

Leticia Avilés

“Verweile doch, Du bist so schön”



Leticia Avilés was born in Quito, Ecuador, the eldest of a family of five children. Already as a high school student Leticia was fascinated with biology and curious about evolution. As a college student at the Pontificia Universidad Católica del Ecuador, she initiated her studies on social spiders. She suspected that these relatively little-studied organisms held the key to important questions in evolutionary biology and population ecology. Leticia continued her studies at Harvard University, where she earned her Ph.D. in 1992. Her dissertation work earned her one of the prestigious Young Investigator Awards from the American Society of Naturalists. Leticia also spent time at the University of California at Berkeley (1988–1990) and later at the University of Arizona, where she was first a post-doctoral fellow (1992–1994) and is currently an Assistant Professor. Inspired by the intriguing biology of social spiders, Leticia’s work brings together issues related to the evolution of sex ratios in subdivided populations, the levels of selection, the biology of metapopulations, population dynamics, and the evolution of social behavior. This work integrates empirical studies in Amazonian rainforests, computer simulations, and laboratory work employing cytological and molecular techniques. Leticia currently lives in Arizona with her husband and two children. – Address: Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721, USA.

A phrase from Goethe’s *Faust* – one of the highlights of my way-too-short stay in Berlin – seems to be the appropriate way to start a report on one of the highlights of my life. Professionally, personally, humanly, these have been, with no question, some of the best months of my life. From conversations about consciousness over a

glass of wine or discussions on the levels of selection during a specialists workshop on social behavior to nights at the opera, two days at a marathon performance of Goethe's Faust, evenings with friends at Prenzlauer Berg, "techno" dancing with my 9-year-old daughter, or waltzing with my husband in the large colloquium room, I have to confess that I have lived life as life was meant to be. So, I am tempted to say, unlike the ever unsatisfied Faust who never reached the moment when he would wish time to freeze: "Verweile doch, Du bist so schön." (Stay with me, you are so beautiful.)

I arrived in February, having unfortunately missed four months of life at the Kolleg and perhaps the opportunity of really nailing this incredibly challenging language of Goethe. Jet lagged, tired, confused, I landed in the middle of an after-dinner discussion about the nature of consciousness. György Ligeti, one of the best-known and well-loved living composers (and a modern-age da Vinci) challenged a group of neurobiologists, ethologists, and computer scientists with the question of what consciousness is. Tired to my bones, but fascinated, I went to bed as if in a cloud. Since then, the cloud has cleared and this new foreign place has become home – home in some unexpected and powerful ways.

I had the fortune of growing up surrounded by books and by friends and family who loved them. My father was an intellectual, a history and social sciences *aficionado* who had amassed one of the largest personal libraries in Quito. As a high school and college student, I religiously attended music school as an after-school activity. I did not do this in the hope of becoming a musician, or even of learning to play the piano (for which I already knew I had no talent), but because at this place I was surrounded by young people like me (except for the talent part, of course), in love with books, theater, music, and with the dream of changing the world. Our concept of a date was to meet at a bookstore to browse through and talk about books; to meet at intermission in the old Teatro Sucre to discuss the music we had just heard; to sit in somebody's living room to ponder the things that could be done to make Ecuador, and even the world, a better place for *all* people. All of this mostly vanished when I went to the United States for graduate school. Not that "Amerika" (as Germans call the United States) does not have a rich intellectual life, which it does, but because the incredibly fast-paced and sink-or-swim environment of academia in the USA does not leave room for such things (I have to admit that having kids has contributed to this paucity of time; that part, though, I am thankful for). So landing in

Berlin and in the Kolleg was like landing back in a time I had almost forgotten I so dearly missed.

Culture, fun, and intellectual stimulation aside, the Kolleg has also been a great place to work. By the time the year was up, three personal computers stood like giants over the no less gigantic desks of my beautiful office at the Villa Jaffé (tall ceilings, wooden floors, a huge window overlooking a garden at first snow-covered, then green and lush). For weeks on end, while obeying my dictatorial instructions, these giants cranked out simulation results that eventually filled 1400 MB of hard drive and now form part of a paper in press, one in review, and at least two others in preparation. Most of my projects fell within the general rubric of social evolution, the central topic of the loosely assembled group of which I was a part (with Raghavendra Gadagkar, Amitabh Joshi, and Somdatta Sinha). Social evolution is a huge field that has occupied ethologists, behavioral ecologists, and evolutionary biologists for many decades. Within such a crowded field, it may not have seemed that many substantial and especially substantially new contributions could be made. I was therefore surprised to discover, as I entered this field a few years ago, that while great progress had been made understanding the genetic aspects of social evolution, much work needed to be done to understand its ecological aspects.

Having discovered through my empirical work^{1,2} that individual fitness may have a “humped” nonlinear relationship with colony size, I have been working on a framework³ that uses the shape and magnitude of this function to make predictions about the origin, size, and dynamics of social groups. This approach simplifies the ecological question by subsuming complex ecological interactions such as cooperation, competition, predation, and resource acquisition in a simple three-parameter model of the relationship between individual fitness and colony size. It also brings to the study of social evolution the theory and methods of nonlinear dynamics while representing a radically different, albeit complementary, approach to the existing paradigm – Hamilton’s inclusive fitness framework⁴ – that has dominated the field for the last few decades. Three projects illustrate the potential of this approach:

Dynamical transitions in the evolution of sociality. Using analytic and simulation methods,^{3,5} I have discovered that the enhanced reproductive success that results from cooperation may allow the colonization of harsh or marginal environments in which solitary individuals would not be able to replace themselves. This effect is dramatically illustrated by the occurrence of eusocial mole rats in

the extremely arid deserts of southern Africa. In contrast, in environments in which group living and cooperation allow access to plentiful resources, I have found^{3,6} that such enhanced reproductive success may lead to intrinsic dynamical instability – i.e., a boom and bust pattern of group and population growth. This finding is consistent with the oscillations in colony size of some social spider species and the global population outbreaks and crashes characteristic of tent caterpillars, voles, migratory locusts, and conifer bark beetles.

Solving the freeloader's paradox. The models I have developed also suggest a possible solution to one of the enduring problems in the study of social evolution – the maintenance of cooperation in the presence of freeloaders.⁷ I have found that even though freeloaders can benefit from cooperators when rare, they are selected against when common because they reduce the productivity of the groups they overburden with their presence. This effect allows the evolution and maintenance of cooperation under a wide range of parameter values, even when groups consist of non-relatives and cooperators suffer a significant relative fitness cost within their groups.

Ecology, demography, and kinship in the evolution of sociality. The models I have developed have also allowed me to explore the interaction between ecology and demography, on the one hand, and kinship – one of the key aspects of Hamilton's inclusive fitness framework –, on the other. I have found that when groups consist of non-relatives, the group carrying capacity and relative fitness costs of cooperation have the greatest effect on the size of the groups and level of sociality that evolve⁶. When groups contain exclusively kin, in contrast, the intrinsic rate of growth becomes a more critical parameter affecting group size and sociality.⁸

While at the Kolleg, I had the opportunity of running these ideas by a select and captive audience during a lively 3-day workshop on Principles of Social Evolution. As we listened to each others' presentations, we pondered about the match between the biology of a variety of social organisms and our understanding of the theories that pertain to why and how they are social. Excellent lectures, but most of all stimulating discussions, made the two-hour slots allocated to each speaker clearly too short (see more on the workshop in Gadagkar's write up about it in this volume).

Thanks to the wonders of technology, I was also able to keep up with my students from across the ocean. We submitted one co-authored paper and made substantial progress towards two others that are now almost ready for submission. I also listened over the phone, as I watched the images on my computer, to a "practice talk"

by one of my students that eventually won her the runner-up prize in the best student paper competition at an international conference in South Africa. Perhaps more amazingly, I was able to participate – live, over a speaker phone – in a stimulating discussion following the presentation by a student in Oregon whose committee I belong to (again, after having listened to his talk over the phone and watched his slides on my computer).

But, above all, these months at the Kolleg have been a period of personal growth – of re-encountering myself, of making friendships as I had not since my college years, of realizing how lucky I am to have the family, the life, and the opportunities I have. Among my blessings I count having shared these past few months with so many wonderful people, both Fellows and staff, while living in a city that grows on you as you discover its diversity and come to terms with its history, a city that manages to be both intimate and monumental, provincial and cosmopolitan, strangely beautiful in its chaos and modernity, and never boring.

Before I close, I would like to reproduce a message I received from a friend during the International Week of Friendship. I direct this message to all former, present, and future Fellows, as a reminder of how lucky we truly are. Here it is:

Etwas zum Nachdenken, mit herzlichen Grüßen von Leticia.

The World and We

Wenn wir die ganze Menschheit auf ein Dorf von 100 Einwohner reduzieren würden, aber auf die Proportionen aller existierenden Völker achtend, würde dieses Dorf so zusammengestellt sein:

- 57 Asiaten
- 21 Europäer
- 14 Amerikaner (Nord und Süd)
- 8 Afrikaner

- 52 Frauen
- 48 Männer

- 70 Nicht-Weiße
- 30 Weiße

70 Nicht-Christen
30 Christen

89 Heterosexuelle
11 Homosexuelle

6 Personen besitzen 59% des gesamten Weltreichtums, und alle
6 kommen aus den USA
80 haben keine ausreichenden Wohnverhältnisse
70 sind Analphabeten

50 sind unterernährt
1 stirbt pro Tag
2 werden pro Tag geboren

1 hat einen PC

1 (nur einer) hat einen akademischen Abschluss

Wenn man die Welt aus dieser Sicht betrachtet, wird jedem klar, dass es ein großes Bedürfnis nach Zusammengehörigkeit, Verständnis, Akzeptanz und Bildung gibt.

Denke auch darüber nach: Falls Du heute Morgen gesund aufgewacht bist, bist Du glücklicher als 1 Million Menschen, welche die nächste Woche nicht erleben werden. Falls Du nie einen Krieg erlebt hast, nie die Einsamkeit durch Gefangenschaft, nie die Agonie der Gequälten oder nie Hunger gespürt hast, dann bist Du glücklicher als 500 Millionen Menschen der Welt.

Falls Du in die Kirche gehen kannst ohne die Angst, dass man Dich bedrohen, verhaften oder umbringen wird, bist Du glücklicher als 3 Milliarden Menschen der Welt. Falls sich in Deinem Kühlschrank Essen befindet, Du angezogen bist, Du ein Dach über dem Kopf hast und ein Bett zum Hinlegen, bist Du reicher als 75% der Einwohner dieser Welt. Falls Du ein Konto bei der Bank hast und etwas Geld im Portemonnaie, gehörst Du zu den 8% der wohlhabenden Menschen auf dieser Welt.

Falls Du diese Nachricht liest, bist Du doppelt gesegnet worden, denn: 1. Jemand hat an Dich gedacht und 2. Du gehörst nicht zu den 2 Milliarden Menschen, die nicht lesen können. Und ... Du hast einen PC!

Jemand hat einmal gesagt:
Arbeitet, als würdet Ihr kein Geld brauchen,

Liebt, als hätte Euch noch nie jemand verletzt,
Tanzt, als würde keiner hinschauen,
Singt, als würde keiner zuhören,
Lebt, als wäre das Paradies auf der Erde.

As I close this essay and the last box of our belongings to be shipped back to America, I am well aware that time cannot be frozen. "Gott sei Dank," Professor Gilliot said to me in his wisdom, "if beautiful things lasted for ever, they wouldn't be so beautiful anymore." So, I am left with the memories, memories that I will treasure for the rest of my life.

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- ¹ Avilés, L. and P. Tufiño. 1998. "Colony size and individual fitness in a social spider." *American Naturalist* 152: 403–418.
 - ² Salazar, P. and L. Avilés, in preparation.
 - ³ Avilés, L. 1999. "Cooperation and non-linear dynamics: An ecological perspective on the Evolution of Sociality." *Evolutionary Ecology Research* 1: 459–477.
 - ⁴ Hamilton, W. D. 1964. "The genetical evolution of social behavior." *Journal of Theoretical Biology* 7: 1–52.
 - ⁵ Avilés, L. and J. Fletcher, in preparation.
 - ⁶ Avilés, L., P. Abbot, and A. Cutter. "Population ecology, nonlinear dynamics, and social evolution. I. Associations among nonrelative." *American Naturalist* 159: 115–127.
 - ⁷ Avilés, L. "Solving the freeloaders paradox: Genetic associations and frequency dependent selection on the evolution of cooperation among non relatives." In review.
 - ⁸ Avilés, L. and A. Cutter, in preparation.