Selection in two-sex structured populations

de Vries, C.

Publication date
2019

Document Version
Other version

License
Other

Link to publication

Bibliography

Abrams, P. A., and H. Matsuda. 1997. Prey adaptation as a cause of predator-prey cycles. Evolution 51:1742–1750.

Altman, P. L., D. S. Dittmer, et al. 1962. Growth, including reproduction and morphological development. Growth, including reproduction and morphological development. .

Alvarez-Buylla, E., R. Garcia-Barrios, C. Lara-Moreno, and M. Martínez-Ramos. 1996. Demographic and genetic models in conservation biology: applications and perspectives for tropical rain forest tree species. Annual Review of Ecology and Systematics 27:387–421.

Anderson, W. W., and T. K. Watanabe. 1974. Selection by fertility in *Drosophila pseudoobscura*. Genetics 77:559–564.

Arnaud, L., E. Haubruge, and M. Gage. 2005. The malathion-specific resistance gene confers a sperm competition advantage in *Tribolium castaneum*. Functional Ecology 19:1032–1039.

Auer, S. K., J. D. Arendt, R. Chandramouli, and D. N. Reznick. 2010. Juvenile compensatory growth has negative consequences for reproduction in trinidadian guppies (*Poecilia reticulata*). Ecology Letters 13:998–1007.

Badyaev, A. V., and G. E. Hill. 2002. Paternal care as a conditional strategy: distinct reproductive tactics associated with elaboration of plumage ornamentation in the house finch. Behavioral Ecology 13:591–597.

Baião, P. C., E. Schreiber, and P. G. Parker. 2007. The genetic basis of the plumage polymorphism in red-footed boobies (sula sula): a melanocortin-1 receptor (mc1r) analysis. Journal of Heredity 98:287–292.

Barfield, M., R. D. Holt, and R. Gomulkiewicz. 2011. Evolution in stage-structured populations. The American Naturalist 177:397–409.

Barrett, R. D., S. M. Rogers, and D. Schluter. 2008. Natural selection on a major armor gene in threespine stickleback. Science 322:255–257.

Beeman, R. W. 1983. Inheritance and linkage of malathion resistance in the red flour beetle. Journal of Economic Entomology 76:737–740.

Bell, A., N. Dingemanse, S. Hankison, M. Langenhof, and K. Rollins. 2011. Early exposure to nonlethal predation risk by size-selective predators increases somatic growth and decreases size at adulthood in threespined sticklebacks. Journal of evolutionary biology 24:943–953.

Berejikian, B. A., D. M. Van Doornik, R. C. Endicott, T. L. Hoffnagle, E. P. Tezak, M. E. Moore, and J. Atkins. 2010. Mating success of alternative male phenotypes and evidence for frequency-dependent selection in chinook salmon, *Oncorhynchus tshawytscha*. Canadian Journal of Fisheries and Aquatic Sciences 67:1933–1941.

Bodmer, W. F. 1965. Differential fertility in population genetics models. Genetics 51:411–424.

Boerlijst, M. C., and A. M. de Roos. 2015. Competition and facilitation between a disease and a predator in a stunted prey population. PloS one 10:e0132251.

Boerner, M., J. Hoffman, W. Amos, N. Chakarov, and O. Kruger. 2013. No correlation between multi-locus heterozygosity and fitness in the common buzzard despite heterozygote advantage for plumage colour. Journal of evolutionary biology 26:2233–2243.

Bolnick, D. I., and M. Doebeli. 2003. Sexual dimorphism and adaptive speciation: two sides of the same ecological coin. Evolution 57:2433–2449.

Bonduriansky, R., and S. F. Chenoweth. 2009. Intralocus sexual conflict. Trends in ecology & evolution 24:280–288.

Bonduriansky, R., A. Maklakov, F. Zajitschek, and R. Brooks. 2008. Sexual selection, sexual conflict and the evolution of ageing and life span. Functional ecology 22:443–453.

Brooks, R. 2000. Negative genetic correlation between male sexual attractiveness and survival. Nature 406:67.

Caswell, H. 1982. Life history theory and the equilibrium status of populations. The American Naturalist 120:317–339.

———. 2001. Matrix Population Models: Construction, Analysis, and Interpretation. Second edition. Sinauer Associates, Sunderland, Massachusetts, USA.

———. 2007*a*. Extrinsic mortality and the evolution of senescence. Trends in ecology & evolution 22:173–174.

———. 2007*b*. Sensitivity analysis of transient population dynamics. Ecology letters 10:1–15.

———. 2008. Perturbation analysis of nonlinear matrix population models. Demographic Research 18:59–116.

———. 2011. Beyond r0: demographic models for variability of lifetime reproductive output. PloS one 6:e20809.

———. 2012. Matrix models and sensitivity analysis of populations classified by age and stage: a vec-permutation matrix approach. Theoretical Ecology 5:403–417.

———. 2018. Sensitivity Analysis: Matrix Methods for Demography and Ecology. Demographic Research Monographs (in press). Springer-Verlag.

Caswell, H., C. de Vries, N. Hartemink, G. Roth, and S. F. van Daalen. 2018. Age × stage-classified demographic analysis: a comprehensive approach. Ecological Monographs 88:560–584.

Caswell, H., J. R. H. Koenig, and Q. Ross. 1972. Systems Analysis and Simulation in Ecology, Vol II., chap. An introduction to systems analysis for ecologists., pages 1–78. Academic Press, N.Y.

Caswell, H., and A. M. John. 1992. From the individual to the population in demographic models. Pages 36–61 *in* Individual-based models and approaches in ecology. Springer.

Caswell, H., and R. Salguero-Gómez. 2013. Age, stage and senescence in plants. Journal of Ecology 101:585–595.

Caswell, H., and E. Shyu. 2017. Senescence, selection gradients and mortality. The evolution of senescence in the tree of life pages 56–82.

Caswell, H., T. Takada, and C. M. Hunter. 2004. Sensitivity analysis of equilibrium in density-dependent matrix population models. Ecology Letters 7:380–387.

Caswell, H., and D. E. Weeks. 1986. Two-sex models: chaos, extinction, and other dynamic consequences of sex. The American Naturalist 128:707–735.

Charlesworth, B. 1970. Selection in populations with overlapping generations. I. The use of Malthusian parameters in population genetics. Theoretical Population Biology 1:352–370.

———. 1971. Selection in density-regulated populations. Ecology 52:469–474.

———. 1972. Selection in populations with overlapping generations. III. Conditions for genetic equilibrium. Theoretical Population Biology 3:377–395.

———. 1994. Evolution in age-structured populations. 2nd ed. Cambridge University Press, Cambridge, UK.

Charlesworth, B., and J. T. Giesel. 1972*a*. Selection in populations with overlapping generations. II. Relations between gene frequency and demographic variables. The American Naturalist 106:388–401.

———. 1972*b*. Selection in populations with overlapping generations. IV. Fluctuations in gene frequency with density-dependent selection. The American Naturalist 106:402–411.

Cheung, W. 2002. The effects of natural selection on nonlinear population dynamics. M.S. thesis. California State University, Los Angeles.

Childs, D. Z., B. C. Sheldon, and M. Rees. 2016. The evolution of labile traits in sex-and age-structured populations. Journal of Animal Ecology 85:329–342.

Chippindale, A. K., J. R. Gibson, and W. R. Rice. 2001. Negative genetic correlation for adult fitness between sexes reveals ontogenetic conflict in drosophila. Proceedings of the National Academy of Sciences 98:1671–1675.

Clark, A. G., and M. W. Feldman. 1986. A numerical simulation of the one-locus, multiple-allele fertility model. Genetics 113:161–176.

Constable, G. W. A., T. Rogers, A. J. McKane, and C. E. Tarnita. 2016. Demographic noise can reverse the direction of deterministic selection. Proceedings of the National Academy of Sciences .

Cooke, F., G. Finney, and R. Rockwell. 1976. Assortative mating in lesser snow geese (anser caerulescens). Behavior genetics 6:127–140.

Cordero, A., S. S. Carbone, and C. Utzeri. 1998. Mating opportunities and mating costs are reduced in androchrome female damselflies, *ischnura elegans* (odonata). Animal Behaviour 55:185–197.

Costantino, R., J. Cushing, B. Dennis, and R. A. Desharnais. 1995. Experimentally induced transitions in the dynamic behaviour of insect populations. Nature 375:227–230.

Costantino, R., R. Desharnais, J. Cushing, and B. Dennis. 1997. Chaotic dynamics in an insect population. Science 275:389–391.

Costantino, R. F., R. A. Desharnais, J. M. Cushing, B. Dennis, S. M. Henson, and A. A. King. 2005. Nonlinear stochastic population dynamics: the flour beetle *Tribolium* as an effective tool of discovery. Advances in Ecological Research 37:101–141.

Coulson, T., T. Benton, P. Lundberg, S. Dall, and B. Kendall. 2006. Putting evolutionary biology back in the ecological theatre: a demographic framework mapping genes to communities. Evolutionary Ecology Research 8:1155–1171.

Coulson, T., D. R. MacNulty, D. R. Stahler, B. vonHoldt, R. K. Wayne, and D. W. Smith. 2011. Modeling effects of environmental change on wolf population dynamics, trait evolution, and life history. Science 334:1275–1278.

Coulson, T., and S. Tuljapurkar. 2008. The dynamics of a quantitative trait in an age-structured population living in a variable environment. The American Naturalist 172:599–612.

Coulson, T., S. Tuljapurkar, and D. Z. Childs. 2010. Using evolutionary demography to link life history theory, quantitative genetics and population ecology.

Journal of Animal Ecology 79:1226–1240.

Crow, J. F., and M. Kimura. 1970. An introduction to population genetics theory. Harper and Row, New York.

Cushing, J. M., R. F. Costantino, B. Dennis, R. Desharnais, and S. M. Henson. 2002. Chaos in ecology: experimental nonlinear dynamics. Academic Press, San Diego, California, USA.

Darwin, C. 1888. The descent of man and selection in relation to sex, vol. 1. John Murray.

de Roos, A. M., and L. Persson. 2013. Population and community ecology of ontogenetic development. Princeton University Press.

De Roos, A. M., T. Schellekens, T. van Kooten, K. van de Wolfshaar, D. Claessen, and L. Persson. 2007. Food-dependent growth leads to overcompensation in stage-specific biomass when mortality increases: the influence of maturation versus reproduction regulation. The American Naturalist 170:E59–E76.

de Vries, C. 2019. Assortative mating in stage-structured Mendelian populations. In preparation.

de Vries, C., and H. Caswell. 2017. Demography when history matters: construction and analysis of second-order matrix population models. Theoretical Ecology .

———. 2018*a*. Combining ecology and genetics: Mendelian matrix population models. In preparation.

———. 2018*b*. Genetics, demography, and polymorphisms in two-sex structured populations. In preparation.

———. 2018*c*. Nonlinear stage genotype matrix population models for eco-evolutionary dynamics: the case of pesticide resistance in tribolium. In preparation.

Dennis, B., R. A. Desharnais, J. Cushing, and R. Costantino. 1995. Nonlinear demographic dynamics: mathematical models, statistical methods, and biological experiments. Ecological Monographs 65:261–282.

Dercole, F., and S. Rinaldi. 2008. Analysis of evolutionary processes: the adaptive dynamics approach and its applications. Princeton University Press, Princeton, New Jersey, USA.

Díaz-Muñoz, S. L., A. M. Boddy, G. Dantas, C. M. Waters, and J. L. Bronstein. 2016. Contextual organismality: Beyond pattern to process in the emergence of organisms. Evolution 70:2669–2677.

Dieckmann, U., and R. Law. 1996. The dynamical theory of coevolution: a derivation from stochastic ecological processes. Journal of mathematical biology

34:579–612.

Diekmann, O. 2004. A beginner's guide to adaptive dynamics. Polish Academy of Sciences, Banach Center Publications 63:47–86.

Diekmann, O., M. Gyllenberg, and J. Metz. 2003. Steady-state analysis of structured population models. Theoretical population biology 63:309–338.

Doherty, P. F., G. Sorci, J. A. Royle, J. E. Hines, J. D. Nichols, and T. Boulinier. 2003. Sexual selection affects local extinction and turnover in bird communities. Proceedings of the National Academy of Sciences 100:5858–5862.

Edmunds, J., J. Cushing, R. Costantino, S. M. Henson, B. Dennis, and R. Desharnais. 2003. Park's *Tribolium* competition experiments: a non-equilibrium species coexistence hypothesis. Journal of Animal Ecology 72:703–712.

Eizirik, E., N. Yuhki, W. E. Johnson, M. Menotti-Raymond, S. S. Hannah, and S. J. O'Brien. 2003. Molecular genetics and evolution of melanism in the cat family. Current biology 13:448–453.

Emlen, J. M. 1970. Age specificity and ecological theory. Ecology 51:588–601.

Engen, S., and B.-E. Sæther. 2017. r-and k-selection in fluctuating populations is determined by the evolutionary trade-off between two fitness measures: Growth rate and lifetime reproductive success. Evolution 71:167–173.

Falconer, D. S. 1960. Introduction to quantitative genetics. Oliver And Boyd, Edinburgh, London.

Feldman, M. W., F. B. Christiansen, and U. Liberman. 1983. On some models of fertility selection. Genetics 105:1003–1010.

Fernandes Martins, M. J., G. Hunt, R. Lockwood, J. Swaddle, and D. J Horne. 2017. Correlation between investment in sexual traits and valve sexual dimorphism in cyprideis species (ostracoda). PLoS ONE 12:e0177791.

Ferriere, R., and S. Legendre. 2013. Eco-evolutionary feedbacks, adaptive dynamics and evolutionary rescue theory. Philosophical Transactions of the Royal Society of London B: Biological Sciences 368.

Ffrench-Constant, R. H., P. J. Daborn, and G. Le Goff. 2004. The genetics and genomics of insecticide resistance. Trends Genet. 20:163–170.

Fieberg, J., and S. P. Ellner. 2001. Stochastic matrix models for conservation and management: a comparative review of methods. Ecology letters 4:244–266.

Fisher, R. 1930. The Genetical Theory of Natural Selection. The Clarendon Press.

Foerster, K., T. Coulson, B. C. Sheldon, J. M. Pemberton, T. H. Clutton-Brock, and L. E. Kruuk. 2007. Sexually antagonistic genetic variation for fitness in red deer. Nature 447:1107.

Fronhofer, E. A., A. Kubisch, T. Hovestadt, and H.-J. Poethke. 2011. Assortative mating counteracts the evolution of dispersal polymorphisms. Evolution 65:2461–2469.

Fussmann, G., M. Loreau, and P. Abrams. 2007. Eco-evolutionary dynamics of communities and ecosystems. Functional Ecology 21:465–477.

Gangoso, L., J. M. Grande, A.-L. Ducrest, J. Figuerola, G. R. Bortolotti, J. Andrés, and A. Roulin. 2011. Mc1r-dependent, melanin-based colour polymorphism is associated with cell-mediated response in the eleonora's falcon. Journal of evolutionary biology 24:2055–2063.

Georghiou, G. 1969. Genetics of resistance to insecticides in houseflies and mosquitoes. Experimental Parasitology 26:224–255.

Geritz, S. A., G. Mesze, J. A. Metz, et al. 1998. Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. Evolutionary ecology 12:35–57.

Giesel, J. T. 1972. Maintenance of genetic variability in natural populations-an alternative implication of the charlesworth-giesel hypothesis. The American Naturalist 106:412–414.

Goldman, N., C. F. Westoff, and C. Hammerslough. 1984. Demography of the marriage market in the united states. Population Index pages 5–25.

Griesemer, J. 2001. The units of evolutionary transition. Selection 1:67–80.

Griesemer, J. R. 2000. Reproduction and the reduction of genetics. The concept of the gene in development and evolution: Historical and epistemological perspectives pages 240–285.

Gross, M. R. 1985. Disruptive selection for alternative life histories in salmon. Nature 313:47–48.

Hadeler, K., and U. Liberman. 1975. Selection models with fertility differences. Journal of Mathematical Biology 2:19–32.

Hadeler, K., R. Waldstätter, and A. Wörz-Busekros. 1988. Models for pair formation in bisexual populations. Journal of mathematical biology 26:635–649.

Hamilton, W. D. 1966. The moulding of senescence by natural selection. Journal of Theoretical Biology 12:12–45.

Harano, T., K. Okada, S. Nakayama, T. Miyatake, and D. J. Hosken. 2010. Intralocus sexual conflict unresolved by sex-limited trait expression. Current Biology 20:2036–2039.

Hartemink, N., T. I. Missov, and H. Caswell. 2017. Stochasticity, heterogeneity, and variance in longevity in human populations. Theoretical population biology 114:107–116.

Hartman, H. 1984. The origin of the eukaryotic cell. Speculations Sci Technol 7:77–81.

Harts, A. M., L. E. Schwanz, and H. Kokko. 2014. Demography can favour female-advantageous alleles. Proceedings of the Royal Society of London B: Biological Sciences 281:20140005.

Hasegawa, M., and E. Arai. 2018. Sexually dimorphic swallows have higher extinction risk. Ecology and evolution 8:992–996.

Hatcher, M. J. 2000. Persistence of selfish genetic elements: population structure and conflict. Trends in ecology & evolution 15:271–277.

Haubruge, E., and L. Arnaud. 2001. Fitness consequences of malathion-specific resistance in red flour beetle (Coleoptera: Tenebrionidae) and selection for resistance in the absence of malathion. Journal of Economic Entomology 94:552–557.

Henderson, H. V., and S. R. Searle. 1981. The vec-permutation matrix, the vec operator and Kronecker products: a review. Linear and Multilinear Algebra 9:271–288.

Henson, S. M., R. Costantino, R. A. Desharnais, J. Cushing, and B. Dennis. 2002. Basins of attraction: population dynamics with two stable 4-cycles. Oikos 98:17–24.

Hoyer, R., and F. Plapp Jr. 1968. Insecticide resistance in the house fly: identification of a gene that confers resistance to organotin insecticides and acts as an intensifier of parathion resistance. Journal of Economic Entomology 61:1269–1276.

Hunter, C. M., and H. Caswell. 2005. The use of the vec-permutation matrix in spatial matrix population models. Ecological modelling 188:15–21.

Hutchinson, G. E. 1965. The ecological theater and the evolutionary play. Yale University Press, New Haven, Connecticut, USA.

Iannelli, M., M. Martcheva, and F. A. Milner. 2005. Gender-structured population modeling: mathematical methods, numerics, and simulations. SIAM, Philadelphia, Pennsylvania,USA.

Jenouvrier, S., H. Caswell, C. Barbraud, and H. Weimerskirch. 2010. Mating behavior, population growth, and the operational sex ratio: a periodic two-sex model approach. The American Naturalist 175:739–752.

Jones, E., R. Ferrière, and J. Bronstein. 2009. Eco-evolutionary dynamics of mutualists and exploiters. The American Naturalist 174:780–794. PMID: 19845459.

Joußen, N., D. G. Heckel, M. Haas, I. Schuphan, and B. Schmidt. 2008. Metabolism of imidacloprid and ddt by p450 cyp6g1 expressed in cell cultures of *Nicotiana tabacum* suggests detoxification of these insecticides in cyp6g1-

overexpressing strains of *Drosophila melanogaster*, leading to resistance. Pest Management Science: formerly Pesticide Science 64:65–73.

Kappers, E. F., C. de Vries, A. Alberda, W. Forstmeier, C. Both, and B. Kempenaers. 2018. Inheritance patterns of plumage coloration in common buzzards *Buteo buteo* do not support a one-locus two-allele model. Biology Letters 14.

Kempthorne, O. 1957. An Introduction to Genetic Statistics. John Wiley & Sons, New York, New York.

Keyfitz, N. 1972. The mathematics of sex and marriage. Pages 89–108 *in* Proceedings of the Sixth Berkeley Symposium on Mathematical Statistics and Probability, Volume 4: Biology and Health. University of California Press, Berkeley, Calif.

Kokko, H., and R. Brooks. 2003. Sexy to die for? Sexual selection and the risk of extinction. Pages 207–219 *in* Annales Zoologici Fennici. JSTOR.

Kokko, H., and M. D. Jennions. 2014. The relationship between sexual selection and sexual conflict. Cold Spring Harbor perspectives in biology page a017517.

Krüger, O., and J. Lindström. 2001. Lifetime reproductive success in common buzzard, *Buteo buteo*: from individual variation to population demography. Oikos 93:260–273.

Krüger, O., J. Lindström, and W. Amos. 2001. Maladaptive mate choice maintained by heterozygote advantage. Evolution 55:1207–1214.

Lande, R. 1982*a*. Elements of a quantitative genetic model of life history evolution. Pages 21–29 *in* Evolution and genetics of life histories. Springer.

———. 1982*b*. A quantitative genetic theory of life history evolution. Ecology 63:607–615.

Lande, R., and S. J. Arnold. 1983. The measurement of selection on correlated characters. Evolution 37:1210–1226.

Lande, R., S. Engen, and B.-E. Sæther. 2009. An evolutionary maximum principle for density-dependent population dynamics in a fluctuating environment. Philosophical Transactions of the Royal Society of London B: Biological Sciences 364:1511–1518.

Levene, H. 1953. Genetic equilibrium when more than one ecological niche is available. The American Naturalist 87:331–333.

Lewontin, R., and J. Krakauer. 1973. Distribution of gene frequency as a test of the theory of the selective neutrality of polymorphisms. Genetics 74:175–195.

Lewontin, R. C. 1974. The genetic basis of evolutionary change, vol. 560. Columbia University Press, New York, New York, USA.

Lindström, J., and H. Kokko. 1998. Sexual reproduction and population dynamics: the role of polygyny and demographic sex differences. Proceedings of the Royal Society of London B: Biological Sciences 265:483–488.

Lorch, P. D., S. Proulx, L. Rowe, and T. Day. 2003. Condition-dependent sexual selection can accelerate adaptation. Evolutionary Ecology Research 5:867–881.

Lumley, A. J., Ł. Michalczyk, J. J. Kitson, L. G. Spurgin, C. A. Morrison, J. L. Godwin, M. E. Dickinson, O. Y. Martin, B. C. Emerson, T. Chapman, et al. 2015. Sexual selection protects against extinction. Nature 522:470.

MacArthur, R. H. 1962. Some generalized theorems of natural selection. Proceedings of the National Academy of Sciences 48:1893–1897.

MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press.

Magnus, J. R., and H. Neudecker. 1979. The commutation matrix: some properties and applications. The Annals of Statistics pages 381–394.

———. 1985. Matrix differential calculus with applications to simple, Hadamard, and Kronecker products. Journal of Mathematical Psychology 29:474–492.

———. 1988. Matrix differential calculus with applications in statistics and econometrics. John Wiley and Sons, New York, New York.

Martínez-Ruiz, C., and R. J. Knell. 2017. Sexual selection can both increase and decrease extinction probability: reconciling demographic and evolutionary factors. Journal of Animal Ecology 86:117–127.

Martins, M. J. F., T. M. Puckett, R. Lockwood, J. P. Swaddle, and G. Hunt. 2018. High male sexual investment as a driver of extinction in fossil ostracods. Nature page 1.

McDaniel, S. F. 2005. Genetic correlations do not constrain the evolution of sexual dimorphism in the moss ceratodon purpureus. Evolution 59:2353–2361.

Merilä, J., B. C. Sheldon, and H. Ellegren. 1997. Antagonistic natural selection revealed by molecular sex identification of nestling collared flycatchers. Molecular Ecology 6:1167–1175.

Merrell, D. J., and C. F. Rodell. 1968. Seasonal selection in the leopard frog, *rana pipiens*. Evolution 22:284–288.

Metcalf, C., K. Rose, D. Childs, A. Sheppard, P. Grubb, and M. Rees. 2008. Evolution of flowering decisions in a stochastic, density-dependent environment. Proceedings of the National Academy of Sciences 105:10466–10470.

Metcalf, C. J. E., and S. Pavard. 2007. Why evolutionary biologists should be demographers. Trends in Ecology & Evolution 22:205–212.

Metz, H. A. 1977. State space models for animal behaviour. Pages 65–109 *in* Annals of Systems Research. Springer.

Metz, J. 2008. Fitness. Evolutionary Ecology. Vol. 2 of Encyclopedia of Ecology. Elsevier, Oxford 2:1599–1612.

Metz, J. A. J., and O. Diekmann. 1986. The dynamics of physiologically structured populations. Lecture Notes in Biomathematics. Springer-Verlag, Berlin.

Metz, J. A. J., R. M. Nisbet, and S. A. H. Geritz. 1992. How should we define 'fitness' for general ecological scenarios? Trends in Ecology and Evolution 7:198–202.

Miller, T. E. X., A. K. Shaw, B. D. Inouye, and M. G. Neubert. 2011. Sex-biased dispersal and the speed of two-sex invasions. The American Naturalist 177:549–561.

Moen, R. A., J. Pastor, and Y. Cohen. 1999. Antler growth and extinction of irish elk. Evolutionary Ecology Research 1:235–249.

Møller, A. P. 2003. Sexual selection and extinction: why sex matters and why asexual models are insufficient. Pages 221–230 *in* Annales Zoologici Fennici. JSTOR.

Mora, C., D. P. Tittensor, S. Adl, A. G. Simpson, and B. Worm. 2011. How many species are there on earth and in the ocean? PLoS biology 9:e1001127.

Moran, E. V., and J. S. Clark. 2012. Causes and consequences of unequal seedling production in forest trees: a case study in red oaks. Ecology 93:1082–1094.

Morrow, E. H., and C. Fricke. 2004. Sexual selection and the risk of extinction in mammals. Proceedings of the Royal Society of London. Series B: Biological Sciences 271:2395–2401.

Muir, W. M., and R. D. Howard. 1999. Possible ecological risks of transgenic organism release when transgenes affect mating success: Sexual selection and the trojan gene hypothesis. Proceedings of the National Academy of Sciences 96:13853–13856.

Mundy, N. I., N. S. Badcock, T. Hart, K. Scribner, K. Janssen, and N. J. Nadeau. 2004. Conserved genetic basis of a quantitative plumage trait involved in mate choice. Science 303:1870–1873.

Mylius, S. D., and J. Metz. 2004. When does evolution optimize? on the relationship between evolutionary stability, optimization and density dependence. Elements of Adaptive Dynamics. Cambridge University Press, Cambridge .

Nagylaki, T. 1992. Introduction to Theoretical Population Genetics. Springer-Verlag, Berlin, Germany.

Neubert, M. G., and H. Caswell. 2000. Demography and dispersal: calculation and sensitivity analysis of invasion speed for structured populations. Ecology 81:1613–1628.

Neve, P., R. Busi, M. Renton, and M. M. Vila-Aiub. 2014. Expanding the eco-evolutionary context of herbicide resistance research. Pest management science 70:1385–1393.

Newton, I. 1985. Lifetime reproductive output of female sparrowhawks. The Journal of Animal Ecology pages 241–253.

Núñez, M. A. B., N. L. Nuckolls, and S. E. Zanders. 2018. Genetic villains: killer meiotic drivers. Trends in Genetics .

Nussbaum, R. D. 1986. Convexity and log convexity for the spectral radius. Linear Algebra and its Applications 73:59–122.

———. 1989. Iterated nonlinear maps and Hilbert's projective metric. Part II, vol. 401. American Mathematical Soc.

Ohlberger, J., Ø. Langangen, E. Edeline, D. Claessen, I. J. Winfield, N. C. Stenseth, and L. A. Vøllestad. 2011. Stage-specific biomass overcompensation by juveniles in response to increased adult mortality in a wild fish population. Ecology 92:2175–2182.

Okasha, S. 2006. Evolution and the levels of selection. Oxford University Press.

Okerblom, J., W. Fletes, H. H. Patel, S. Schenk, A. Varki, and E. C. Breen. 2018. Human-like cmah inactivation in mice increases running endurance and decreases muscle fatigability: implications for human evolution. Proceedings of the Royal Society B: Biological Sciences 285:20181656.

Orive, M. E. 1995. Senescence in organisms with clonal reproduction and complex life histories. The American Naturalist 145:90–108.

———. 2001. Somatic mutations in organisms with complex life histories. Theoretical population biology 59:235–249.

Orive, M. E., M. Barfield, C. Fernandez, and R. D. Holt. 2017. Effects of clonal reproduction on evolutionary lag and evolutionary rescue. The American Naturalist 190:469–490.

Owen, A. 1953. A genetical system admitting of two distinct stable equilibria under natural selection. Heredity 7:97.

Pelletier, F., D. Garant, and A. Hendry. 2009. Eco-evolutionary dynamics. Philosophical Transactions of the Royal Society of London B: Biological Sciences 364:1483–1489.

Penrose, L. 1947. The meaning of 'fitness 'in human populations. Annals of Human Genetics 14:301–304.

Pigliucci, M. 2010. Genotype–phenotype mapping and the end of the 'genes as blueprint'metaphor. Philosophical Transactions of the Royal Society B: Biological Sciences 365:557–566.

Pincheira-Donoso, D., and J. Hunt. 2017. Fecundity selection theory: Concepts and evidence. Biological Reviews 92:341–356.

Pittendrigh, B., R. Reenan, B. Ganetzky, et al. 1997. Point mutations in the drosophila sodium channel gene para associated with resistance to ddt and pyrethroid insecticides. Molecular and General Genetics MGG 256:602–610.

Plard, F., S. Schindler, R. Arlettaz, and M. Schaub. 2018. Sex-specific heterogeneity in fixed morphological traits influences individual fitness in a monogamous bird population. The American Naturalist 191:106–119.

Pollak, E. 1978. With selection for fecundity the mean fitness does not necessarily increase. Genetics 90:383–389.

Pollak, R. A. 1990. Two-sex demographic models. Journal of Political Economy 98:399–420.

Price, D. K., and N. T. Burley. 1994. Constraints on the evolution of attractive traits: selection in male and female zebra finches. The American Naturalist 144:908–934.

Promislow, D. E., R. Montgomerie, and T. E. Martin. 1992. Mortality costs of sexual dimorphism in birds. Pages 143–150 *in* Proc. R. Soc. Lond. B. Vol. 250. The Royal Society.

Prout, T. 1968. Sufficient conditions for multiple niche polymorphism. The American Naturalist 102:493–496.

Rankin, D. J., and H. Kokko. 2007. Do males matter? The role of males in population dynamics. Oikos 116:335–348.

Rees, M., and S. P. Ellner. 2016. Evolving integral projection models: evolutionary demography meets eco-evolutionary dynamics. Methods in Ecology and Evolution 7:157–170.

Rice, W., and A. Chippindale. 2001. Intersexual ontogenetic conflict. Journal of Evolutionary Biology 14:685–693.

Rice, W. R., and B. Holland. 1997. The enemies within: intergenomic conflict, interlocus contest evolution (ICE), and the intraspecific Red Queen. Behavioral Ecology and Sociobiology 41:1–10.

Roff, D. A. 1992. The evolution of life histories. Chapman and Hall, New York, New York, USA.

Roth, W. 1934. On direct product matrices. Bulletin of the American Mathematical Society 40:461–468.

Roughgarden, J. 1971. Density-dependent natural selection. Ecology 52:453–468.

———. 1979. Theory of Population Genetics and Evolutionary Ecology: an Introduction. New York: Macmillan Publishing Co.,.

Roush, R. T., and J. A. McKenzie. 1987. Ecological genetics of insecticide and acaricide resistance. Annual Review of Entomology 32:361–380.

Rueffler, C., M. Egas, and J. A. Metz. 2006. Evolutionary predictions should be based on individual-level traits. The American Naturalist 168:E148–E162.

Saastamoinen, M., G. Bocedi, J. Cote, D. Legrand, F. Guillaume, C. W. Wheat, E. A. Fronhofer, C. Garcia, R. Henry, A. Husby, et al. 2018. Genetics of dispersal. Biological Reviews 93:574–599.

Schilthuizen, M. 2018. Darwin comes to town. Quercus, London, England.

Schoen, R. 1983. Measuring the tightness of a marriage squeeze. Demography 20:61–78.

———. 1988. Modeling multigroup populations. Plenum Press, New York.

Sheldon, B. C. 2000. Differential allocation: tests, mechanisms and implications. Trends in Ecology & Evolution 15:397–402.

Shine, R. 1989. Ecological causes for the evolution of sexual dimorphism: a review of the evidence. The Quarterly Review of Biology 64:419–461.

Shyu, E., and H. Caswell. 2016*a*. A demographic model for sex ratio evolution and the effects of sex-biased offspring costs. Ecology and evolution 6:1470–1492.

———. 2016*b*. Frequency-dependent two-sex models: a new approach to sex ratio evolution with multiple maternal conditions. Ecology and evolution 6:6855–6879.

———. 2018*a*. Mating, births, and transitions: a flexible two-sex matrix model for evolutionary demography. Population Ecology 60:21–36.

———. 2018*b*. Mating, births, and transitions: a flexible two-sex matrix model for evolutionary demography. Population Ecology pages 1–16.

Silvertown, J., M. Franco, I. Pisanty, and A. Mendoza. 1993. Comparative plant demography–relative importance of life-cycle components to the finite rate of increase in woody and herbaceous perennials. Journal of Ecology pages 465–476.

Slatkin, M. 1984. Ecological causes of sexual dimorphism. Evolution 38:622–630.

Snyder, R. E., and S. P. Ellner. 2018. Pluck or luck: Does trait variation or chance drive variation in lifetime reproductive success? The American Naturalist 191:E90–E107. PMID: 29570408.

Sousa, W. P. 1979. Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. Ecology 60:1225–1239.

Stearns, S. C. 1992. The evolution of life histories. Oxford University Press, Oxford, England.

Stern, D. L. 2008. Aphids. Current Biology 18:R504–R505.

Sullivan, L. L., B. Li, T. E. Miller, M. G. Neubert, and A. K. Shaw. 2017. Density dependence in demography and dispersal generates fluctuating invasion speeds. Proceedings of the National Academy of Sciences page 201618744.

Szathmáry, E., and J. M. Smith. 1995. The major evolutionary transitions. Nature 374:227–232.

Székely, T., F. Weissing, and J. Komdeur. 2014. Adult sex ratio variation: implications for breeding system evolution. Journal of evolutionary biology 27:1500–1512.

Takada, T., and H. Nakajima. 1992. An analysis of life history evolution in terms of the density-dependent lefkovitch matrix model. Mathematical biosciences 112:155–176.

———. 1998. Theorems on the invasion process in stage-structured populations with density-dependent dynamics. Journal of Mathematical Biology 36:497–514.

Temeles, E. J., I. L. Pan, J. L. Brennan, and J. N. Horwitt. 2000. Evidence for ecological causation of sexual dimorphism in a hummingbird. Science 289:441–443.

ten Brink, H., A. M. de Roos, and U. Dieckmann. 2018. The evolutionary ecology of metamorphosis. The American Naturalist In press.

Theron, E., K. Hawkins, E. Bermingham, R. E. Ricklefs, and N. I. Mundy. 2001. The molecular basis of an avian plumage polymorphism in the wild: a melanocortin-1-receptor point mutation is perfectly associated with the melanic plumage morph of the bananaquit, coereba flaveola. Current Biology 11:550–557.

Toscano, B. J., V. Hin, and V. H. Rudolf. 2017. Cannibalism and intraguild predation community dynamics: Coexistence, competitive exclusion, and the loss of alternative stable states. The American Naturalist 190:617–630.

Travis, J. 1988. Differential fertility as a major mode of selection. Trends in ecology & evolution 3:227–230.

Tuljapurkar, S., and H. Caswell, eds. 1996. Structured-Population Models in Marine, Terrestrial, and Freshwater Systems. New York: Chapman & Hall.

Tuljapurkar, S. D. 1982. Population dynamics in variable environments. iii. Evolutionary dynamics of r-selection. Theoretical Population Biology 21:141–165.

Tuljapurkar, S. D., C. O. Puleston, and M. D. Gurven. 2007. Why men matter: mating patterns drive evolution of human lifespan. PloS one 2:e785.

Vamosi, J. C., and S. P. Otto. 2002. When looks can kill: the evolution of sexually dimorphic floral display and the extinction of dioecious plants. Proceedings of the Royal Society of London. Series B: Biological Sciences 269:1187–1194.

van Daalen, S. F., and H. Caswell. 2017. Lifetime reproductive output: individual stochasticity, variance, and sensitivity analysis. Theoretical Ecology 10:355–374.

Van Doorn, G. S. 2009. Intralocus sexual conflict. Annals of the New York Academy of Sciences 1168:52–71.

Van Geel, B., J. Sevink, D. Mol, B. Langeveld, R. Van Der Ham, C. Van Der Kraan, J. Van Der Plicht, J. Haile, A. Rey-Iglesia, and E. Lorenzen. 2018. Giant deer (megaloceros giganteus) diet from mid-weichselian deposits under the present north sea inferred from molar-embedded botanical remains. Journal of Quaternary Science 33:924–933.

Van Leeuwen, A., A. De Roos, and L. Persson. 2008. How cod shapes its world. Journal of Sea Research 60:89–104.

van Tienderen, P. H. 2000. Elasticities and the link between demographic and evolutionary dynamics. Ecology 81:666–679.

Verdy, A., and H. Caswell. 2008. Sensitivity analysis of reactive ecological dynamics. Bulletin of Mathematical Biology 70:1634–1659.

Wagner, G. P., and J. Zhang. 2011. The pleiotropic structure of the genotype–phenotype map: the evolvability of complex organisms. Nature Reviews Genetics 12:204.

Wahid, I., T. Sunahara, and M. Mogi. 2003. Maxillae and mandibles of male mosquitoes and female autogenous mosquitoes (diptera: Culicidae). Journal of medical entomology 40:150–158.

Waples, R. S. 1989. Temporal variation in allele frequencies: testing the right hypothesis. Evolution 43:1236–1251.

Webb, J. K., B. W. Brook, and R. Shine. 2002. What makes a species vulnerable to extinction? comparative life-history traits of two sympatric snakes. Ecological Research 17:59–67.

Werren, J. H., U. Nur, and C.-I. Wu. 1988. Selfish genetic elements. Trends in Ecology & Evolution 3:297–302.

Whitlock, M. C., and A. F. Agrawal. 2009. Purging the genome with sexual selection: reducing mutation load through selection on males. Evolution: International Journal of Organic Evolution 63:569–582.

Willson, M. F., et al. 1983. Plant reproductive ecology. John Wiley & Sons.

Wool, D., S. Noiman, O. Manheim, and E. Cohen. 1982. Malathion resistance in *Tribolium* strains and their hybrids: inheritance patterns and possible enzymatic mechanisms (coleoptera, tenebrionidae). Biochemical Genetics 20:621–636.

Wright, S. 1931. Evolution in Mendelian populations. Genetics 16:97–159.

Zweerus, N. L., S. Sommer, D. Fontaneto, and A. Ozgul. 2017. Life-history responses to environmental change revealed by resurrected rotifers from a historically polluted lake. Hydrobiologia pages 1–10.

Summary

Selection in two-sex stage-structured populations

A hungry caterpillar emerges from an egg. After stuffing itself with leaves, it hangs upside down, dissolves his entire body into a mush, and finally an elegant butterfly emerges from the soup. Helpless, fluffy chicks morph into fierce birds of prey (Figure 2). That is, if the hungry caterpillar and the fluffy chicks do not get eaten by a hungry predator. Helpless, chubby babies turn into hungry PhD students, who morph into full-fledged doctors if fed with enough scientific papers and writing courses. That is, if they survive their defense. These are all examples of life cycles.

Organisms have complex life cycles. Each life cycle represents a different solution to the problem of staying alive. And there are many solutions: the number of species on earth is estimated to be anywhere between 2 million and 10^{12}. Some species survive because individuals of the species live for a very long time, such as corals and sponges, that can live thousands of years. Other species live only very briefly, like mayflies, whose adult lifespan can be as short as 5 minutes for females of the mayfly species *Dolania americana*.

Organisms also have genes, which affect their size, color, and shape, how fast they run, grow, and reproduce, how fast they kill their host, and how fast they kill their parasites. A gene will increase in frequency if the individuals carrying it contribute more offspring to the next generation than individuals without the gene. Individuals procreate and die at rates that are influenced by both their genes and the environment they live in. The environment they live in is shaped by the population they live in. If the population grows very large, there may not be enough food, and individuals may starve. If the population is very sparse, individuals may struggle to find a mate. As a consequence of individuals starving or failing to mate, populations grow or shrink, and gene frequencies increase or decrease.

In summary, genes affect individuals, which affect populations, which affect individuals, which affect how many genes make it into the next generation, etc. For more than a hundred years, biologists have been studying how these two things, genes and complex life cycles, interact. When there are so many interactions and feedbacks, it can be difficult to understand what is happening through verbal reasoning alone. Mathematical models are helpful tools in such a situation. In this thesis, we combine genetics and complex life cycles into a new mathematical framework to learn more about their interaction.

But so far I have not mentioned any of the words in the title of the thesis yet: "Selection in two-sex stage-structured populations". What is "selection", and what are "structured" populations? The term selection refers to the preferential survival and reproduction of individuals with certain genes, or the preferential elimination of individuals with certain genes. That is, when a gene is "selected for", it means that gene will increase in frequency in the next generation.

A "structured" population refers to a population in which individuals differ due to their age, developmental stage, size, colour, mood, or marital status. You might be thinking, "Surely all populations are structured by that definition?" And I would agree with you. However, including structure into mathematical models of populations makes them a lot more complicated. Biologists therefore often treat all individuals, fluffy or fierce, caterpillar or butterfly, PhD student or professor, as if they are the same in mathematical models.[1]

Finally, the thesis title also mentions "two-sex"; so what is that about? We found that the existence of two sexes has a profound impact on the evolution of populations. In sexually reproducing populations, genes live in both males and females[2], but a gene that is good for males might not be good for females, and vice versa.

To investigate how sex and population structure impact evolution, we calculated under which conditions a gene will be able to invade a resident population of individuals with a different, competing gene at that particular location in the genome (the genetic material of an organism, its DNA). When males and females are identical, we found that new genes can only invade if they lead to individuals that are better somehow, for example by having a higher survival, or reaching maturation faster. When males and females differ, however, genes can invade that benefit males at the expense of females, or vice versa.

Imagine one of our hominoid ancestors, for example. When their brains started getting bigger and babies' heads grew bigger, it became a huge advantage for females to have wider hips. However, wide hips made males slower runners. So the same gene increased female survival but decreased male survival. Such a gene would have established itself in the population nevertheless, if the positive impact

[1] Some argue that this is the fault of physicists and mathematicians, because the people who started modeling populations in this way were mathematicians, chemists, and physicists (e.g. Alfred J. Lotka, Pierre François Verhulst, Vito Volterra). That said, Lotka is also one of the most prominent historical figures in demography.

[2] Except in some crazy fungi, like *Schizophyllum commune*, which has around 23,000 different sexes or mating types.

of wide hips on female survival was much larger than the negative impact on male survival.

Once the wide-hip gene has spread through the hominoid population, a different gene that can stop the wide-hip gene from being expressed in males would give those small-hipped males an advantage. Males and females would evolve towards having different-sized hips. Differences between the sexes evolve to resolve the conflicting interests of males and females.

Females are usually more important for the survival of a species, because one male can fertilize lots of females, but each female can only produce a limited number of eggs, babies, pups, kittens, or cubs. Therefore if a gene spreads that benefits males over females, the population will grow a little slower, or maybe even shrink. Of course, eventually another mutation might occur that suppresses the expression of the gene in females, or otherwise solve the problem. But if the original male-benefitting gene is sufficiently bad for females, the population can go extinct before the savior gene has managed to save the day.

The fact that sex is dangerous in this way has been known for longer than the author of this thesis has been alive. However, the impact that sexual conflict has on the evolution of life-cycles, referred to as life-history evolution by biologists, has not received much attention.

Demographers and biologists are particularly obsessed with the final stage of every individuals' life-cycle: death. Why do some species live thousands of years, like sponges and corals, and others only 24 hours, like the mayflies? Traditionally, demographers have tried to answer these questions using models that only contained females. In general, males are the neglected sex in biology. The results of this thesis suggest that the conflict between males and females might be an important factor in the evolution of such life-history characteristics. By neglecting males, demographers are missing out on the consequences of the ongoing evolutionary tug of war between males and females.

How important the evolutionary tug of war has been in shaping life-history evolution remains an open question. This thesis provides a set of tools (and maybe some motivation) for biologists and evolutionary demographers to answer that question.

Figure 1: Adult Cooper's hawk (*Accipiter cooperii*) feeding his fluffy offspring. Credits: Tom Muir

Samenvatting

Hoe werkt de evolutie als individuen van elkaar verschillen in meer dan alleen hun geslacht?

Een hongerige rups kruipt uit z'n eitje. Nadat de rups zich helemaal heeft volgepropt met sappige blaadjes, gaat hij op z'n kop aan een takje hangen en verpopt. Binnenin de pop verandert het lijfje van de rups in een papje van cellen, en van dat papje wordt weer een schitterende vlinder gemaakt die zich ten slotte losworstelt uit de pop en de wereld in vliegt. Maar niet alleen vlinders veranderen enorm gedurende hun leven. Hulpeloze, donzige kuikens worden imponerende roofvogels (Figuur 2). Hulpeloze, mollige baby's worden hongerige promovendi. Tenminste, als de kleine rups en het donzige kuiken niet door een roofdier worden opgesmikkeld, en als de promovenda haar verdediging overleeft. Dit zijn allemaal voorbeelden van levenscycli.

Levende wezens hebben allemaal verschillende, en soms erg ingewikkelde, levenscycli. Elke levenscyclus is een andere manier om te overleven op onze planeet. En er zijn heel veel verschillende manieren om in leven te blijven: het aantal soorten op aarde wordt tussen de 2 miljoen en de 10^{12} geschat (10^{12} is een korte manier om een 1 met 12 nullen op te schrijven). Sommige soorten overleven dankzij de gigantische levensduur van fortuinlijke individuen, zoals koralen en sponzen, die duizenden jaren oud kunnen worden. Individuen van andere soorten leven daarentegen maar hééél even, zoals eendagsvliegen. De volwassen vrouwtjes van sommige soorten eendagsvliegen (*Dolania americana*) leven zelfs maar 5 minuten, maar krijgen het desondanks voor elkaar om zich voort te planten!

Levende wezens hebben ook allemaal verschillende genen. Genen zijn stukjes erfelijk materiaal die onder andere de grootte, kleur, en vorm van de drager van het gen bepalen. Maar genen bepalen, samen met de omgeving van een individu, ook hoe snel de drager van het gen kan rennen, groeien, en zich voortplanten. Als een gen ervoor zorgt dat individuen met dat stukje erfelijk materiaal meer kinderen krijgen dan individuen zonder dat stukje erfelijk materiaal, dan zullen er steeds meer individuen met dat gen in de populatie komen. Het aantal kinderen dat een individu krijgt wordt niet uitsluitend bepaald door zijn of haar genen, maar is ook sterk afhankelijk van de omgeving waarin hij of zij leeft. Een zaadje met fantastische genen zal bijvoorbeeld niet erg oud worden in de schaduw van een grote boom. De omgeving waarin een individu leeft wordt dus sterk bepaald door de populatie waarin hij of zij geboren is. Als de populatie heel groot is, en er maar beperkt voedsel is, dan zal een nieuwkomer misschien verhongeren. Als de populatie heel klein is, en verspreid over een groot gebied, dan zullen individuen misschien moeite hebben om een maatje te vinden om zich mee voort te planten. Doordat individuen verhongeren, sterven, of zich al dan niet voortplanten, verandert vervolgens de grootte van de populatie en daarmee de frequentie van verschillende genen in de populatie.

Dus genen beïnvloeden het overleven en voortplanten van de individuen die de genen dragen, het overleven en voortplanten van individuen beïnvloedt vervolgens de grootte en samenstelling van de populatie, en dat beïnvloedt dan weer de overlevingskans en het voortplantingssucces van de individuen in de populatie, enzovoort en zo verder. Al ruim honderd jaar proberen biologen deze interactie tussen genen en levenscycli uit te pluizen. Met zoveel interacties en feedback is het vrijwel onmogelijk om te begrijpen wat er aan de hand is door alleen maar hard na te denken over het systeem. Omdat genetica al ingewikkeld genoeg is, wordt er in de meeste wiskundige modellen van de genetica gekozen om de ontwikkeling van een individu door de verschillende stadia in de levenscyclus te negeren. Maar hetzelfde gen heeft vaak een heel ander effect op verschillende levensstadia; in dit proefschrift combineren we daarom een genetisch model met een model van de verschillende levensstadia om de interacties tussen individuele ontwikkeling, de populatie en genen beter te begrijpen.

Tot nu toe heb ik nog geen van de woorden in de titel van mijn proefschrift, *Selection in two-sex stage-structured populations*, gebruikt. Wat is *selection* (selectie), en wat zijn *structured* (gestructureerde) populaties? Selectie slaat op het feit dat individuen met bepaalde genen meer kinderen krijgen dan individuen zonder die genen. We zeggen dan dat zo'n gen “geselecteerd” wordt, omdat dat gen sneller in aantal toeneemt dan de andere genen.

Een *structured population* (gestructureerde populatie) is een populatie waarin individuen van elkaar verschillen, bijvoorbeeld door hun leeftijd, ontwikkeling, lengte, de kleur van hun vacht, hun humeur, of burgerlijke status. Nu denk je misschien terecht, “Ok, maar dan zijn (bijna) alle populaties toch gestructureerd? Zelfs in een klonale populatie is niet iedereen even oud!” En in dat geval heb je helemaal gelijk. Maar een wiskundig model waarin al die verschillen worden meegenomen is best wel ingewikkeld. Biologen maken daarom bij voorkeur modellen waarin alle individuen in een populatie hetzelfde zijn, dus rupsen hetzelfde als vlinders, donzige kuikens hetzelfde als indrukwekkende roofvogels, en gretige promovendi hetzelfde als ervaren hoogleraren.

Ten slotte staat er ook nog iets over twee seksen in de titel van dit proefschrift; wat heeft dat met dit alles te maken? Tijdens mijn onderzoek kwam ik erachter dat het bestaan van twee verschillende seksen een enorm effect heeft op de interacties tussen de genen, individuen, en populaties die ik hierboven beschreef. Oftewel, het bestaan van twee verschillende seksen heeft een enorm effect op de evolutie. In populaties die aan seksuele voortplanting doen, leven genen in zowel mannen als vrouwen[3], maar een gen dat goed is voor mannetjes is misschien helemaal niet zo goed voor vrouwtjes, en andersom.

Om uit te zoeken wat het effect is van seks op de evolutie, hebben we uitgerekend onder welke voorwaarden een mutatie in een stukje erfelijk materiaal (een nieuw gen) zal toenemen in een populatie van individuen die zich seksueel voortplanten. We kwamen erachter dat in soorten waarbij de mannetjes en de vrouwtjes min of meer hetzelfde zijn, een stukje erfelijk materiaal alleen maar kan toenemen in een populatie als dat stukje erfelijk materiaal ook daadwerkelijk het leven van zijn dragers beter maakt, door ze bijvoorbeeld een grotere overlevingskans te geven, of door ze extra sexy te maken voor soortgenoten. Maar als de mannetjes en vrouwtjes van een soort sterk van elkaar verschillen, dan kan een gen verspreiden dat weliswaar het leven van de mannetjes beter maakt, maar dat het leven van de vrouwtjes juist moeilijker maakt, of andersom.

Stel je bijvoorbeeld een van onze eigen verre voorouders voor. Toen onze/hun hersenen steeds groter werden en de hoofdjes van baby's daardoor ook steeds groter werden, hadden vrouwen met bredere heupen een veel betere kans om het baren van een kindje te overleven. Mannen met wijde heupen kunnen daarentegen niet zo snel rennen als mannen met smallere heupen. Dus het "wijde heupen gen" geeft vrouwelijke dragers een veel grotere overlevingskans, maar zorgt er bij de mannen juist voor dat ze langzamer gaan rennen. Omdat de negatieve impact van minder hard rennen op de overleving van mannen waarschijnlijk kleiner is dan de positieve impact op vrouwen, zal een "wijde heupen gen" zich verspreiden door een populatie. Als dat gen eenmaal een groot deel van de populatie heeft overgenomen, dan kan een tweede mutatie dat het gen uitzet in mannetjes, verspreiden in de populatie, omdat het goed is voor de mannetjes en geen effect heeft op vrouwtjes.

Vrouwtjes zijn voor de overleving van de meeste soorten belangrijker dan mannetjes, Omdat één mannetje heel veel vrouwen kan bevruchten, maar één vrouwtje maar een beperkt aantal eitjes, baby's, puppy's, of kittens kan produceren. Genen die goed zijn voor de mannetjes maar slecht voor de vrouwtjes, zijn dus eigenlijk ook slecht voor de hele soort. Gelukkig kan de evolutie dit weer oplossen door mutaties die zo'n gen uitzetten in vrouwtjes, maar zo'n reddende mutatie moet dan wel optreden voordat de populatie uitsterft.

[3]Behalve als je een schimmel bent, sommige schimmels hebben wel 23,000 verschillende geslachten, zoals *Schizophyllum commune*.

Dit soort gevaarlijke neveneffecten van seksuele voortplanting zijn al heel lang bekend. Maar de gevolgen hiervan op de evolutie van levenscycli zijn nog vrijwel onbekend.

Biologen (en levensverzekeringen) zijn vooral erg geïnteresseerd in de laatste fase van elke levenscyclus: de dood. Waarom leven sommige soorten duizenden jaren, en anderen nog geen dag? Waarom leven sommige vrouwen tot ze 116 zijn, ondanks dat ze door de menopauze al decennia geen kinderen meer kunnen krijgen? Traditioneel worden dit soort vragen onderzocht met modellen waarin alleen de vrouwen worden gemodelleerd. Over het algemeen zijn mannen het verwaarloosde geslacht in de biologie. De resultaten van dit proefschrift benadrukken dat zulke modellen een heel belangrijk onderdeel missen, namelijk het feit dat de evolutie telkens het conflict tussen de belangen van mannen en vrouwen moet oplossen. Door de mannen te verwaarlozen, zijn dergelijke modellen blind voor het evolutionaire getouwtrek dat constant plaatsvindt tussen de seksen.

Hoe belangrijk dit getouwtrek tussen de seksen geweest is voor de evolutie van de verschillende levenscycli op onze planeet, en hoe belangrijk dat zal zijn in de wedstrijd van soorten om zich snel genoeg aan te passen aan een veranderend klimaat, blijft een open vraag. De bijdrage van dit proefschrift bestaat vooral uit het benodigde wiskundige gereedschap om die vraag te beantwoorden.

Figuur 2: Een volwassen Coopers sperwer mannetje (*Accipiter cooperii*) geeft zijn donzige nageslacht te eten. Credits: Tom Muir

Author Contributions

2 **Selection in one-sex stage-structured populations**
Charlotte de Vries and Hal Caswell
HC designed the research, CdV contributed to further development of the idea. CdV analyzed the model and wrote the first version of chapter. HC contributed significantly to later versions of the chapter.

3 **Selection in two-sex stage-structured populations**
Charlotte de Vries and Hal Caswell
CdV designed the research, analyzed the model, and wrote the first version of chapter. HC contributed significantly to the structure of the chapter and to the writing of later versions of the chapter.

4 **Density-dependent selection in one-sex stage-structured populations**
Charlotte de Vries, Robert A. Desharnais, Hal Caswell
CdV and HC constructed the model, CdV analyzed the model. RAD designed the experimental part of the paper, and supervised a student (W. Cheung) who performed the research and statistical fitting. CdV analyzed the model and wrote the first version of chapter. RAD, and HC contributed significantly to later versions of chapter.

5 **Density-dependent selection in two-sex stage-structured populations**
Charlotte de Vries
CdV designed the research and wrote the chapter.

Author Affiliations

Lotte de Vries is at the:
Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, P.O. Box 94248, 1090 GE Amsterdam, The Netherlands

Hal Caswell is at the:
Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, P.O. Box 94248, 1090 GE Amsterdam, The Netherlands

Robert A. Desharnais is at the:
Department of Biological Sciences, California State University, Los Angeles, USA
Control and Dynamical Systems, California Institute of Technology, Pasadena, USA