results with a study that measures variation in altruism among neighborhoods at the behavioral level. We have performed a number of additional validations that will be reported in more detail elsewhere and will briefly be described here.

At this point, we would like to introduce a terminological change. We began with the terms "altruism" and "selfishness" because they have been influential in framing the debate within evolutionary theory. However, the term altruism has a strong connotation of self-sacrifice in addition

to helping others. While helping others *sometimes* requires extreme self-sacrifice, often it is possible to benefit others at a low cost to oneself or to benefit along with others in the provision of public goods (Sober & Wilson, 1998). As we have already seen, punishment and other forms of social control can turn "selfish" into "inadvisable" and "altruistic" into "prudent," although social control is itself a second-order public good. We prefer the term "prosocial" to "altruistic" because it focuses on other- and society-oriented behaviors while remaining agnostic about the degree of individual self-sacrifice that might be involved. Thus, an individual who routinely does favors for others or who agrees with the survey item "I am helping to make my community a better place" qualifies as prosocial, regardless of the degree of self-sacrifice involved.

1. Methods

1.1. The Binghamton Neighborhood Project

Binghamton is a small city (population approximately 50,000) in a region of New York that has been economically depressed over the last few decades. It is ethnically diverse, both from past immigrations from various parts of Europe and current immigrations from all over the world. Over 18 different primary languages are spoken by students in Binghamton's single high school. Binghamton's proximity to New York City introduces elements of the drug trade and other criminal activity, in addition to more positive influences such as an art scene. In short, Binghamton shares the same problems and potentials as many other cities, but its relatively small size makes it manageable as a "field site" for basic and applied research. The Binghamton Neighborhood Project (http://evolution.binghamton.edu/bnp/) was initiated in 2006 to create a general infrastructure for community-based research from an evolutionary perspective, in coordination with EvoS, Binghamton University's campus-wide evolutionary studies program (http://evolution.binghamton.edu/evos/).

1.2. The developmental assets profile

In collaboration with the Binghamton City School District, a survey was administered to 1942 public school students in Grades 6–12 in May 2006. Basic demographic information is provided in Table 1. The survey included a 58-item "Developmental Assets Profile (DAP)" developed by Search Institute, a nonprofit organization dedicated to the scientific study and improvement of communities (http://www.search-institute.org/). The DAP is widely used and highly regarded nationwide as an instrument that can help school districts and other community organizations measure and improve the quality of life for youth. Items on the DAP include questions about the individual (e.g., "I think it is important to help other people") and questions about their social environment (e.g., "I have good neighbors who help me succeed"), which make it a useful instrument for measuring prosociality and its environmental correlates.

Table 1
Demographic information for individual survey participants

Gender	
Male	983
Female	959
Ethnicity	
Caucasian	1348
Black	406
Hispanic	105
Asian	79
Pacific Islander	1
Native American	3

The DAP organizes the 58 items into subscales in two different ways, but we found it useful to create our own subscales for this analysis. Eight items are clearly related to other- and society-oriented behavior and were combined to form a prosociality subscale. Items relevant to social support were grouped into six subscales: *family*, *school*, *neighborhood*, *religion*, *extracurricular activities* and *general*. The *general* subscale included questions that did not reference a specific social context (i.e., "I am given useful roles and responsibilities."). The items on the *neighborhood* subscale are similar to items on scales measuring social capital and collective efficacy (e.g., Sampson, Raudenbush, & Earls, 1997). The items comprising each scale and the inter-correlation between these items (in the form of Cronbach's alphas) are reported in Table 2. Other DAP items found to be theoretically unrelated to these constructs were excluded from analysis.

Agreement on each item was indicated on a four-point Likert scale (1=Not at all or rarely, 2=Somewhat or sometimes, 3=Very or often, 4=Extremely or almost always). For each student, a score was calculated for each subscale by summing the score for each item and normalizing so that the lowest (all 1's) and highest (all 4's) possible scores were assigned values of 0 and 100, respectively. If a student did not answer one or more questions on a subscale, this was taken into account so that the score still spanned the 0–100 range. An individual's score for a given scale or subscale was not calculated if more than 15% of the questions were omitted. Before analysis, cases were removed if the student failed to answer fewer than 52 of the 58 questions or answered all questions identically or in a discernable pattern (e.g., 2-4-2-4-2-4, etc.). During analysis, 12 additional data points were removed as multivariate outliers (Mahalanobis distances: df=3, p<.001). The total remaining sample size of students was N=1840.

1.3. Background information and spatial analysis

Background information gathered in addition to the DAP included gender, age, parent's education (a reliable surrogate for socioeconomic status), ethnicity, religious affiliation, residential address and number of years lived at the current address. Student identity was protected in accordance with human subject review board guidelines by having school

Table 2
Scales and associated Cronbach's alpha scores

Prosociality	α=.807	n=8
"I think it is important to help other people."		
"I resolve conflicts without anyone getting hurt."		
"I tell the truth even when it is not easy."		
"I am helping to make my community a better place."		
"I am trying to help solve social problems."		
"I am developing respect for other people."		
"I am sensitive to the needs and feelings of others."		
"I am serving others in my community"		
Total social support	α=.903	n=27
Social support: family	α=.849	n=8
"I feel safe and secure at home"		
"I am included in family tasks and decisions"		
"I am spending quality time at home with my parents/guardians"		
"I have parents/guardians who help me succeed"		
"I have parents/guardians who urge me to do well in school"		
"I have a family that gives love and support"		
"I have parents/guardians who are good at talking with me about things"		
"I have a family that knows where I am and what I am doing"		
Social support: school	α=.787	n=5
"I feel safe at school"		
"I have a school that gives students clear rules"		
"I have a school that cares about kids and encourages them"		
"I have teachers who urge me to develop and achieve"		
"I have a school that enforces rules fairly"		
Social support: religion	α=.708	n=2
"I am involved in a religious group or activity"		
"How often do you attend religious services?"		
Social support: neighborhood	α=.724	n=3
"I have a safe neighborhood"		
"I have good neighbors who help me succeed"		
"I have neighbors who help watch out for me"		
Social support: extracurricular activities	α=.310	n=2
"I am involved in a sport"		
"I am involved in creative things such as music"		
Social support: general	α=.788	n=7
"I feel valued and appreciated by others"		
"I am encouraged to try things that might be good for me"		
"I am encouraged to help others"		
"I am given useful roles and responsibilities"		
"I have friends who set good examples for me"		
"I have adults who are good role models for me"		
"I have support from adults other than my parents/guardians"		

Questions are those from the DAP chosen to comprise each scale and the Cronbach's alpha describes the extent to which those items intercorrelate.

personnel replace the student names with arbitrary ID numbers and aggregating the data so that no individual could be traced to an individual address. Residential location enabled us to measure variation among neighborhoods and relate our survey to other spatially based information, such as US Census statistics. Spatial mapping was performed using ArcGIS v. 9.0. To visualize variation among neighborhoods, we employed the technique of kriging, which creates a continuous surface by calculating an extrapolated value for each location, based on the value of nearby data points. Kriging reveals the actual "hills" and "valleys" representing variation among neighborhoods, without regard to preestablished boundaries such as census block groups. However, it is also difficult to convert the topography revealed by kriging into discrete units for hierarchical statistical analysis. We therefore used census block groups as the group level in our multilevel statistical analysis. The division of Binghamton into 64 census block groups does not necessarily conform to the "hills" and "valleys" of a krig map, but the census block groups are sufficiently small, compared to the city as a whole, that much of the variation among actual neighborhoods will be reflected in variation among census block groups. Using census block groups has the additional advantage of allowing us to relate the survey data to other information based on census block groups, such as US census statistics. Hierarchical analysis was performed using HLM v. 6.02 (Raudenbush, 2004). All individual cases with missing data are excluded from analysis when using HLM, as are census block groups containing fewer data points than predictors in the model. The models below included 62 of the 64 census block groups and 1551 subjects.

1.4. Lost-letter study

To validate self-report information on neighborhood quality, we used the lost-letter method (Milgram, Mann, & Harter, 1965; Shotland, Berger, & Forsythe, 1970) to directly measure the likelihood that people walking through a given neighborhood are willing to perform a small act of kindness. On July 10, 2007, 22 Binghamton University students participating in a summer school course dropped 216 envelopes on the sidewalks at predetermined points throughout the city. The envelopes were stamped and addressed to "Job Search Committee, Department of Biological Sciences, Binghamton University." The return address included a fictitious name that could be either male or female (Terry Atwater) and a fictitious address coded to indicate the drop location. Each letter was given a code of "1" if was returned in the mail and a code of "0" if it was not returned. Each letter was also coded for the following predictor variables: (a) average prosociality score for the census block group that included the drop location (from the DAP); (b) average neighborhood quality score for the census block group that included the drop location (from the DAP); and (c) median income of the census block group that included the drop location (from US Census Statistics).

2. Results

2.1. DAP and background variables

Table 3 reports means and standard deviations in measures of prosociality and social support for males and females, with females scoring significantly higher in many of the categories. Across the age range, there is a tendency for older individuals to score lower on all scales. ANOVAs also demonstrate differences among ethnic groups; post hoc tests

Table 3
Scores (and standard deviations) on the prosociality and social support scales, by gender

	Male	Female	
Prosociality	58.87 (19.57)	63.77 (19.29)	$p<.001$
Social support (SS)	67.88 (16.53)	70.69 (16.53)	$p<.001$
SS Extracurricular Activities	64.66 (27.91)	68.23 (30.68)	$p<.01$
SS Family	79.22 (19.10)	80.21 (19.46)	n.s.
SS General	70.16 (19.23)	75.02 (18.47)	$p<.001$
SS Neighborhood	55.18 (28.71)	58.34 (28.92)	$p<.05$
SS Religion	41.84 (32.82)	46.49 (33.60)	$p<.01$
SS School	65.34 (23.30)	67.13 (23.40)	n.s.

The p-values reflect the results of a t-test between the genders. n.s. = not significant.

Table 4
Final result of two stepwise regressions using social support subscales to predict prosociality

Subscales in model	Standardized beta (semi-partial)[a]	Standardized beta (semi-partial)[b]
General	.522 (.376)***	–
Extracurricular activities	.146 (.133)***	.218 (.204)***
School	.119 (.094)***	.248 (.208)***
Neighborhood	.109 (.091)***	.174 (.145)***
Religion	.070 (.066)***	.115 (.109)***
Family	.015[c]	.258 (.211)***

Semi-partial correlation reflects the unique relationship between each subscale and prosociality.
[a] Total model was significant at $p<.001$ with $R=.758$.
[b] Total model was significant at $p<.001$ with $R=.691$.
[c] Not entered into model as $p>.05$.
*** $p<.001$.

show this to be primarily a result of low reports on all relevant scales by black subjects. These differences will be examined in more detail elsewhere. Here we concentrate on the relationship between prosociality and social support for the population as a whole.

To relate prosociality to social support, we first summed the social support subscales to create a total social support variable. There is a strong positive association between the self-reported prosociality of the student and the total social support reported by the student (Pearson $r=.723$, $R^2=.523$, $p<.001$; see Fig. 1). We then broke total social support into the six subscales in a stepwise multiple regression analysis with a threshold of $p=.05$, as shown in the second column of Table 4. Each of the subscales except *family* was entered successfully into the model and entering them separately accounts for 5% more variance ($R^2=.574$, $p<.001$) than when they are lumped into a total social support variable.

The exclusion of *family* appears to be an artifact of strong collinearity with the *general* subscale (see Table 5), as we can see by family's strength when *general* is removed in the model shown in the third column of Table 4. In fact, collinearity appears to play an important part in these models, being that most pair-wise comparisons of subscales feature strong correlations. In both models, though, no specific subscale fully mediates the effects of the others, and each accounts for its own small fraction of the variance, suggesting that *individual prosociality requires multiple sources of social support*. According to the second model, the subscales can be ranked in the order *family*, *school*, *extracurricular activities*, *neighborhood* and *religion*.

Mapping the residential locations of the students shows that self-reported prosociality is distributed highly nonran-

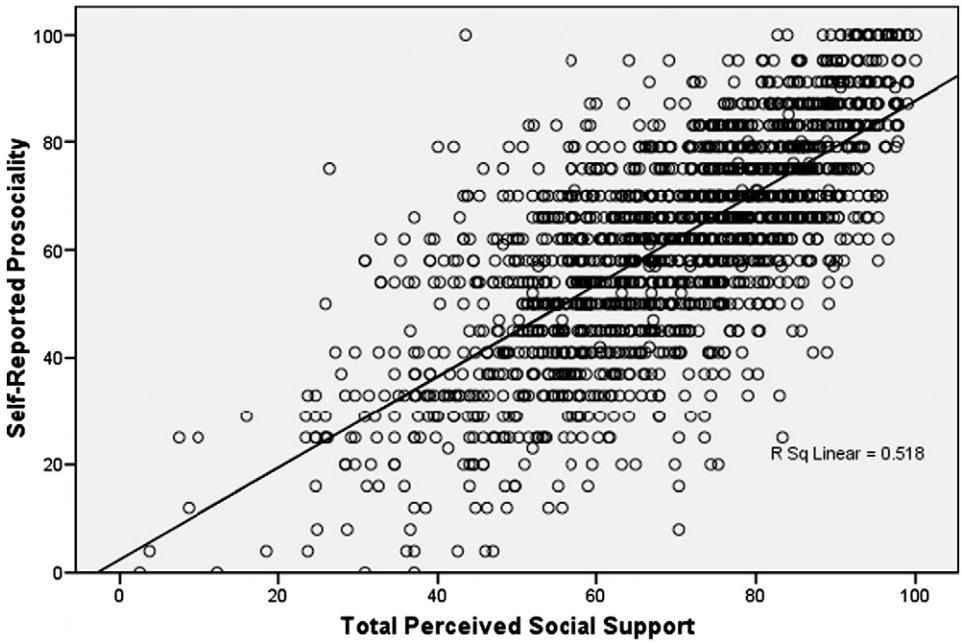

Fig. 1. Scatter plot of an individual's self-reported prosociality against perceived social support.

Table 5
Correlation matrix for social support subscales

	Family	Gender	School	Religion	Extracurricular activities	Neighborhood
Family	1	.690 (***)	.462 (***)	.188 (***)	.258 (***)	.468 (***)
General	.690 (***)	1	.589 (***)	.281 (***)	.385 (***)	.524 (***)
School	.462 (***)	.589 (***)	1	.180 (***)	.235 (***)	.443 (***)
Religion	.188 (***)	.281 (***)	.180 (***)	1	.249 (***)	.219 (***)
Extracurricular activities	.258 (***)	.385 (***)	.235 (***)	.249 (***)	1	.242 (***)
Neighborhood	.468 (***)	.524 (***)	.443 (***)	.219 (***)	.242 (***)	1

*** $p<.001$.

domly among the neighborhoods of the city (Fig. 2). The average prosociality score of students living in a given neighborhood can vary from a low in the mid-30s to a high in the mid-70s. Even though the 64 census block groups do not correspond exactly to the peaks and valleys of the krig map, much of the variation among neighborhoods is captured as variation among census block groups, making them suitable as a second level in a hierarchical regression analysis. Descriptive statistics on the primary neighborhood-level variables can be seen in Table 6.

For the hierarchical analysis, first-level variables included the six social support subscales. Second-level variables were *neighborhood quality* (the average value of the *neighborhood* subscale score for students living in each census block group) and *median income* (from the 2000 US Census Bureau statistics, log-transformed due to its nonnormal distribution). Two census block groups were omitted from the analysis because they contained fewer students than variables in the model. All first-level variables were grand-centered and included error terms. Cross-level interaction effects were included for the two second-level predictors and the *neighborhood* subscale. Such interactions were deemed inappropriate for the other first-level predictors (e.g., *school*), which are not descriptors of the neighborhood. As with the multiple regression analysis, the model was run both with and without the general subscale.

The hierarchical analysis mirrors the multiple regression analysis, explaining 58% of the variance ($\eta^2 = \frac{s_1^2 - s_2^2}{s_1^2}$; see Table 7 for values) and even repeating the same order of importance for the five subscales when the *general* subscale is removed (Compare the second and fourth columns of Table 7). Again, each subscale is significant when *general* is excluded, but all effect sizes are on the order of .2 or below, the majority showing what Cohen (1992) describes as effects too small to be apparent to the naked eye. These separate effects of small magnitude contribute to an overall effect of large magnitude. Of the two second-level variables, only *neighborhood quality* is associated with higher self-reported prosociality. In other words, the degree to which an individual reports being prosocial is influenced not only by the *individual's* assessment of neighborhood social support, but also by the *average assessment* of neighborhood social support by students in the same census block group. In the second model, the group-level effect of *neighborhood quality* was stronger than the individual-level effects of *neighborhood*, *extracurricular activities* and *religion*.

In addition, there is an interaction between the group-level variable *neighborhood quality* and the individual-level

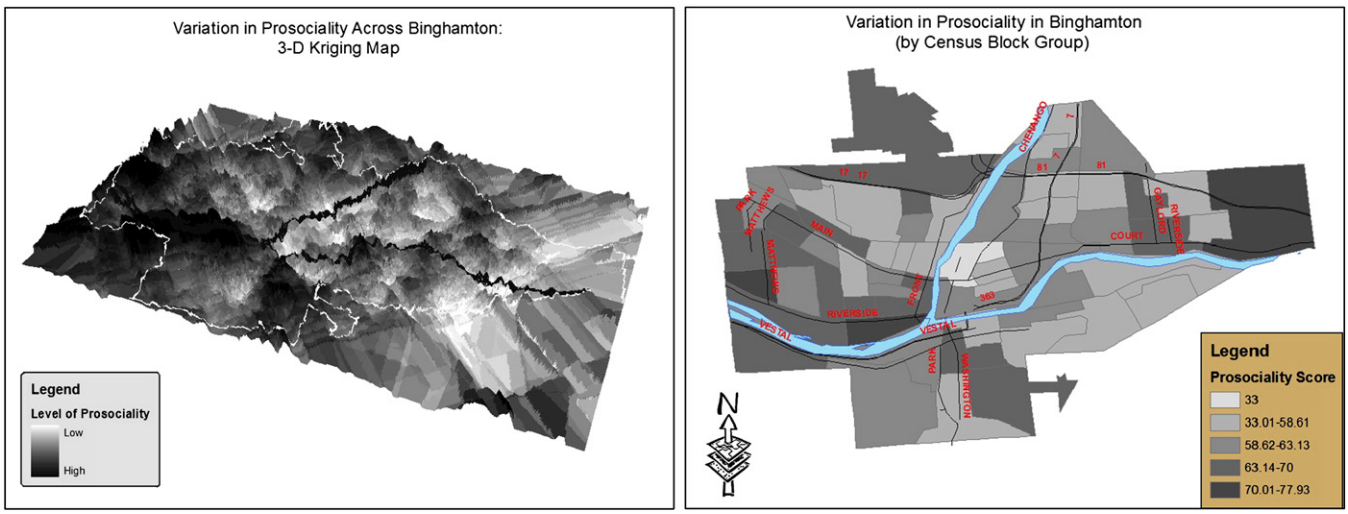

Fig. 2. Mapping Binghamton's prosociality with two different methods. On the left is a continuous map using kriging; on the right the city is split into discrete census block groups with scores. Both use the responses from the DAP.

Table 6
Descriptive statistics for prosociality, neighborhood social support and median income as measurements of the census block groups

	Mean (S.D.)	Range
Prosociality	61.12 (6.51)	33.00–77.93
Neighborhood social support	54.66 (11.23)	11.11–80.56
Median income	29,385 (16,465)	8430–90,143

variable *neighborhood*, suggesting that the social support of a neighborhood is itself a resource. The effect of this resource on an individual resident's prosociality is both a result of its own quality and the extent to which the person feels connected to the resource. For example, a person who feels very positively about a neighborhood that is generally rated as having a quality social support system reports a higher level of prosociality in comparison to one who feels just as highly about a neighborhood rated to have a lower quality social environment.

2.2. The lost-letter method

Of the 216 envelopes, 143 (66%) were returned. Three variables were considered as predictors of return rate: (1) log-transformed median income of the census block where the letter was dropped; (2) *neighborhood quality* of the census block where the letter was dropped (as defined above); and (3) the average *prosociality* score of students living in the census block where the letter was dropped. One logistic regression analysis used these three predictors as continuous variables. In a second analysis, the predictors were converted into dichotomous variables by assigning values of '0' and '1' to block groups below and above the median, respectively. This was done to accommodate threshold effects.

Table 8
Odds ratios (and 95% confidence intervals) for logistic regression models used to predict envelope return rates

	Model 1	Model 2*
Neighborhood social capital	1.017 (.967–1.069)	
Local prosociality	.977 (.917–1.041)	
Local median income	1.652 (.696–3.921)	
Underaverage social capital		.387 (.187–.802)*
Underaverage prosociality		.989 (.530–1.844)
Underaverage median income		1.065 (.531–2.135)
−2*log likelihood	266.514	261.982
Nagelkerke R^2	.033	.062

* $p<.05$. Significance of a model refers to the omnibus test of coefficients.

None of the variables are significantly associated with return rate in the first analysis. In the second model, return rate is strongly predicted by neighborhood quality but not the other two variables (Table 8). According to the second analysis, an envelope dropped in a below-average neighborhood is approximately 60% less likely to be mailed than in an above-average neighborhood.

3. Discussion

Prosociality is such an important theme in human life that it is considered by all branches of the basic and applied human behavioral sciences. One goal of our research was to create an empirical infrastructure for studying prosociality in the real world, at the scale of an entire city, that can be

Table 7
Results of multilevel model with prosociality as the dependent variable

	Model 1		Model 2	
	Parameter size (S.E.)[a]	Effect size[b]	Parameter size (S.E.)[a]	Effect size[b]
First-level predictors				
Family	.019 (.031)	.015	.265 (.031)***	.210
General	.518 (.028)***	.420	–	–
School	.103 (.023)***	.113	.206 (.026)***	.199
Religion	.037 (.011)***	.090	.060 (.012)***	.125
Extracurricular activities	.090 (.013)***	.179	.132 (.014)***	.231
Neighborhood	.065 (.015)***	.106	.114 (.017)***	.170
Second-level predictors				
Neighborhood social capital	.157 (.062)*	.064	.149 (.070)*	.054
Median income (log transformed)	−3.09 (2.690)	.029	−3.856 (3.057)	.032
Cross-level interactions on neighborhood				
Neighborhood social capital	.002 (.002)	.028	.006 (.002)*	.065
Median income (log transformed)	−.06 (.086)	.018	−.143 (.097)	.037
Parameters estimated	40		32	
Deviance	12,241		12,544	
Remaining variance[c]	148.841		179.194	

[a] All error terms included.

[b] Effect sizes calculated using $r = \sqrt{\frac{t^2}{(df + t^2)}}$.

[c] Variance of the intercept-only model was 355.618.

* $p<.05$.

*** $p<.001$.

examined from any theoretical perspective. Another goal is to integrate the perspectives on prosociality that have developed in separate fields, such as evolutionary biology, experimental economics and the social capital literature within sociology.

As our first step, we modified the subscales of a widely used instrument (especially among schools and other organizations that are actively trying to improve the quality of life for youth) to measure prosociality at the individual level and a number of possible environmental correlates. We showed that prosociality correlates strongly with social support. Moreover, prosociality appears to require social support from *multiple* sources. Each source explained a small fraction of the variation by itself and only collectively accounted for a large fraction of the variation. Evidently, it really does take a village to raise a highly prosocial child. Needless to say, these are correlations and additional studies are required to determine whether they signify causal relationships.

When self-reported prosociality is mapped spatially, there is substantial variation among neighborhoods. This variation does not necessarily reflect the importance of neighborhood quality per se, because students who score low on the other sources of support might be concentrated in certain neighborhoods, perhaps for economic reasons. However, the fact that neighborhood quality is significant as both a group- and an individual-level variable in the hierarchical analysis suggests a causal role for neighborhood quality. It is difficult to otherwise explain how self-reported prosociality can be influenced, not only by the student's assessment of neighborhood quality, but by the assessment of *other* students living in the same census block group.

The lost-letter method adds credence to the fact that the students are accurately reporting differences in the prosociality of their neighborhood social environments. In the same neighborhoods that score high with respect to the DAP item "I have neighbors who help watch out for me," pedestrians are more likely to perform a small act of kindness by picking up and mailing a dropped letter. In other studies that will be reported elsewhere, numerous lines of evidence confirm the reality of student-reported neighborhood quality in the city of Binghamton, including crime statistics, school delinquency notices, the evaluation of photographs of neighborhoods by nonresidents and even the degree to which the neighborhoods become decorated during Halloween and Christmas.

It is common to assume that prosociality is mostly a matter of economics. There is indeed a positive correlation between median income and neighborhood quality, but two results of our study indicate that median income matters only insofar as it contributes to neighborhood quality, with no other additional effect on prosociality. First, neighborhood quality but not income is retained as a group-level variable in our hierarchical regression analysis. Second, neighborhood quality but not median income is the significant predictor in our lost-letter study. In a study that will be reported elsewhere, median income has an independent *negative* effect on tendency to initiate cooperation, as measured by an experimental economics game. By this measure, the most prosocial students live in neighborhoods that are high in quality and low in median income — perhaps because, in the absence of financial capital, they need to rely more on social capital in their everyday lives.

These are our basic empirical results, which can be interpreted from any theoretical perspective. We will now attempt to relate the results to three separate fields in the hope of integrating them: evolutionary theory, experimental economics and social capital.

3.1. Evolutionary theory

The primary challenge for evolutionary theory is to explain how behaviors that benefit others or one's group as a whole can evolve, when these behaviors often involve a cost in time, energy and risk for the individual performing the behavior. This basic fact, which Wilson and Wilson (2007) termed "the fundamental problem of social life," makes prosociality locally disadvantageous or at best neutral, compared to free-riding or downright exploitation. The solution to the problem is that prosociality can be selectively advantageous at larger scales. *Groups* of prosocial individuals robustly outcompete less prosocial groups, even if they are vulnerable to free-riding and exploitation from within. Although the evolution of prosociality (usually conceptualized in terms of altruism) is often discussed in terms of genetic models involving discrete groups, the basic dynamic applies more widely, including groups with fuzzy boundaries that are not necessarily spatially based, the expression of behaviorally flexible behaviors (phenotypic plasticity) and traits that are transmitted culturally rather than genetically. Thus, evolutionary theory writ large is highly relevant to contemporary human social dynamics and not just the distant past of human genetic evolution.

In nonhuman species, genetic relatedness and reciprocity are thought to be the primary mechanisms that cause altruists to associate with each other and avoid interactions with nonaltruists. This happens automatically in interactions among genetic relatives, to the extent that altruism is genetically based. In the extreme case of interactions among identical twins, altruists always interact with other altruists and nonaltruists with other nonaltruists. There are no mixed pairs; therefore, no advantage for selfishness. In the case of reciprocity, flexible strategies such as tit-for-tat accomplish the same matching by acting altruistically toward partners who behave altruistically and selfishly toward partners who behave selfishly, eliminating mixed pairs at the behavioral level. Selfishness requires access to altruism to succeed as an evolutionary strategy, and it does not matter whether the access is denied automatically by virtue of genetic relatedness or behaviorally by virtue of flexible strategies such as tit-for-tat.

There is widespread agreement among evolutionists that human prosociality goes beyond genetic relatedness and narrow reciprocity. It is simply a fact of human life that

people cooperate in large groups of unrelated individuals (Wilson, 2006). The challenge for the evolutionist is to explain how such large-scale cooperation can succeed against the threat of subversion from within. Numerous possibilities have been suggested, including indirect reciprocity (Alexander, 1987), honest signaling (Cronk, 2005), low-cost social control (Boyd & Richerson, 1992; Sober & Wilson, 1998) and cultural transmission mechanisms that increase phenotypic variation among groups (Richerson & Boyd, 2005). Most of the discussions are theoretical or based on laboratory experiments. Against this background, our study fills a void by actually measuring the correlation between individual prosociality and the prosociality of the individual's social environment in the real world. At a very crude level, the correlation between prosociality and total social support (Pearson r in the range of 0.7) is comparable to the genetic coefficient of relatedness (r). Astonishingly, the chance of a highly prosocial student interacting with other highly prosocial individuals in the city of Binghamton is considerably higher than the chance of an altruist having an altruist for a full sibling in a simple genetic model! It is important to stress that this r value includes all forms of social support, including but not restricted to neighborhood support.

This empirical result explains why it is possible for prosociality to succeed as a behavioral strategy in contemporary human life. Very simply, those who give to others also get from others (see also Wilson & Csikszentmihalyi, 2007). Much more work will be required, however, to identify the specific mechanisms that cause this phenotypic matching to occur and to explain how variation in prosociality is maintained in the population. According to the simplest evolutionary models, selfishness is maintained by exploiting altruism, despite incomplete access. There are human behavioral strategies that are genuinely predatory in this way (Oakley, 2007; Wilson, Near, & Miller, 1996). However, another form of low prosociality occurs when individuals who are willing and able to cooperate "turn off" their prosociality in response to harsh social environments, similar to the tit-for-tat strategy defecting in response to selfishness (Wilson & Csikszentmihalyi, 2007). We look forward to investigating these more refined issues in future studies.

3.2. Experimental economics

The field of experimental economics attempts to identify human social preferences empirically, rather than rely upon the individual utility maximizing assumption of rational choice theory. It was motivated in part because rational choice theory failed to explain the human propensity to cooperate, even when individual incentives are removed in carefully controlled laboratory experiments. In many ways, this reflects a return to Adam Smith's (1759) *Theory of Moral Sentiments*, which also claimed that people have a fundamental concern for the welfare of others in addition to themselves.

Theoretically, experimental economics is already converging with evolutionary theory in two respects. First, human social preferences require a deep explanation in terms of genetic evolution, even if they are highly variable in their individual and cultural expression. Second, fast paced processes of behavioral change count as evolutionary to the extent that they cause the most successful behavioral strategies to increase in frequency over time. There is a generalized replicator dynamic that includes, but goes beyond, genetic evolution (Bowles, 2003; Gintis, 2000). A growing number of experimental economists have thoroughly incorporated both perspectives into their own thinking.

One of the greatest contributions of experimental economics is the development of experimental protocols ("games") that measure human preferences in a standardized fashion. These games can be used to measure differences between individuals, contexts and cultures at the behavioral level, providing a valuable complement to self-report surveys. Instead of merely *asking* someone about the importance of helping others, for example, an experimental game reveals whether they actually do help others in situations that involve real financial loss and gain.

Increasingly, experimental economics games are being taken outside the laboratory to study human social preferences in everyday life (e.g., Carpenter & Cardenas, 2008; Carpenter et al., 2005). In a widely cited study (Henrich et al., 2004), the ultimatum game was played in small-scale traditional societies around the world. These cultures were already known to be different from each other, but the ultimatum game enabled the differences to be measured with more precision than before and to relate the differences to theoretical models of human social dynamics.

The results reported here set the stage for an equivalent study of small-scale spatial variation. Are the differences between neighborhoods that we have documented reflected in how the residents play experimental economics games? If so, then how does variation among neighborhoods compare with worldwide variation? Can small-scale and large-scale variation be attributed to the same causes? In results that will be reported elsewhere, we have shown that the tendency to initiate cooperation in a sequential prisoner's dilemma game provides a sensitive indicator of neighborhood quality, not only for students who live in the neighborhoods (as described previously), but even for nonresidents who merely view photographs of the neighborhoods. In general, we look forward to using the empirical methods developed within the field of experimental economics to ask theoretical questions that are already shared by experimental economics and evolutionary theory.

3.3. Social capital

The term social capital refers to the benefits that can be obtained from social relationships, similar to financial capital, physical capital (e.g., a dwelling) and individual

capital (e.g., an education). It is worth quoting the first recorded use of the term, by Hanifan (1916), who was the state supervisor of rural schools in West Virginia:

> …those tangible substances [that] count for most in the daily lives of people: namely good will, fellowship, sympathy, and social intercourse among the individuals and families who make up a social unit.…The individual is helpless socially, if left to himself.…If he comes into contact with his neighbor, and they with other neighbors, there will be an accumulation of social capital, which may immediately satisfy his social needs and which may bear a social potentiality sufficient to the substantial improvement of living conditions in the whole community. The community as a whole will benefit by the cooperation of all its parts, while the individual will find in his associations the advantages of the help, the sympathy, and the fellowship of his neighbors (p. 130).

This original usage is synonymous with what we mean by prosociality, and it is interesting that Hanifan was motivated primarily by the practical desire to increase the quality of life for youth, similar to Search Institute and its Developmental Assets Profile.

Social capital became an important concept within the social sciences starting in the 1960s, based in part on Coleman's (1990) *Foundations of Social Theory* and Putnam's (2000) *Bowling Alone*. An especially influential research program is the Project on Human Development in Chicago Neighborhoods, or PHDCN (http://www.icpsr.umich.edu/PHDCN) headed by Robert J. Sampson and his colleagues, which provides a model for the kind of research program that we are trying to establish for the city of Binghamton. Unsurprisingly for such a large literature, the concept of social capital has become elaborated in a number of ways, including a distinction between bridging vs. bonding social capital (Putnam, 2000), and collective efficacy (Sampson, 2004).

In some respects, the research reported in this article follows in the footsteps of the social capital literature. For example, readers familiar with the PHDCN will not be surprised by the variation among neighborhoods that we have shown for the city of Binghamton. In other respects, however, the social capital literature reflects a lack of convergence with other disciplines that are centrally concerned with human prosociality, including evolutionary theory and experimental economics. For example, even while becoming sophisticated in other respects, the social capital literature has not attempted to identify a set of social preferences that underlie human social dynamics and requires a deep explanation in terms of genetic evolution. Although it richly documents changes in social capital over time (the main subject of *Bowling Alone*), it tends not to focus on the relative success of alternative behavioral strategies in game theoretical terms, nor does it emphasize the inherent local instability of prosociality that Wilson and Wilson (2007) term "the fundamental problem of social life."

A good example of how our approach differs from the social capital literature is the high correlation that we have demonstrated between prosociality at the level of the *individual* and the *individual's social environment*. For an evolutionist or (increasingly) an experimental economist, this is the first piece of information that we need to know, because a sufficiently high correlation is required for prosociality to succeed as a behavioral strategy. In the social capital literature, there are many demonstrations that high social capital increases the welfare of individuals, but almost no demonstrations that the benefits accrue mostly to individuals who are themselves prosocial, as a requirement for the long-term maintenance of prosociality in a Darwinian world of competition among alternative forms.

It is not our purpose to disparage the social capital literature, which is more firmly grounded in field studies and more sophisticated than the evolutionary and experimental economics literatures in many respects. Rather, we want to encourage the integration of fields that all have prosociality as their central focus. Everyone can gain by creating a unified theoretical perspective, sharing empirical methodologies and becoming aware of each other's literatures. This includes the integration of basic and applied research. It is common to imagine a negative tradeoff between the two, such that the most important contributions to basic knowledge only eventually result in practical applications. However, evolution is fundamentally about the relationship between organisms and their environments. It follows that basic scientific research on humans from an evolutionary perspective should be centered on people from all walks of life, as they go about their daily lives — similar to the detailed field studies that provide the foundation for evolutionary research on nonhuman species. With the exception of projects such as the PHDCN, field-oriented experimental economics research and our newly formed Binghamton Neighborhood Project, this kind of naturalistic approach is sorely lacking in the human behavioral sciences. The best way to study prosociality from an evolutionary perspective is in everyday life, where advances in knowledge can quickly be used to improve the quality of life, creating a positive trade-off between basic and applied research.

This article describes the theoretical foundation and initial results for a study that is designed to continue over the long-term, including administering the DAP at 3-year intervals to create a longitudinal database and controlled intervention programs designed to increase prosociality in targeted neighborhoods. Only by studying cultural evolution in action can we properly identify the causal mechanisms that create the correlations observed in this preliminary study.

Acknowledgments

The Binghamton Neighborhood Project reflects a unique "whole university/whole city approach" to community based research from an evolutionary perspective. EvoS, Binghamton University's campus-wide evolutionary studies program,

provides a network of over 60 faculty participants and 100 students representing all academic disciplines, who interact with a comparable network of partners reflecting all sectors of the city. For this study, we especially thank Peggy Wozniak, Doug Stento and Eben Bullock from the Binghamton City School District; Peter Benson from Search Institute; Matthew Johnson, Shelley Dionne and Donald Spangler for statistical advice; and Jeffrey Carpenter and Robert Sampson from among our academic colleagues.

References

Alexander, R. D. (1987). *The Biology of Moral Systems.* New York: Aldine de Gruyter.

Bingham, P. M. (1999). Human uniqueness: A general theory. *Quarterly Review of Biology, 74*, 133−169.

Boehm, C. (1999). *Hierarchy in the forest: Egalitarianism and the evolution of human altruism.* Cambridge, MA: Harvard University Press.

Bowles, S. (2003). *Microeconomics: Behavior, institutions, and evolution.* Princeton: Princeton University Press.

Boyd, R., & Richerson, P. J. (1992). Punishment allows the evolution of cooperation (or anything else) in sizable groups. *Ethology and Sociobiology, 13*, 171−195.

Carpenter, J. P., & Cardenas, J. -C. (2008). Behavioral development economics: Lessons from field labs in the developing world. *Journal of Development Studies, 44*, 337−364.

Carpenter, J. P., Harrison, G. W., & List, J. A. (Eds.). (2005). *Field Experiments in Economics.* Greenwich: JAI Press.

Cohen, J. (1992). A power primer. *Quantitative Methods in Psychology, 112*, 155−159.

Coleman, J. S. (1990). *Foundations of social theory.* Cambridge, MA: Harvard University Press.

Cronk, L. (2005). The application of animal signaling theory to human phenomena: Some thoughts and clarifications. *Social Science Information Sur Les Sciences Sociales, 44*, 603−620.

Fehr, E., & Fischbacher, U. (2003). The nature of human altruism. *Nature, 425*, 785−791.

Fehr, E., & Fischbacher, U. (2005). The economics of strong reciprocity. In H. Gintis, S. Bowles, R. Boyd, & E. Fehr (Eds.), *Moral Sentiments and Material Interests: The Foundations of Cooperation in Economic Life.* Cambridge, MA: MIT Press.

Gintis, H. (2000). *Game theory evolving.* Princeton, NJ: Princeton University Press.

Gintis, H., Bowles, S., Boyd, R., & Fehr, E. (Eds.). (2005). *Moral Sentiments and Material Interests.* Cambridge, MA: MIT Press.

Halpern, D. (2004). *Social capital.* New York: Polity.

Hammerstein, P. (Ed.). (2003). *Genetic and Cultural Evolution of Cooperation.* Cambridge, MA: MIT press.

Hanifan, L. J. (1916). The rural school community center. *Annals of the American Academy of Political and Social Science, 67*, 130−138.

Henrich, J., Boyd, R., Bowles, S., Camerer, C., Fehr, E., & Gintis, H. (2004). *Foundations of human sociality: Economic experiments and ethnographic evidence from fifteen small-scale societies.* Oxford, UK: Oxford University Press.

Kerr, B., Neuhauser, C., Bohannan, B. J. M., & Dean, A. M. (2006). Local migration promotes competitive restraint in a host-pathogen 'tragedy of the commons'. *Nature, 442*, 75−78.

Milgram, S., Mann, L., & Harter, S. (1965). The lost-letter technique: A tool of social research. *Public Opinion Quarterly, 29*, 437−438.

Oakley, B. (2007). *Evil genes: Why Rome fell, Hitler rose, Enron collapsed and my sister stole my mother's boyfriend.* New York: Prometheus.

Putnam, R. D. (2000). *Bowling Alone: The collapse and revival of American community.* New York: Simon and Schuster.

Raudenbush, S., Bryk, A., Cheong, Y. F., Congdon, R., & du Toit, M. (2004). *HLM 6: Heirarchical Linear & Nonlinear Modeling.* Lincolnwood, IL: Scientific Software International.

Richerson, P. J., & Boyd, R. (2005). *Not by genes alone: How culture transformed human evolution.* Chicago: University of Chicago Press.

Sampson, R. J. (2004). Neighborhood and community: Collective efficacy and community safety. *New Economy, 11*, 106−113.

Sampson, R. J., McAdam, D., MacIndoe, H., & Weffer-Elizondo, S. (2005). Civil society reconsidered: The durable nature and community structure of collective civic action. *American Journal of Sociology, 111*, 673−714.

Sampson, R. J., Raudenbush, S. W., & Earls, F. (1997). Neighborhoods and violent crime: A multilevel study of collective efficacy. *Science, 277*, 918−924.

Seeley, T. (1995). *The wisdom of the hive.* Cambridge, MA: Harvard University Press.

Shotland, R. L., Berger, W. G., & Forsythe, R. (1970). A validation of the lost-letter technique. *Public Opinion Quarterly, 34*, 278−281.

Smith, A. (1982 (1759)). *The theory of moral sentiments.* Indianapolis: Liberty Fund.

Sober, E., & Wilson, D. S. (1998). *Unto others: The evolution and psychology of unselfish behavior.* Cambridge, MA: Harvard University Press.

Wilson, D. S. (2006). Human groups as adaptive units: Toward a permanent consensus. In P. Carruthers, S. Laurence, & S. Stich (Eds.), *The Innate Mind: Culture and Cognition* (pp. 78−90). Oxford: Oxford University Press.

Wilson, D. S., & Csikszentmihalyi, M. (2007). Health and the ecology of altruism. In S. G. Post (Ed.), *The Science of Altruism and Health* (pp. 314−331). Oxford: Oxford University Press.

Wilson, D. S., Near, D., & Miller, R. R. (1996). Machiavellianism: A synthesis of the evolutionary and psychological literatures. *Psychological Bulletin, 199*, 285−299.

Wilson, D. S., & Wilson, E. O. (2007). Rethinking the theoretical foundation of sociobiology. *Quarterly Review of Biology, 82*, 327−348.

Wilson, E. O., & Holldobler, B. (2009). *The superorganism.* New York: W.W. Norton.