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Curriculum Vitae
STEVEN A. FRANK

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Education

University of Michigan, Ann Arbor	1987	Ph.D. (Biology)
University of Florida, Gainesville	1983	M. Statistics
University of Florida, Gainesville	1983	M.S. (Zoology)
University of Michigan, Ann Arbor	1979	B.S. (Biology)

Positions

Professor, Ecology and Evolutionary Biology, University of California, Irvine	1997-
Associate Professor, Ecology and Evolutionary Biology, University of California, Irvine	1992-1997
Assistant Professor, Ecology and Evolutionary Biology, University of California, Irvine	1988-1992

Major Grants

2009-2012	NSF Grant, Theoretical Biology
2006-2011	NIH/MIDAS Grant, Influenza epidemiology & evolution, Co-PI w/R. Bush
2001-2006	NIH Grant, Antigenic variation in <i>Borrelia</i> , Co-PI w/A. Barbour
2001-2007	NSF Grant, Population Biology
1996-2001	NSF Grant, Population Biology
1990-1998	NSF Presidential Young Investigator Award
1990-1996	NIH FIRST Award

Fellowships

2011	Hogge-Baer Visiting Professor in Cancer Research, University of Chicago
2006-2007	Institute for Advanced Study (Wissenschaftskolleg), Berlin
2002	Member, Institute for Advanced Study, Princeton
1996-1997	Institute for Advanced Study (Wissenschaftskolleg), Berlin
1995-1996	John Simon Guggenheim Fellowship
1987-1989	Miller Research Fellowship, University of California, Berkeley
1984-1987	NIH Genetics Traineeship, University of Michigan

Prizes and Honors

2009	Elected fellow, American Association for the Advancement of Science
1988	Theodosius Dobzhansky Prize, Society for the Study of Evolution
1986	Young Investigator Prize, American Society of Naturalists

Ten key publications

Frank, S. A. 2007. *Dynamics of Cancer: Incidence, Inheritance, and Evolution*. Princeton University Press.

Frank, S. A. and Nowak, M. A. 2003. Developmental predisposition to cancer. *Nature* 422:494.

Frank, S. A. 2002. *Immunology and Evolution of Infectious Disease*. Princeton University Press.

Frank, S. A. 1996. Models of parasite virulence. *Quarterly Review of Biology* 71:37-78.

Frank, S. A. 1998. *Foundations of Social Evolution*. Princeton University Press.

Frank, S. A. 1995. Mutual policing and repression of competition in the evolution of cooperative groups. *Nature* 377:520-522.

Frank, S. A. 1989. The evolutionary dynamics of cytoplasmic male sterility. *American Naturalist* 133:345-376.

Frank, S. A. 1991. Divergence of meiotic drive-suppression systems as an explanation for sex-biased hybrid sterility and inviability. *Evolution* 45:262-267.

Frank, S. A. 2009. The common patterns of nature. *Journal of Evolutionary Biology* 22:1563-1585.

Frank, S. A. and Smith, D. E. 2011. A simple derivation and classification of common probability distributions based on information symmetry and measurement scale. *Journal of Evolutionary Biology* 24:469-484.

All publications available at <http://stevefrank.org>

Publications

129. Frank, S. A. 2012. Natural selection. III. Selection versus transmission and the levels of selection. *Journal of Evolution Biology* 25:227-243.
128. Frank, S. A. 2012. Wright's adaptive landscape versus Fisher's fundamental theorem. Pages 00-00 in *The Adaptive Landscape in Evolutionary Biology*, E. Svensson and R. Calsbeek, eds. Oxford University Press.
127. Frank, S. A. 2011. Natural selection. II. Developmental variability and evolutionary rate. *Journal of Evolution Biology* 24:2310-2320.
126. Frank, S. A. 2011. Natural selection. I. Variable environments and uncertain returns on investment. *Journal of Evolution Biology* 24:2299-2309.
125. Frank, S. A. and Crespi, B. J. 2011. Pathology from evolutionary conflict, with a theory of X chromosome versus autosome conflict over sexually antagonistic traits. *Proceedings of the National Academy of Sciences USA* 108 (Suppl. 2):10886-10893.
124. Frank, S. A. 2011. Cancer: the whole story [book review]. *PLoS Biology* 9:e1001044.
123. Frank, S. A. and Smith, E. 2011. A simple derivation and classification of common probability distributions based on information symmetry and measurement scale. *Journal of Evolution Biology* 24:469-484.
122. Frank, S. A. 2011. Measurement scale in maximum entropy models of species abundance. *Journal of Evolution Biology* 24:485-496.
121. Frank, S. A. and Smith, D. E. 2010. Measurement invariance, entropy, and probability. *Entropy* 12:289-303.
120. Frank, S. A. 2010. History of science: belief, reason, and insight [book review]. *Science* 329:279-280.
119. Frank, S. A. 2010. A general model of the public goods dilemma. *Journal of Evolutionary Biology* 23: 1245-1250.
118. Frank, S. A. 2010. The trade-off between rate and yield in the design of microbial metabolism. *Journal of Evolutionary Biology* 23:609-613.
117. Frank, S. A. 2010. Microbial secretor-cheater dynamics. *Philosophical Transactions of the Royal Society of London B* 365:2515-2522.
116. Frank, S. A. 2010. Demography and the tragedy of the commons. *Journal of Evolutionary Biology* 23:32-39.
115. Frank, S. A. 2010. Somatic evolutionary genomics: Mutations during development cause highly variable genetic mosaicism with risk of cancer and neurodegeneration. *Proceedings of the National Academy of Sciences USA* 107:1725-1730.

114. Frank, S. A. 2009. The common patterns of nature. *Journal of Evolutionary Biology* 22:1563–1585.
113. Frank, S. A. 2009. Natural selection maximizes Fisher information. *Journal of Evolutionary Biology* 22:231–244.
112. Frank, S. A. 2009. Evolutionary foundations of cooperation and group cohesion. Pages 3–40 in *Games, Groups, and the Global Good*, S. A. Levin, ed. Springer-Verlag.
111. Frank, S. A. and Schmid-Hempel, P. 2008. Mechanisms of pathogenesis and the evolution of parasite virulence. *Journal of Evolutionary Biology* 21:396–404.
110. Frank, S. A. 2008. Evolutionary dynamics of redundant regulatory control. *Journal of Theoretical Biology* 255:64–68.
109. Frank, S. A. 2007. *Dynamics of Cancer: Incidence, Inheritance, and Evolution*. Princeton University Press.
108. Frank, S. A. 2007. Maladaptation and the paradox of robustness in evolution. *PLoS ONE* 2(10):e1021.
107. Frank, S. A. 2007. All of life is social. *Current Biology* 17:R648–R650.
106. Frank, S. A. 2007. Evolution of antigenic variation. Pages 225–242 in *Encyclopedia of Infectious Diseases: Modern Methodologies*, M. Tibayrenc, ed. Wiley.
105. Frank, S. A. and Bush, R. M. 2007. Barriers to antigenic escape by pathogens: trade-off between reproductive rate and antigenic mutability. *BMC Evolutionary Biology* 7:229.
104. Schmid-Hempel, P. and Frank, S. A. 2007. Pathogenesis, virulence, and infective dose. *PLoS Pathogens* 3(10):e147.
103. Barbour, A. G., Dai, Q., Restrepo, B. I., Stoenner, H. G., and Frank, S. A. 2006. Pathogen escape from host immunity by a genome program for antigenic variation. *Proceedings of the National Academy of Sciences USA* 103:18290–18295.
102. Frank, S. A. and Barbour, A. G. 2006. Within-host dynamics of antigenic variation. *Infection, Genetics and Evolution* 6:141–146.
101. Frank, S. A. 2006. Social selection. Pages 350–363 in *Evolutionary Genetics: Concepts and Case Studies*, C. W. Fox and J. B. Wolf, eds. Oxford University Press.
100. Frank, S. A. and McKenzie, R. B. 2006. The male-female pay gap driven by coupling between labor markets and mating markets. *Journal of Bioeconomics* 8:269–274.
99. Frank, S. A. 2006. Mathematical biology: Master class in evolutionary modeling [book review]. *Science* 314:1878–1879.

98. Frank, S. A. 2005. Age-specific incidence of inherited versus sporadic cancers: A test of the multistage theory of carcinogenesis. *Proceedings of the National Academy of Sciences USA* 102:1071-1075.
97. Frank, S. A., Chen, P.-C. and Lipkin, S. M. 2005. Kinetics of cancer: a method to test hypotheses of genetic causation. *BMC Cancer* 5:163.
96. Frank, S. A. 2004. A multistage theory of age-specific acceleration in human mortality. *BMC Biology* 2:16.
95. Frank, S. A. 2004. Genetic predisposition to cancer—insights from population genetics. *Nature Reviews Genetics* 5:764-772.
94. Frank, S. A. 2004. Genetic variation in cancer predisposition: mutational decay of a robust genetic control network. *Proceedings of the National Academy of Sciences USA* 101:8061-8065.
93. Frank, S. A. 2004. Age-specific acceleration of cancer. *Current Biology* 14:242-246.
92. Frank, S. A. and Nowak, M. A. 2004. Problems of somatic mutation and cancer. *BioEssays* 26:291-299.
91. Frank, S. A. 2004. Inheritance of cancer. *Discovery Medicine* 4:396-400.
90. Frank, S. A. 2004. Mathematical models of cancer progression and epidemiology in the age of high throughput genomics [invited commentary on Armitage and Doll's classic 1954 paper]. *International Journal of Epidemiology* 33:1179-1181.
89. Lin, S.-C. J., Lee, J.-F., Nikitin, A. Y., Hilsenbeck, S. G., Cardiff, R. D., Li, A., Kang, K.-W., Frank, S. A., Lee, W.-H., and Lee, E. Y.-H. P. 2004. Somatic mutation of *p53* leads to estrogen receptor α -positive and -negative mouse mammary tumors with high frequency metastasis. *Cancer Research* 64:3525-3532.
88. André, J.-B., Gupta, S., Frank, S., Tibayrenc, M. 2004. Evolution and immunology of infectious disease: what's new? *Infection, Genetics and Evolution* 4:69-75.
87. Frank, S. A. 2003. Viral genetics: deadly partnerships [News and Views]. *Nature* 425:251-252.
86. Frank, S. A. and Nowak, M. A. 2003. Developmental predisposition to cancer. *Nature* 422:494.
85. Frank, S. A. 2003. Somatic mutation: early cancer steps depend on tissue architecture. *Current Biology* 13:R261-R263.
84. Frank, S. A., Iwasa, Y. and Nowak, M. A. 2003. Patterns of cell division and the risk of cancer. *Genetics* 163:1527-1532.
83. Frank, S. A. 2003. Somatic mosaicism and cancer: inference based on a conditional Luria-Delbrück distribution. *Journal of Theoretical Biology* 223:405-412.
82. Michor, F., Nowak, M. A., Frank, S. A., and Iwasa, Y. 2003. Stochastic elimination of cancer. *Proceedings of the Royal Society of London B* 270:2017-2024.

81. Michor, F., Frank, S. A., May, R. M., Iwasa, Y., and Nowak, M. A. 2003. Somatic selection for and against cancer. *Journal of Theoretical Biology* 225:377-382.
80. Frank, S. A. and Barr, C. M. 2003. Programmed cell death and hybrid incompatibility. *Journal of Heredity* 94:181-183.
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74. Frank, S. A. 2002. Immune response to parasitic attack: evolution of a pulsed character. *Journal of Theoretical Biology* 219:281-290.
73. Frank, S. A. 2002. George Price. Pages 930-931 in *Encyclopedia of Evolution*, M. Pagel, ed. Oxford University Press.
72. Frank, S. A. 2001. Multiplicity of infection and the evolution of hybrid incompatibility in segmented viruses. *Heredity* 87:522-529.
71. Frank, S. A. and Barr, C. M. 2001. Spatial dynamics of cytoplasmic male sterility. Pages 219-243 in *Integrating Ecology and Evolution in a Spatial Context*, J. Silvertown and J. Antonovics, eds. Blackwell Scientific, Oxford.
70. Frank, S. A. and Jeffrey, J. S. 2001. The probability of severe disease in zoonotic and commensal infections. *Proceedings of the Royal Society of London B* 268:53-60.
69. Frank, S. A. 2000. Within-host spatial dynamics of viruses and defective interfering particles. *Journal of Theoretical Biology* 206:279-290.
68. Frank, S. A. 2000. Polymorphism of attack and defense. *Trends in Ecology and Evolution* 15:167-171.
67. Frank, S. A. 2000. Specific and non-specific defense against parasitic attack. *Journal of Theoretical Biology* 202:283-304.
66. Frank, S. A. 2000. Sperm competition and female avoidance of polyspermy mediated by sperm-egg biochemistry. *Evolutionary Ecology Research* 2:613-625.

65. Frank, S. A. 1999. Development of colony phenotype in social insects controlled by frequency-dependent thresholds among workers. *Evolutionary Ecology Research* 1:1003-1007.
64. Frank, S. A. 1999. A model for the sequential dominance of antigenic variants in African trypanosome infections. *Proceedings of the Royal Society of London B* 266:1397-1401.
63. Frank, S. A. 1999. Population and quantitative genetics of regulatory networks. *Journal of Theoretical Biology* 197:281-294.
62. Frank, S. A. 1998. Inducible defence and the social evolution of herd immunity. *Proceedings of the Royal Society of London B* 265:1911-1913.
61. Frank, S. A. and Amarasekare, P. 1998. Increasing resource specialization among competitors shifts control of diversity from local to spatial processes. *Ecology Letters* 1:3-5.
60. Frank, S. A. 1998. Dynamics of cytoplasmic incompatibility with multiple *Wolbachia* infections. *Journal of Theoretical Biology* 192:213-218.
59. Frank, S. A. 1998. *Foundations of Social Evolution*. Princeton University Press.
58. Frank, S. A. 1997. Multivariate analysis of correlated selection and kin selection, with an ESS maximization method. *Journal of Theoretical Biology* 189:307-316.
57. Frank, S. A. 1997. The Price Equation, Fisher's fundamental theorem, kin selection, and causal analysis. *Evolution* 51:1712-1729.
56. Frank, S. A. 1997. Models of symbiosis. *American Naturalist* 150:S80-S99.
55. Frank, S. A. 1997. Cytoplasmic incompatibility and population structure. *Journal of Theoretical Biology* 184:327-330.
54. Frank, S. A. 1997. The design of adaptive systems: optimal parameters for variation and selection in learning and development. *Journal of Theoretical Biology* 184:31-39.
53. Frank, S. A. 1997. Developmental selection and self-organization. *BioSystems* 40:237-243.
52. Frank, S. A. 1997. Spatial processes in host-parasite genetics. Pages 325-352 in *Metapopulation Biology: Ecology, Genetics, and Evolution*, I. Hanski and M. Gilpin, eds. Academic Press, New York.
51. Frank, S. A. 1996. Policing and group cohesion when resources vary. *Animal Behaviour* 52:1163-1169.
50. Frank, S. A. and Hurst, L. D. 1996. Mitochondria and male disease. *Nature* 383:224.
49. Frank, S. A. 1996. Host control of symbiont transmission: the separation of symbionts into germ and soma. *American Naturalist* 148:1113-1124.
48. Frank, S. A. 1996. Host-symbiont conflict over the mixing of symbiotic lineages. *Proceedings of the Royal Society of London B* 263:339-344.
47. Taylor, P. D. and Frank, S. A. 1996. How to make a kin selection model. *Journal of Theoretical Biology* 180:27-37.

46. Frank, S. A. 1996. Problems inferring the specificity of plant-pathogen genetics [a reply to M. Parker]. *Evolutionary Ecology* 10:323-325.
45. Frank, S. A. 1996. Statistical properties of polymorphism in host-parasite genetics. *Evolutionary Ecology* 10:307-317.
44. Frank, S. A. 1996. The design of natural and artificial adaptive systems. Pages 451-505 in *Adaptation*, M. R. Rose and G. V. Lauder, eds. Academic Press, New York.
43. Frank, S. A. 1996. Models of parasite virulence. *Quarterly Review of Biology* 71:37-78.
42. Frank, S. A. 1995. The origin of synergistic symbiosis. *Journal of Theoretical Biology* 176:403-410.
41. Frank, S. A. 1995. Mutual policing and repression of competition in the evolution of cooperative groups. *Nature* 377:520-522.
40. Frank, S. A. 1995. George Price's contributions to evolutionary genetics. *Journal of Theoretical Biology* 175:373-388.
39. Frank, S. A. 1995. Sex allocation in solitary bees and wasps. *American Naturalist* 146:316-323.
38. Frank, S. A. 1994. Recognition and polymorphism in host-parasite genetics. *Philosophical Transactions of the Royal Society of London B* 346:283-293.
37. Frank, S. A. 1994. Kin selection and virulence in the evolution of protocells and parasites. *Proceedings of the Royal Society of London B* 258:153-161.
36. Frank, S. A. 1994. Genetics of mutualism: the evolution of altruism between species. *Journal of Theoretical Biology* 170:393-400.
35. Frank, S. A. 1994. Polymorphism of bacterial restriction-modification systems: the advantage of diversity. *Evolution* 48:1470-1477.
34. Frank, S. A. 1994. Spatial polymorphism of bacteriocins and other allelopathic traits. *Evolutionary Ecology* 8:369-386.
33. Olivieri, I. and Frank, S. A. 1994. The evolution of nodulation in *Rhizobium*: altruism in the rhizosphere. *Journal of Heredity* 85:46-47.
32. Frank, S. A. 1994. Coevolutionary genetics of hosts and parasites with quantitative inheritance. *Evolutionary Ecology* 8:74-94.
31. Frank, S. A. 1993. Evolution of host-parasite diversity. *Evolution* 47:1721-1732.
30. Frank, S. A. 1993. Specificity versus detectable polymorphism in host-parasite genetics. *Proceedings of the Royal Society of London B* 254:191-197.
29. Frank, S. A. 1993. A model of inducible defense. *Evolution* 47:325-327.
28. Frank, S. A. 1993. Coevolutionary genetics of plants and pathogens. *Evolutionary Ecology* 7:45-75.

27. Frank, S. A. 1992. A kin selection model for the evolution of virulence. *Proceedings of the Royal Society of London B* 250:195–197.
26. Frank, S. A. 1992. Models of plant-pathogen coevolution. *Trends in Genetics* 8:213–219.
25. Frank, S. A. and Slatkin, M. 1992. Fisher's fundamental theorem of natural selection. *Trends in Ecology and Evolution* 7:92–95.
24. Frank, S. A. 1991. Haldane's rule: a defense of the meiotic drive theory. *Evolution* 45:1714–1717.
23. Frank, S. A. 1991. Ecological and genetic models of host-pathogen coevolution. *Heredity* 67:73–83.
22. Frank, S. A. 1991. Divergence of meiotic drive-suppression systems as an explanation for sex-biased hybrid sterility and inviability. *Evolution* 45:262–267.
21. Frank, S. A. 1991. Spatial variation in coevolutionary dynamics. *Evolutionary Ecology* 5:193–217.
20. Frank, S. A. 1990. Sex allocation theory for birds and mammals. *Annual Review of Ecology and Systematics* 21:13–55.
19. Frank, S. A. and Slatkin, M. 1990. Evolution in a variable environment. *American Naturalist* 136:244–260.
18. Frank, S. A. 1990. When to copy or avoid an opponent's strategy. *Journal of Theoretical Biology* 145:41–46.
17. Frank, S. A. and Slatkin, M. 1990. The distribution of allelic effects under mutation and selection. *Genetical Research* 55:111–117.
16. Slatkin, M. and Frank, S. A. 1990. The quantitative genetic consequences of pleiotropy under stabilizing and directional selection. *Genetics* 125:207–213.
15. Frank, S. A. 1989. Ecological and evolutionary dynamics of fig communities. *Experientia* 45:674–680.
14. Frank, S. A. and Crespi, B. J. 1989. Synergism between sib rearing and sex ratio in Hymenoptera. *Behavioral Ecology and Sociobiology*. 24:155–162.
13. Frank, S. A. 1989. The evolutionary dynamics of cytoplasmic male sterility. *American Naturalist* 133:345–376.
12. Frank, S. A. and Swingland, I. R. 1988. Sex ratio under conditional sex expression. *Journal of Theoretical Biology* 135:415–418

11. Frank, S. A. 1987. Demography and sex ratio in social spiders. *Evolution* 41:1267-1281
10. Frank, S. A. 1987. Variable sex ratio among colonies of ants. *Behavioral Ecology and Sociobiology* 20:195-201.
9. Frank, S. A. 1987. Individual and population sex allocation patterns. *Theoretical Population Biology* 31:47-74.
8. Frank, S. A. 1987. Weapons and fighting in fig wasps. *Trends in Ecology and Evolution* 2:259-260.
7. Frank, S. A. 1986. Dispersal polymorphisms in subdivided populations. *Journal of Theoretical Biology* 122:303-309.
6. Frank, S. A. 1986. The genetic value of sons and daughters. *Heredity* 56:351-354.
5. Frank, S. A. 1986. Hierarchical selection theory and sex ratios. I. General solutions for structured populations. *Theoretical Population Biology* 29:312-342.
4. Frank, S. A. 1985. Hierarchical selection theory and sex ratios. II. On applying the theory, and a test with fig wasps. *Evolution* 39:949-964.
3. Frank, S. A. 1985. Are mating and mate competition by the fig wasp *Pegoscapus assuetus* (Agaonidae) random within a fig? *Biotropica* 17:170-172.
2. Frank, S. A. 1984. The behavior and morphology of the fig wasps *Pegoscapus assuetus* and *P. jimenezi*: Descriptions and suggested behavioral characters for phylogenetic studies. *Psyche* 91:289-308.
1. Frank, S. A. 1983. A hierarchical view of sex-ratio patterns. *Florida Entomologist* 66:42-75.