Perspectives

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A Kingpin of Academic Inclusive Fitness: The History and Contributions of Bruce Grant

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ONE of the most difficult decisions facing postdocs on the academic job market is where they should apply for jobs. They seek the advice of their supervisors, but their supervisors' world view is colored by their own decisions and experiences. Because most postdocs are at research universities, their supervisors typically overtly or subtly encourage them to apply to similar schools. The implication is that, for scientists to have an impact on their discipline, they must be able to recruit top Ph.D. students and postdocs, which cannot be done as effectively at smaller institutions such as liberal arts colleges. Accepting a job at a smaller institution is often called the "kiss of death" because new faculty members supposedly will be overwhelmed with teaching responsibilities, their research record will suffer, and a later move to a research university will be far more difficult.

We do not dispute that teaching responsibilities are often greater at smaller institutions or liberal arts colleges. Because our time is finite, this greater load will likely take a toll on research productivity. However, we use the example of our recently retired mentor, Professor Bruce S. Grant, to demonstrate that the impact of faculty at liberal arts colleges on a scientific discipline can nonetheless be immense when measured by a combination of their own research, their mentoring of future researchers, and their service to their field. Although we discuss all three elements, in this article we emphasize Grant's mentoring contributions. Our title derives from a nickname given to Grant by his former students: the "Kingpin." Grant's research career (and research students) can be roughly divided into three temporal "phases" by taxonomic group of study: Drosophila, wasps (primarily Nasonia), and the peppered moth *Biston betularia*.

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DROSOPHILA PHASE: THE EARLY YEARS

Grant grew up in Pennsylvania and New York as a devout fan of the New York Yankees. After high school, he spent some time in various jobs, including pressing shirts, cashiering, and performing custodial tasks. Although he was very proficient at these jobs, he soon decided to pursue higher education. He enrolled in his local college, Bloomsburg University of Pennsylvania. There, like many of us, he was positively influenced by some of his biology professors and decided that he wanted to pursue biology in general and population genetics in particular. His genetics professor, Donald Rabb, recommended that, given his interests, he would be well advised to apply for the Ph.D. program at North Carolina State University.

Grant pursued his Ph.D. under the tutelage of Lawrence Mettler, studying disruptive selection on escape behavior of *Drosophila melanogaster* in vertical I-mazes. Disruptive selection and its associated effects on mate discrimination were "the rage" at that time, following the provocative classic disruptive selection experiment of Thoday and Gibson (1962) and its implication of the plausibility of sympatric speciation. In that study, Thoday and Gibson (1962) simultaneously selected for high and low bristle number in a *D. melanogaster* laboratory population, and the resultant flies appeared to mate assortatively: they had effectively speciated. Many subsequent studies failed to produce such reproductive isolation through disruptive selection. Grant and Mettler (1969) also failed to obtain any significant mating discrimination in their I-maze disruptive selection study, but they did get some mating discrimination between their divergently selected directional selection lines.

Upon completion of his Ph.D., and without the benefit of a postdoctoral position, Grant accepted a position at the College of William & Mary in Virginia. The biology department at William & Mary did not then and

Bruce Grant

does not now offer a Ph.D. program. At the time of his hire, the department had only ~15 faculty members, Grant was given essentially no "startup" funds, and his lab space was only 280 square feet. His teaching load was consistently heavy by research university standards with, at minimum, one class per semester and typically two or more.

In Grant's first spring semester at William & Mary, he admitted a promising sophomore undergraduate, Jerry Coyne, into the junior-level genetics class. One of the exercises in the associated lab involved having students map a white-eyed mutant of Drosophila by crossing it to other lines. In the F_2 between white-eyed males and wild-type females, four phenotypes were observed: wild type, bright red, brown, and white eyes. To a Drosophila geneticist, this cross was obviously between wild type and a cinnabar-brown double mutant, but the strange results of this cross puzzled Coyne deeply until he figured it out some days later. A year later, Coyne enrolled in an National Science Foundation-funded undergraduate honors project drawing on Grant's dissertation work. Coyne and Grant worked closely together and obtained statistically significant differences in activity and significant sexual isolation in their I-maze disruptive selection experiment (Coyne and Grant 1972), confirming in principle the controversial results of Thoday and Gibson (1962). Note that, at the time, it was exceedingly rare for undergraduates to have first-authored papers in Genetics! Coyne recalls, "I went to college as a prospective marine biologist and left as an evolutionary geneticist. This was due entirely to Bruce Grant, whose enthusiasm for science was as strong as his commitment to his undergraduate students." Coyne was heavily inspired by Grant's interest in speciation and published a related article on selection for hybrid inviability in his first year as a Ph.D. student at Harvard (Coyne 1974). Coyne is currently a professor at the University of Chicago, still studying the genetics of speciation.

Grant's influence in this era was not only on his research students. For example, he served on the thesis committee for Virginia Institute of Marine Science masters student Walt Eanes, who was studying allozyme polymorphisms in herring. Eanes also enrolled in Grant's population genetics course, and he and Grant talked extensively about career goals. Eanes was strongly influenced by these discussions and went on to pursue a Ph.D. in butterfly genetics at SUNY Stony Brook. Today he is a professor at SUNY Stony Brook studying population genetics and molecular evolution of Drosophila. Around the same time, Kenneth Weber took Grant's population genetics course as a masters student at William & Mary. Ken asked to do his thesis with Bruce, but Bruce felt that his proposed project was too large in scale for an M.S. degree. However, he talked Ken into pursuing a Ph.D. at Harvard University with Richard Lewontin. Interestingly, the project that he pursued for his Ph.D. with Lewontin was essentially the one that he had asked Grant to supervise as a masters thesis! Weber is currently an associate professor at the University of Southern Maine studying the genetics of adaptation in Drosophila.

WASP PHASE

Grant soon became interested in unusual findings of frequency-dependent male selection, and in particular the so-called "rare male advantage," and he decided to pursue this question in the parasitoid wasp *Nasonia vitripennis*. Confirming this hypothesis, Grant and his students (Grant *et al.* 1974) found that the mating success of males with a visible mutation depended upon the marker's frequency; when the mutant males were common, they were at a disadvantage but when they were rare in comparison to the wild type, they had a mating advantage. In a follow-up study, Grant's student, Harry White, found that olfactory cues were the proximal mechanism behind this rare male advantage (White and Grant 1977). Grant *et al.* (1980) also showed that female Nasonia are able to distinguish between males raised on two different kinds of host. Moreover, these females will tend to mate with the rarer of the male types (by host origin). They suggested that this rare male mating advantage had evolved to promote outbreeding.

During this era, in 1978, Grant allowed into his junior-level genetics course a *freshman*: Greg Wray. Wray recalls the same laboratory experiment with the cross of white-eyed flies as highly influential, and he subsequently joined Grant's laboratory for a 1-year project. Wray studied speciation genetics of Nasonia, but he spent a large amount of time trying to find a way to rear parasitoid Nasonia on pupae bought from a scientific supply company. Normally, the host pupae are found on rotting meat, but for obvious reasons, Grant's colleagues did not approve of the maintenance of large masses of rotting liver. Wray attempted to coat the host pupae with several appropriately named diamines, such as putricine and cadaverine. Wray and Grant interacted strongly on the tasks at hand, the overall projects, and on science in general. Wray recalls, "A lot of what I learned on how to approach a complex problem came from that interaction." Wray later went into developmental biology, but the seed planted by Grant regarding an evolutionary perspective eventually sprouted. Today, Wray is a full professor at Duke University studying the evolution of developmental mechanisms.

Around this same time, H. Allen Orr, a philosophy major, took Grant's evolution course as a junior. Immediately taken with evolutionary biology, Orr arranged to pursue an independent research project in his senior year with Grant. The particular project, which considered the effect of body size on mating interference between competing males of *N. vitripennis*, proved less important than the time spent interacting with Grant. Orr recalls, "We talked nearly every day and we talked about everything: evolution, Nasonia, philosophy, music, you name it. But mostly we talked about—and I learned about—scientific skepticism. Bruce believed in hard, rigorous experiments that yield yes or no answers, and he taught me to think critically about biological claims in the literature. We talked so much (and so loudly) that I remember other faculty coming by and closing our lab door in an attempt to muffle us." Deciding that his future lay in biology, not in philosophy, Orr stayed on with Bruce as a masters student in biology and was particularly taken with the study of speciation. Grant advised him to pursue his Ph.D. with his first former student, Jerry Coyne. The result was tremendously successful, and Orr continues to study the genetics of speciation as a full professor at the University of Rochester. Coyne and Orr dedicated a classic article in Evolution to Grant (Coyne and Orr 1989, an article cited >300 times and mentioned in the David Duchovny film "Evolution") and gave Grant a hearty acknowledgment in their book *Speciation* (Coyne and Orr 2004).

Another undergraduate, Norman Johnson, was inspired by both Grant's genetics and evolution courses a few years later. Prior to these courses, Johnson was a premed student, but he was inspired by Grant's emphasis on the spirit of Dobzhansky's famous quote, "Nothing in biology makes sense except in the light of evolution." He appreciated both the problem-solving aspects of the courses (such as the white-eyed fly experiment again) and how up-to-date they were. Grant would even talk about the work of Nobel laureates from that year. He guided Johnson's honors research, testing whether female wasps would adjust the proportion of males in their broods depending upon whether they were related to the other females to which they were exposed (Johnson 1987). Reflecting on this experience, Johnson says, "I learned the importance of experimental design and replication, as well as the nuts and bolts of writing a scientific paper. Most importantly, I learned how to think like a scientist. Over the years, our relationship has evolved from student-mentor to colleague, but I will always think of Bruce Grant as a wise friend." Today, Johnson, an adjunct assistant research professor at the University of Massachusetts, has research interests in speciation genetics and the evolution of development.

Biston betularia PHASE

Grant's most recent line of research began in the mid-1980s, when he took an interest in the classic peppered moth, *B. betularia*. This species is famous for providing textbook evidence of industrial melanism and observable evolution by natural selection within human lifetimes. Grant dissected this system by examining parallels between the temporal patterns of industrial melanism in multiple locations in the United Kingdom, United States, and Japan and the details of what drove the temporal changes in melanic allele frequencies. For example, Grant and his collaborators noted the lack of change in lichen floras coincident with the melanic allele frequency changes and concluded that "the role of lichens has been inappropriately emphasized in chronicles about the environment of the melanism in peppered moths" (Grant *et al.* 1996, p. 351). He also tested (and refuted) the "contrast/conflict" model, wherein moths select resting sites on the basis of comparison of their own color to that of the surface (Grant and Howlett 1988). One of his most visually striking observations was his documentation of the decline of the melanic morphs in multiple localities within the United States (see Grant and Wiseman 2002, Figure 1): one can observe an almost perfectly linear decline in the frequency of melanics in Michigan and Pennsylvania between 1959 and 2001, whereas melanics were extremely rare in Virginia and are now apparently absent altogether. These frequencies were strongly correlated with atmospheric SO_2 levels both in the United States and in the United Kingdom (Grant *et al.* 1998). Grant (2004) further showed that the same alleles are responsible for melanism on multiple continents in 2004.

In the course of these projects, Grant interacted extensively with several renowned experts in the classic system, including Sir Cyril Clarke. Grant's energy and enthusiasm in the classroom described by his students also came across in these collaborations. For example, Rory Howlett's memories of his collaboration are "of having long, jovial late-night conversations with [Grant] about all aspects of evolutionary biology—I seem to remember the molecular drive was much discussed at that time, but he seemed to be interested in everything, and very well read!"

Some details of the classic Kettlewell work on industrial melanism have come under much scrutiny, such as the role of lichens as a background for these moths, but Grant has been a vigorous defender of the work and the clear evidence of evolution by natural selection that it provides. For example, Coyne (1998, p. 36), in a book review that emphasized some points of Majerus's (1998) book that were critical of Kettlewell's results, suggested that "we must discard *Biston* as a well-understood example of natural selection in action." While it is certainly true that we do not understand all the factors affecting industrial melanism in this (or any) species, Coyne's (1998) review and the associated book were unfortunately and inappropriately grabbed by the Discovery Institute and other fanatical antievolution groups as having provided evidence against natural selection driving the changes in melanic moth frequencies over time. Grant (1999) vigorously and eloquently defended Kettlewell's results against this misinterpretation in a subsequent review of the book. He calls the evidence for natural selection "indisputable" and points to many unequivocal lines of evidence supporting it, including the parallel rise and fall of these morphs on two continents concomitant with changes in industrial practices and pollution. He concluded that "none of the complications so far identified have challenged the role assigned to selective predation as the primary explanation for industrial melanism in peppered moths" (p. 984). Grant (2002) similarly defended Kettlewell against a "character assassination" by Judith Hooper (2002), and his position has been supported in subsequent years (Rudge 2005).

Less known is that Grant's laboratory also worked extensively on the color polymorphism of *B. betularia* caterpillars (illustrated in Harris 1766). He confirmed E. B. Poulton's early work showing that body color was induced by visual cues from the shoots on which the caterpillars were reared (Parnell 1992): caterpillars reared on birch branches turned brown while those on willow turned green irrespective of the leaves that they consumed. His group also studied how long into development the caterpillars retain the ability to adjust their body color to new surroundings (Noor 1992).

Mohamed Noor, a B-average student when he came to work with Grant, had a successful project, but of more importance was that he received extensive one-on-one mentoring with Grant. Initially prompted by his excitement over Grant's evolutionary genetics class, Noor asked to work in Grant's lab starting the summer after his junior year. Every day, without exception, Grant spent 30 min or longer (often hours) talking about the project and about evolutionary genetics in general, ranging from concepts to amusing anecdotes about the players. Grant saw something in Noor that his other professors did not see (another William & Mary biology professor had advised Noor that he should take "easier classes" that would be more consistent with his ability). Grant engaged Noor to think harder and more independently about his project and about evolution. Grant was then able to convince Jerry Coyne at the University of Chicago to take a chance on another prospective Ph.D. student. The result was pretty good, as Noor had a successful graduate career and is currently an associate professor at Duke University in evolutionary genetics.

SYNOPSIS

This essay by no means presents the sum total of Grant's contributions to research, mentoring, or the advance of science in the discipline or at large. Indeed, Grant was unaware of this article at the time of its preparation, so we have merely skimmed the surface of his contributions using information volunteered by his colleagues and former students. For example, we have not discussed Grant's service on numerous boards, including as an associate editor for the Journal of Heredity for 5 years. He also fought publicly for evolution education, illustrated by his book review for Skeptic magazine exposing many flaws of so-called "intelligent design." Finally, we have certainly described only a small sampling of his influence even on the particular students mentioned; all with whom we spoke said things along the lines of, "There's simply no way I would have become a scientist if it weren't for Bruce." All commented repeatedly on the highly influential and beneficial effect of his ability to engage them and make them think critically.

Nonetheless, we feel the example of this outstanding scientist, mentor, colleague, and advocate of science to the public is one from which we can all learn. Too often, faculty at research universities view teaching as a burden keeping them from research and look upon undergraduates as distractions from "really doing science." They fail to think in a context vaguely akin to inclusive fitness: one's own productions are only part of their scientific net worth, and aiding others to produce research increases one's scientific net worth. How many more undergraduates would have gone into our subdisciplines and made great scientific achievements if we had worked harder to stimulate their interest, following Grant's example? How many potential future publications are actually lost when we fail to stimulate our students? If our scientific net worths ever amount to half that of Bruce Grant, or others who have similarly inspired such a great many future scientists, we can retire knowing we have had truly successful careers. Do not forget to put a little extra effort into your next lecture and/or lab assignment: a future Jerry Coyne may be sitting in the audience.

Bruce Grant's website is at http://bsgran.people.wm.edu/.

First, foremost, and rather obviously, we wholeheartedly thank Bruce Grant for his mentoring of us and for his service to evolutionary genetics in general. We also hope he can forgive us for bringing so much attention to his contributions. In addition, we thank J. Coyne, R. Howlett, A. Orr, K. Weber, L. Wiseman, and G. Wray for providing us material to prepare this tribute. Finally, we thank A. Moehring and K. Zimmerman for comments on the manuscript.

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