

Short Curriculum vitae Franz J. ('Franjo') Weissing

Recent academic positions:

Professor of Theoretical Biology (since 2005; emeritus since 2022)
Founding director, Erasmus Mundus Joint MSc Programme Evolutionary Biology (2009-2019)
Founding, Groningen Graduate School of Science (2007-2012)
Dean of Research, Faculty of Science, University of Groningen (2008-2011)
Distinguished Lorentz Fellow Netherlands Institute for Advanced Study (KNAW-NIAS, 2017-2018)

Major grants:

ERC Advanced Grant (2017, 2.5 M€); Erasmus Mundus Joint MSc Programme Evolutionary Biology (2015, 1.9 M€, 2009, 4.5 M€); NWO Graduate Programme (2012, 1 M€); Groningen Systems Biology Centre (2010, 4 M€); co-PI of Marie Curie Initial Training Network on Speciation (2008, 3 M€).

Honours and Awards:

Honorary Membership of Dutch Society for Theoretical Biology (2023); Mercator Fellowship (2018); Distinguished Lorentz Fellowship Award (2017); Teaching Excellence Fellowship (2015); highest score ('outstanding') for Erasmus Mundus Programme MEME (2015) by Netherlands-Flemish Accreditation Organisation; highest score ('international excellence') in research evaluation by international Peer Review Committee (2012).

Editorial Boards:

American Naturalist (2002-2018), *Frontiers in Zoology* (2004-2020), *Oikos* (2007-2012); guest editor *PLoS Computational Sciences* (2016-2022).

Supervision of PhD theses:

Since 1994, I have supervised 48 PhD students until the defence of their thesis. Thirteen of these received the distinction *cum laude* (which is reserved for the top 3% of all PhD theses), and eighteen received prizes or personal grants on the basis of their PhD work. Of the PhD students and post-doctoral fellows (10) supervised by me, 43 are still active in academic research. Three of these have a full professorship, six have a tenure-track position, four are (senior) lecturers, eight are (senior) scientists at a research institute, and ten are independent research fellows funded by a personal grant.

Research themes:

- Adaptive response strategies // Mechanisms of adaptation
- Animal personalities
- Cultural evolution
- Evolution of self-organisation // Evolution of cooperation
- Evolutionary game theory
- Evolvability
- Life history evolution
- Non-equilibrium dynamics
- Phytoplankton competition
- Segregation distortion // Sex determination // Sex allocation
- Sexual selection // Sex roles // Sex ratios
- Speciation

All articles listed below can be downloaded from the following websites:

<https://www.rug.nl/research/gelifes/tres/publications/allpubs> (until 2018) and
<https://www.marmgroup.eu/publications> (after 2018).

Selected publications per research theme:

Adaptive response strategies // Mechanisms of adaptation

- Adrian-Kalchauer, I., Sultan, S.E., Shama, L.N.S., Spence-Jones, H., Tiso, S., Valsecchi, C.I.K. & **Weissing, F.J.** 2020. Understanding 'non-genetic' inheritance: Insights from molecular-evolutionary crosstalk. *Trends Ecol. Evol.* 35: 1078-1089. doi: 10.1016/j.tree.2020.08.011.
- Botero, C.A., **Weissing, F.J.**, Wright, J. & Rubenstein, D.R. 2015. Evolutionary tipping points in the capacity to adapt to environmental change. *Proc. Natl. Acad. Sci. USA* 112:184-189.
- Fawcett, T.W., Kuijper, A., **Weissing, F.J.** & Pen, I. 2011. Sex-ratio control erodes sexual selection, revealing evolutionary feedback from adaptive plasticity. *Proc. Natl. Acad. Sci. USA* 108: 15925-15930.
- Gupte, P.R., Albery, G.F., Gismann, J., Sweeny, A.R. & **Weissing, F.J.** 2023. Novel pathogen introduction triggers rapid evolution in animal social movement strategies. *eLife*, 12: e81805, doi: 10.7554/eLife.81805.
- Gupte, P.R., Netz, C. & **Weissing, F.J.** 2023. The joint evolution of animal movement and competition strategies. *American Naturalist*, doi: 10.1086/725394.
- Kozielska, M.A. & **Weissing, F.J.** 2024. A neural network model for the evolution of learning in changing environments. *PLoS Comp Biol* 20: e1011840, doi: 10.1371/journal.pcbi.1011840.
- Moreno-Gómez, S., Sorg, R.A., Kjos, M., **Weissing, F.J.**, Van Doorn, G.S. & Veening, J.W. 2017. Quorum sensing integrates environmental cues, cell density and cell history to control bacterial competence. *Nature Comm.* 8: 854.
- Netz, C., Hildenbrandt, H. & **Weissing, F.J.** 2022. Complex eco-evolutionary dynamics induced by the coevolution of predator-prey movement strategies. *Evol. Ecol.* 36: 1-17, doi: 10.1007/s10682-021-10140-x.
- Romero-Mujalli, D., Fuchs, L.I.R., Haase, M., Hildebrandt, J.-P., **Weissing, F.J.**, & Revilla, T.A. 2024. Emergence of phenotypic plasticity through epigenetic mechanisms. *Evolution Letters*, in press.
- Solopova, A., Van Gestel, J., **Weissing, F.J.**, Bachmann, H., Teusink, B., Kok, J., Kuipers, O.P. 2014. Bet-hedging during bacterial diauxic shift. *Proc. Natl. Acad. Sci. USA* 111: 7427-7432.
- Van den Berg, P. & **Weissing, F.J.** 2015. The importance of mechanisms for the evolution of cooperation. *Proc. R. Soc. B* 282:20151382.
- Van Gestel, J. & **Weissing, F.J.** 2016. Regulatory mechanisms link phenotypic plasticity to evolvability. *Scientific Rep.* 6:24524, doi: 10.1038/srep24524
- Van Gestel, J. & **Weissing, F.J.** 2018. Is plasticity caused by single genes? *Nature* 555: E19-E23.
- Visser, B., Alborn, H.T., Rondeaux, S., Haillot, M., Hance, T., Rebar, D., Riederer, J.M., Tiso, S., van Eldijk, T.J.B., **Weissing, F.J.** & Nieberding, C.M. 2021. Phenotypic plasticity explains apparent reverse evolution of fat synthesis in parasitic wasps. *Scientific Reports* 11: 7751. doi: 10.1038/s41598-021-86736-8.

Animal personalities

- Botero, C.A., Pen, I., Komdeur, J. & **Weissing, F.J.** 2010. The evolution of individual variation in communication strategies. *Evolution*, 64: 3123-3133.
- Molleman, L., Van den Berg, P. & **Weissing, F.J.** 2014. Consistent individual differences in human social learning strategies. *Nature Communications* 5: 3570.
- Netz, C., Ramesh, A., Gismann, J., Gupte, P.R. & **Weissing, F.J.** 2022. Details matter when modelling the effects of animal personality on the spatial distribution of foragers. *Proc. R. Soc. B* 289: 20210903, doi: 10.1098/rspb.2021.0903.
- Netz, C., Ramesh, A. & **Weissing, F.J.** 2023. Ideal free distribution of unequal competitors: spatial assortment and evolutionary diversification of competitive ability. *Animal Behaviour* 201: 13-21; doi: 10.1016/j.anbehav.2023.04.004

- Ramesh, A., Gismann, J., Groothuis, T.G.G., **Weissing, F.J.** & Nicolaus, M. 2023. Mesocosm experiments reveal the loss of migratory tendencies in a recently isolated population of three-spined sticklebacks. *Biology Letters* 19: 20220602, doi: 10.1098/rsbl.2022.0602.
- Wolf, M., Van Doorn, G.S., Leimar, O. & **Weissing, F.J.** 2007. Life-history trade-offs favour the evolution of animal personalities. *Nature* 447: 581-584.
- Wolf, M., Van Doorn, G.S. & **Weissing, F.J.** 2008. Evolutionary emergence of responsive and unresponsive personalities. *Proc. Natl. Acad. Sci. USA* 105: 15825-15830.
- Wolf, M. & **Weissing, F.J.** 2010. An explanatory framework for adaptive personality differences. *Phil. Trans. R. Soc. B* 365: 3959-3968.
- Wolf, M. & **Weissing, F.J.** 2012. Animal personalities: consequences for ecology and evolution. *Trends Ecol. Evol.* 27: 452-461.

Cultural evolution

- Boon, E., van den Berg, P., Molleman, L. & **Weissing, F.J.** (eds) 2021. *Foundations of Cultural Evolution*. Theme issue of *Phil. Trans. R. Soc. B* 376, issue 1828.
- Erten, E.Y., van den Berg P. & **Weissing F.J.** 2018. Effect of acculturation on the evolution of a multicultural society. *Nature Comm* 9: 58, doi: 10.1038/s41467-017-02513-0.
- Henrich, J., Bowles, S., Boyd, R.T., Hopfensitz, A., Richerson, P.J., Sigmund, K., Smith, E.A., **Weissing, F.J.** & Young, H.P. 2003. The cultural and genetic evolution of human cooperation. In: Hammerstein, P. (ed.). *Genetic and Cultural Evolution of Cooperation*. MIT Press, pp 445-468.
- Molleman, L., Quiñones, A.E. & **Weissing, F.J.** 2013. Cultural evolution of cooperation: the interplay between forms of social learning and group selection. *Evol. Hum. Behav.* 34: 342-349.
- Molleman, L., Van den Berg, P. & **Weissing, F.J.** 2014. Consistent individual differences in human social learning strategies. *Nature Communications* 5: 3570.
- Rostovtseva, V.V., Butovskaya, M.L., Mezentseva, A.A. & **Weissing, F.J.** 2023. Effects of sex and sex-related facial traits on trust and trustworthiness: An experimental study. *Frontiers in Psychology* 13: 925601, doi: 10.3389/fpsyg.2022.925601.
- Rostovtseva, V.V., Puurtinen, M., Méndez Salinas, E., Cox, R.F.A., Groothuis, A.G.G., Butovskaya, M.L. & **Weissing, F.J.** 2023. Unravelling the many facets of human cooperation in an experimental study. *Scientific Reports* 13: 19573, doi: 10.1038/s41598-023-46944-w.
- Smolla, M., Jansson, F., Lehmann, L., Houkes, W., **Weissing, F.J.**, Hammerstein, P., Dall, S.R.X., Kuijper, B. & Enquist, M. 2021. Underappreciated features of cultural evolution. *Phil. Trans. R. Soc. B* 376: 20200259. doi: 10.1098/rstb.2020.0259
- Van den Berg, P., Fawcett, T.W., Buunk, A.P. & **Weissing, F.J.** 2013. The evolution of parent-offspring conflict over mate choice. *Evol. Human Behav.*, 34: 405-411.
- Van den Berg, P., Molleman, L. & **Weissing, F.J.** 2015. Focus on the success of others leads to selfish behavior. *Proc. Natl. Acad. Sci. USA* 112:2912-2917.
- Weissing, F.J.** & Ostrom, E. 1993. Irrigation institutions and the games irrigators play. Rule enforcement on government- and farmer-managed systems. In: Scharpf, F.W. (ed.). *Games in Hierarchies and Networks*. Boulder: Westview, pp 387-428.

Evolution and self-organization // Evolution of cooperation

- De Jager, M., van de Koppel, J., Weerman, E.J. & **Weissing, F.J.** 2020. Patterning in mussel beds explained by the interplay of multi-level selection and spatial self-organization. *Front. Ecol. Evol.* 8:7. doi: 10.3389/fevo.2020.00007
- De Jager, M., **Weissing, F.J.**, Herman, P.M.J., Nolet, B.A. & Van de Koppel, J. 2011 Lévy walks evolve through interaction between movement and environmental complexity. *Science* 332: 1551-1553.
- De Jager, M., **Weissing, F.J.** & Van de Koppel, J. 2017. Why mussels stick together: spatial self-organization affects the evolution of cooperation. *Evol Ecol* 31: 547-558.

- Duarte, A., Keller, L., Pen, I. & **Weissing, F.J.** 2011. An evolutionary perspective on self-organized division of labor in social insects. *Annu. Rev. Ecol. Evol. Syst.* 42: 91–110.
- Duarte, A., Scholtens, E. & **Weissing, F.J.** 2012. Implications of behavioral architecture for the evolution of self-organized division of labor. *PLoS Comput. Biol.* 8: e1002430.
- Kreider, J.J., Janzen, T., Bernadou, A., Elsner, D., Kramer, B. H. & **Weissing, F.J.** 2022. Resource sharing is sufficient for the emergence of division of labour. *Nature Communications* 13: 7232, doi: 10.1038/s41467-022-35038-2.
- Pen, I. & **Weissing, F.J.** 2000. Towards a unified theory of cooperative breeding: the role of ecology and life history re-examined. *Proc. R. Soc. Lond. B* 267: 2411-2418.
- Quiñones, A.E., Van Doorn, G.S., Pen, I., **Weissing, F.J.** & Taborsky, M. 2016. Negotiation and appeasement can be more effective drivers of sociality than kin selection. *Phil. Trans. R. Soc. B* 371:20150089.
- Ramazi, P., Cao, M. & **Weissing, F.J.** 2016. Evolutionary dynamics of homophily and heterophily. *Scientific Rep.* 6:22766, doi: 10.1038/srep22766
- Van den Berg, P., Molleman, L. & **Weissing, F.J.** 2015. Focus on the success of others leads to selfish behavior. *Proc. Natl. Acad. Sci. USA* 112:2912-2917.
- Van den Berg, P. & **Weissing, F.J.** 2015. The importance of mechanisms for the evolution of cooperation. *Proc. R. Soc. B* 282:20151382.
- Van Gestel, J., **Weissing, F.J.**, Kuipers, O.P. & Kovács, A.T. 2014. Density of founder cells affects spatial pattern formation and cooperation in *Bacillus subtilis* biofilms. *ISME Journal* 8: 2069-2079.

Evolutionary game theory

- McNamara, J.M. & **Weissing, F.J.** 2010. Evolutionary game theory. In: Székely, T., Moore, A.J. & Komdeur, J. (eds). *Social Behaviour: Genes, Ecology and Evolution*. Cambridge University Press, pp 109-133.
- Van Doorn, G.S., Hengeveld, G.M. & **Weissing, F.J.** 2003ab. The evolution of social dominance. *Behaviour* 140: 1305-1332 & 1333-1358.
- Weissing, F.J.** 1991. Evolutionary stability and dynamic stability in Rock-Scissors-Paper games. In: Selten, R. (ed.). *Game Equilibrium Models I. Evolution and Game Dynamics*. Berlin: Springer-Verlag, pp. 29-97.

Evolvability

- Gupte, P.R., Albery, G.F., Gismann, J., Sweeny, A.R. & **Weissing, F.J.** 2023. Novel pathogen introduction triggers rapid evolution in animal social movement strategies. *eLife*, 12: e81805, doi: 10.7554/eLife.81805.
- Netz, C., Hildenbrandt, H. & **Weissing, F.J.** 2022. Complex eco-evolutionary dynamics induced by the coevolution of predator-prey movement strategies. *Evol. Ecol.* 36: 1-17, doi: 10.1007/s10682-021-10140-x.
- Riederer, J.M., Tiso, S., Van Eldijk, T.J.B. & **Weissing, F.J.** 2022. Capturing the facets of evolvability in a mechanistic framework. *Trends Ecol. Evol.* 37: 430-439, doi: 10.1016/j.tree.2022.01.004.
- Van Gestel, J. & **Weissing, F.J.** 2016. Regulatory mechanisms link phenotypic plasticity to evolvability. *Scientific Rep.* 6:24524, doi: 10.1038/srep24524
- Van Gestel, J. & **Weissing, F.J.** 2018. Is plasticity caused by single genes? *Nature* 555: E19-E23, doi: 10.1038/nature25495.

Life history evolution

- Borger, M.J., Komdeur, J., Richardson, D.S. & **Weissing, F.J.** 2023. The estimation of reproductive values from pedigrees. *Behavioral Ecology*, doi: 10.1093/beheco/arad049.
- Ens, B.J., **Weissing, F.J.** & Drent, R.H. 1995. The despotic distribution and deferred maturity: two sides of the same coin. *American Naturalist* 146: 625-650.

- Kramer, B.H., Van Doorn, G.S., **Weissing, F.J.** & Pen, I. 2016. Lifespan divergence between social insect castes: challenges and opportunities for evolutionary theories of aging. *Curr. Opin. Insect Sci.* 16, 76-80.
- Long, X., Liu, Y., Liker, A., **Weissing, F.J.**, Komdeur, J. & Székely, T. 2022. Does ecology and life history predict parental cooperation in birds? – A comparative analysis. *Behav. Ecol. Sociobiol.* 76: 92, doi: 10.1007/s00265-022-03195-5.
- Pen, I. & **Weissing, F.J.** 2000. Towards a unified theory of cooperative breeding: the role of ecology and life history re-examined. *Proceedings of the Royal Society of London, Series B* 267: 2411-2418.
- Port, M., Hildenbrandt, H., Pen, I., Schülke, O., Ostner, J. & **Weissing, F.J.** 2020. The evolution of social philopatry in female primates. *Amer. J. Phys. Anthropol.* 173: 397-410, doi: 10.1002/ajpa.24123.
- Van Boven, M. & **Weissing, F.J.** 2004. The evolutionary economics of immunity. *American Naturalist* 163: 277-294.

Non-equilibrium dynamics

- Baldauf, S.A., Engqvist, L. & **Weissing, F.J.** 2014. Diversifying evolution of competitiveness. *Nature Comm.* 5: 5233
- Huisman, J., Johansson, A.M., Folmer, E.O. & **Weissing, F.J.** 2001. Towards a solution of the plankton paradox: the importance of physiology and life history. *Ecology Letters* 4: 408-411.
- Huisman, J. & **Weissing, F.J.** 1999. Biodiversity of plankton by species oscillations and chaos. *Nature* 402: 407-410.
- Huisman, J. & **Weissing, F.J.** 2001. Fundamental unpredictability in multispecies competition. *American Naturalist* 157: 488-494.
- Huisman, J. & **Weissing, F.J.** 2001. Biological conditions for oscillations and chaos generated by multispecies competition. *Ecology* 82: 2682-2695.
- Netz, C., Hildenbrandt, H. & **Weissing, F.J.** 2022. Complex eco-evolutionary dynamics induced by the coevolution of predator-prey movement strategies. *Evol. Ecol.* 36: 1-17, doi: 10.1007/s10682-021-10140-x.
- Van Doorn, G.S. & **Weissing, F.J.** 2006. Sexual conflict and the evolution of female preferences for indicators of male quality. *American Naturalist* 168: 743-757.

Phytoplankton competition

- Huisman, J., Jonker, R.R., Zonneveld, C. & **Weissing, F.J.** 1999. Competition for light between phytoplankton species: experimental tests of mechanistic theory. *Ecology* 80: 211-222.
- Huisman, J., van Oostveen, P. & **Weissing, F.J.** 1999. Critical depth and critical turbulence: two different mechanisms for the development of phytoplankton blooms. *Limnology and Oceanography* 44: 1781-1787.
- Huisman, J. & **Weissing, F.J.** 1995. Competition for nutrients and light in a mixed water column: a theoretical analysis. *American Naturalist* 146: 536-564.
- Huisman, J. & **Weissing, F.J.** 1994. Light-limited growth and competition for light in well-mixed aquatic environments: an elementary model. *Ecology* 75: 507-520.

Segregation distortion // Sex determination // Sex allocation

- Daan, S., Dijkstra, C. & **Weissing, F.J.** 1996. An evolutionary explanation for seasonal trends in avian sex ratios. *Behavioral Ecology* 7: 426-430.
- Fawcett, T.W., Kuijper, A., **Weissing, F.J.** & Pen, I. 2011. Sex-ratio control erodes sexual selection, revealing evolutionary feedback from adaptive plasticity. *Proc. Natl. Acad. Sci. USA* 108: 15925-15930.
- Kalita, I.K., Marois, E., Kozielska, M., **Weissing, F.J.**, Jaouen, E., Möckel, M.M., Rühle, F., Butter, F., Basilicata, M.F. & Keller Valsecchi, C.I. 2023. The sex-specific factor SOA controls dosage

- compensation in *Anopheles* mosquitoes. *Nature* 623: 175-182, doi: 10.1038/s41586-023-06641-0.
- Kozielska, M., **Weissing, F.J.**, Beukeboom, L.W. & Pen, I. 2010. Segregation distortion and the evolution of sex-determining mechanisms. *Heredity* 104: 100-112.
- Manser, A., Lindholm, A. & **Weissing, F.J.** 2017. The evolution of costly mate choice against segregation distorters. *Evolution* 71: 2817-2828.
- Pen, I. & **Weissing, F.J.** 1999. Sperm competition and sex allocation in simultaneous hermaphrodites: A new look at Charnov's invariance principle. *Evolutionary Ecology Research* 1: 517-525.
- Pen, I. & **Weissing, F.J.** 2002. Optimal sex allocation: steps towards a mechanistic theory. In: Hardy, I. (ed). *Sex Ratios: Concepts and Research Methods*. Cambridge University Press, pp. 26-45.
- Van Boven, M. & **Weissing, F.J.** 1999. Segregation distortion in a deme-structured population: Opposing demands of gene, individual, and group selection. *Journal of Evolutionary Biology* 12: 80-93.
- Weissing, F.J.** & M. van Boven 2001. Selection and segregation distortion in a sex-differentiated population. *Theoretical Population Biology* 60: 327-341.

Sexual selection // Sex roles // Adult sex ratios

- Fawcett, T.W., Kuijper, A., **Weissing, F.J.** & Pen, I. 2011. Sex-ratio control erodes sexual selection, revealing evolutionary feedback from adaptive plasticity. *PNAS* 108: 15925-15930.
- Heisler, L., Andersson, M.B., Arnold, S.J., Boake, C.R., Borgia, G., Hausfater, G., Kirkpatrick, M., Lande, R., Maynard Smith, J., O'Donald, P., Thornhill, A.R. & **Weissing F.J.** 1987. The evolution of mating preferences and sexually selected traits. In: Bradbury, J.W. and Andersson, M.B. (eds). *Sexual Selection: Testing the Alternatives*. New York: John Wiley and Sons, pp. 96-118.
- Kuijper, A.L.W., Pen, I. & **Weissing, F.J.** 2012. A guide to sexual selection theory. *Annu. Rev. Ecol. Evol. Syst.* 43: 287-311.
- Long, X. & **Weissing, F.J.** 2023. Transient polymorphisms in parental care strategies drive divergence of sex roles. *Nature Communications* 14: 6805, doi: 10.1038/s41467-023-42607-6
- Manser, A., Lindholm, A. & **Weissing, F.J.** 2017. The evolution of costly mate choice against segregation distorters. *Evolution* 71: 2817-2828.
- Schacht, R., Beissinger, S.R., Wedekind, C., Jennions, M.D., Geffroy, B., Liker, A., Kappeler, P.M., **Weissing, F.J.**, Kramer, K.L., Hesketh, T., Boissier, J., Uggla, C., Hollinghaus, M. & Székely, T. 2022. Adult sex ratios: causes of variation and implications for animal and human societies. *Communications Biology* 5: 1273, doi 10.1038/s42003-022-04223-w.
- Van Doorn, G.S. & **Weissing, F.J.** 2004. The evolution of female preferences for multiple indicators of quality. *American Naturalist* 164: 173-186.
- Van Doorn, G.S. & **Weissing, F.J.** 2006. Sexual conflict and the evolution of female preferences for indicators of male quality. *American Naturalist* 168: 743-757.
- Zheng, J., Komdeur, J. & **Weissing, F.J.** 2023 Effects of season length and uniparental care efficacy on the evolution of parental care. *Journal of Animal Ecology*, doi: 10.1111/1365-2656.13967.

Speciation

- Etienne, R.S., Apol, M.E.F., Olf, H. & **Weissing F.J.** 2007. Modes of speciation and the neutral theory of biodiversity. *Oikos* 116: 241-258.
- Qvarnström, A., Veen, T., Husby, A., Ålund, M. & **Weissing, F.J.** 2023. Assortative mating in an ecological context: Effects of mate choice errors and relative species abundance on the frequency and asymmetry of hybridization. *American Naturalist* 201: 125-137, doi: 10.1086/722156.
- Van Doorn, G.S., Dieckmann, U. & **Weissing, F.J.** 2004. Sympatric speciation by sexual selection: a critical re-evaluation. *American Naturalist* 163: 709-725.
- Van Doorn, G.S., Edelaar, P. & **Weissing, F.J.** 2009. On the origin of species by natural and sexual selection. *Science* 326: 1704-1707.

Van Doorn, G.S., Luttikhuizen, P.C. & **Weissing, F.J.** 2001. Sexual selection at the protein level drives the extraordinary divergence of sex related genes during sympatric speciation. *Proceedings Royal Society London, Series B* 268: 2155-2161.

Weissing, F.J., Edelaar, P. & van Doorn, G.S. 2011. Adaptive speciation theory: a conceptual review. *Behav. Ecol. Sociobiol.* 65: 461–480.